# Temperature sensitivity increases with decreasing soil carbon quality in forest ecosystems across northeast China



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## Abstract

Soil respiration universally exhibits exponential temperature dependence (Respiration =  $R_0 e^{\beta T} \& Q_{10} = e^{10\beta}$ , and temperature sensitivity (Q<sub>10</sub>) and soil organic carbon quality (as expressed by basal respiration rate at 0 °C, R<sub>0</sub>) are the key parameters. Despite their importance for predicting the responses of forest ecosystems to climate change and quantifying the magnitude of soil CO<sub>2</sub> efflux, the controlling factors of temperature sensitivity and soil carbon quality and their relationships among various forest types at a regional scale are as yet unknown. Here, we present a comprehensive analysis of  $Q_{10}$ , R<sub>0</sub>, and their related variables by assembling 154 independent temperature-respiration functions under a common standard in forest ecosystems across northeast China (41°51'-51°24' N, 118°37'-129°48' E). The R<sub>0</sub> values ranged from 0.1700 to 2.1194  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> (mean = 0.8357  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>), and the Q<sub>10</sub> values from 1.29 to 5.42 (mean = 2.72). The relationships between Q<sub>10</sub> and R<sub>0</sub> could be best expressed with exponential decay equations  $(R^2 = 0.460 - 0.611, P < 0.01)$ . They indicated that the temperature sensitivity decreased with increasing the soil carbon quality, and then tended to level off when the R<sub>0</sub> values were larger than ~1  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>. Soil carbon quality (R<sub>0</sub>) was closely related with the minimum soil temperature and its corresponding soil respiration rate during the growing season ( $R^2 = 0.696 - 0.857$ , P < 0.01). Such a synthesis is necessary to fully understand the spatial heterogeneity in the temperature sensitivity of soil respiration and to increase our ability to make robust predictions about the future carbon budget.

**Keywords** Soil respiration  $\cdot Q_{10} \cdot Basal respiration \cdot Carbon quality-temperature hypothesis <math>\cdot$  Forest ecosystem  $\cdot$  China

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## 1 Introduction

Soil respiration is the second largest flux (~80 Pg C year<sup>-1</sup>) in the global carbon cycle, and small changes in the magnitude of soil CO<sub>2</sub> flux could lead to a large effect on the concentration of CO<sub>2</sub> in the atmosphere (Schlesinger and Andrews 2000; Raich et al. 2002). Therefore, soil respiration plays a critical role in regulating the global carbon budget. Recent studies provided multiaspect evidence that warming-induced soil carbon losses are currently occurring at local and global scales (Schuur et al. 2015; Crowther et al. 2016; Prietzel et al. 2016; Melillo et al. 2017; Bond-Lamberty et al. 2018; Vaughn and Torn 2018). In the past decades (2008–2017), the global carbon budget imbalance could be attributed to imperfect data and understanding of the contemporary carbon cycle (Le Quéré et al. 2018). Forest ecosystems in northeast China play an important role in both local and national carbon budgets because of their large area (more than 30% of total forest area in China, Wang 2006; Wang et al. 2013), great soil carbon storage (Liu et al. 2014; Yang et al. 2014), and high temperature sensitivity of soil respiration (~3, Peng et al. 2009; Zheng et al. 2009; Song et al. 2014; Xu et al. 2015).

Temperature is often the primary factor determining rates of soil respiration (Raich et al. 2002; Chen and Tian 2005; Peng et al. 2009). Temperature sensitivity of soil respiration (i.e.,  $Q_{10}$ ) is defined as the factor by which soil respiration is multiplied when temperature increases by 10 °C (Davidson et al. 2006).  $Q_{10}$  is an important parameter in modeling and evaluating the effects of global warming on soil carbon release (Davidson and Janssens 2006). The van't Hoff equation ( $R_s = R_0 e^{\beta T} \& Q_{10} = e^{10\beta}$ , van't Hoff 1899) is widely used to describe the relationship between soil respiration and temperature, where  $R_s$  is the instantaneous soil CO<sub>2</sub> emissions to temperature variation, and  $R_0$  denotes basal respiration rate at a reference temperature of 0 °C (µmol m<sup>-2</sup> s<sup>-1</sup>) and is also regarded as an index of soil organic carbon quality (the availability and lability) in many studies (Mikan et al. 2002; Fierer et al. 2005; Inglett et al. 2012; Xu et al. 2012; He and Yu 2016). The van't Hoff equation is only valid within a certain temperature range, because biological activity cannot increase indefinitely with temperature. The temperature sensitivity ( $Q_{10}$ ) and basal respiration rate ( $R_0$ ) are key parameters in empirical models for quantifying soil CO<sub>2</sub> emissions.

It is not surprising that basal respiration rate varied spatially given its underlying mechanisms, including changes in carbon substrate supply from photosynthesis and quantity of respiring biomass (Davidson and Janssens 2006). Spatial variations of R<sub>0</sub> are rarely studied, and an adequate algorithm is lacking to predict  $R_0$  variation across the globe (Yuan et al. 2011). Meanwhile, due to the complexity of factors affecting soil  $CO_2$  emissions, high spatial heterogeneity in temperature sensitivities have been reported. The Q<sub>10</sub> values varied with temperature (r = -0.37 to -0.77, Chen and Tian 2005; Peng et al. 2009; Zheng et al. 2009; Song et al. 2014; Xu et al. 2015), precipitation (r = -0.36 to 0.45, Peng et al. 2009; Zhou et al. 2009; Xu et al. 2015), soil organic carbon (r = 0.32 to 0.75, Zhou et al. 2009; Zheng et al. 2009; Song et al. 2014), or biotic factors, e.g., normalized difference vegetation index (NDVI), leaf area index (LAI), or gross primary productivity (GPP) (r = 0.60 to 0.89, Wang et al. 2010b; Yuste et al. 2004; Sampson et al. 2007). The correlations of the Q<sub>10</sub> values with these factors showed large fluctuations from weak to strong, even from negative to positive in precipitation, and the mechanisms that underlie these effects are still poorly understood. Temperature sensitivity remains one of the major uncertainties in predicting climate-carbon cycle feedback (Conant et al. 2011). If the spatially heterogeneity in  $Q_{10}$  is considered, then the magnitude and even direction of the terrestrial carbon budget feedbacks to climate warming could be significantly changed (Jones et al. 2003; Chen and Tian 2005). Thus, quantifying the influence of environmental factors on the key parameters ( $Q_{10} \& R_0$ ) across different forest ecosystems can be of paramount importance to better understand soil carbon feedbacks to climate change and to improve soil respiration models at the regional and global scales, which are primary tools for estimating and predicting soil carbon emissions.

Currently, a consensus has not yet been reached on the relationship between temperature sensitivity of decomposition and substrate quality. On the basis of enzyme kinetics, Bosatta and Ågren (1999) proposed that temperature sensitivity should be negatively related to substrate quality (i.e., the carbon quality-temperature hypothesis), which has been tested by many studies (Mikan et al. 2002; Fierer et al. 2005; Leifeld and Fuhrer 2005; Conant et al. 2008; Inglett et al. 2012; Xu et al. 2012). However, Fang et al. (2005) found the temperature sensitivity was not significantly different between resistant and labile carbon pools. Additionally, the abovementioned results were derived mainly from laboratory incubation experiments (i.e., heterotrophic respiration), but few in situ data (including heterotrophic and autotrophic respiration) exist to address the hypothesis directly. Thus, we collected and synthesized the key parameters of  $Q_{10}$  and  $R_0$  from field measurements across different forest ecosystems in northeast China.

## 2 Methods

## 2.1 Data collection

We collected available soil respiration data of forest ecosystems across northeast China from China Knowledge Resource Integrated Database (http://www.cnki.net/), China Science and Technology Journal Database (http://www.cqvip.com/), ISI Web of Science (http://isiknowledge.com/), ScienceDirect (http://www.sciencedirect.com/), and Springer Link (http://link.springer.com/). The related terms of "soil respiration", "soil CO<sub>2</sub> flux", "soil carbon flux" or "soil carbon emission" were searched for in the literature published before 2017.

The following criteria were used to ensure data consistency and accuracy: (1) Soil respiration was measured in the field without obvious disturbances or manipulation experiments, e.g., fire, cutting, and nitrogen addition treatments. (2) Most soil respiration measurements were conducted during the growing season in northeast China. The  $Q_{10}$  values were usually derived from more than 3–6 months of measurements in the previous syntheses (see Table 1). In this study, the investigation time was no less than 4 months during the growing season (April–October). (3) Soil respiration was measured by Li-6400, Li-8100 or gas chromatograph (GC), which are the most popular methods in China (~95% of the data) and measurements are consistent between methodologies (Peng et al. 2009; Zheng et al. 2009, 2010). (4) The  $Q_{10}$  and  $R_0$  values were estimated using the van't Hoff equations based on soil temperature at 5 cm ( $T_5$ ) or 10 cm depth ( $T_{10}$ ), which were the common layers of temperature measurement (Wang et al. 2010b; Song et al. 2014; Xu et al. 2015), accounting for more than 90% of the data. (5) The determination coefficients ( $R^2$ ) of the van't Hoff equations were greater than 0.50.

Within these constraints, 154 groups of  $Q_{10}$  &  $R_0$  (101 with  $T_5$  and 53 with  $T_{10}$ ) were assembled from 68 published studies across forest ecosystems in northeast China (between 41°51' N and 51°24' N; 118°37' E and 129°48' E), including Heilongjiang, Liaoning, and

Study region	Mean	Range	Sample	Period	Source
Japanese	2.12 (NA)	1.30-3.17	40	NA	Hashimoto, 2005
China	2.65 (NA)	1.33-5.53	48 (18)	NA	Chen et al. 2008
China	2.28 (T <sub>5</sub> ), 3.00 (T <sub>10</sub> )	1.09-5.51	89 (28)	> 3 months	Peng et al. 2009
China	2.51 (T <sub>5</sub> )	1.28-4.75	34 (16)	NA	Zheng et al. 2009
Globe	2.55 (T <sub>5</sub> ), 3.01 (T <sub>10</sub> )	0.98-6.27	185 (20)	NA	Wang et al. 2010a
Globe	2.70 (T <sub>5</sub> ), 3.31 (T <sub>10</sub> )	1.10-8.90	267 (31)	NA	Wang et al. 2010b
China	2.46 (T <sub>5</sub> ), 2.74 (T <sub>10</sub> )	1.09-5.47	173 (~22)	> 3 months	Song et al. 2014
China	$2.51(T_5)$	1.10-5.18	145 (NA)	> 6 months	Xu et al. 2015
Northeastern China	2.63(T <sub>5</sub> ), 2.90 (T <sub>10</sub> )	1.29-5.42	154 (154)	> 4 months	This study

**Table 1** Mean temperature sensitivity  $(Q_{10})$  for soil respiration across different forest ecosystems at large spatial scales.  $T_5$  and  $T_{10}$  represent the average  $Q_{10}$  values from soil temperature at 5 cm and 10 cm depths, respectively

The number of samples from northeastern China are in parentheses

NA: not available

Jilin provinces and the eastern part of the Inner Mongolia Autonomous Region (see supplementary Dataset). In total, these studies measured 38 different forest types across northeast China, covering most of the typical forest ecosystems in local sites. The measurement year was between 2001 and 2016, and 88% of the investigation time was at least 6 months. In addition to  $Q_{10}$ ,  $R_0$ , and the determination coefficients ( $R^2$ ), the factors related to the van't Hoff equations during the growing seasons were also collected or digitized from the fitted figures with the Web-based program WEBPLOTDIGITIZER (Burda et al. 2017), including the minimum soil respiration rates ( $R_{min}$ ) and their corresponding soil temperatures ( $T_{Rmin}$ ), the minimum soil temperatures ( $T_{min}$ ) and their corresponding soil temperatures ( $T_{max}$ ). In addition, the supporting information was recorded, including geographical location (province, study site, latitude, longitude, and elevation), forest type, measurement period, and method. In our dataset, all  $Q_{10}$  values were estimated by in situ soil respiration measurements (including heterotrophic and autotrophic respiration), representing the apparent temperature sensitivity.

## 2.2 Statistical analysis

Because the  $Q_{10}$  values were related to the measurement depths of soil temperature (Peng et al. 2009), we conducted analyses by splitting our data set into soil temperature at 5 cm (T<sub>5</sub>) and 10 cm depth (T<sub>10</sub>). Basal respiration across northeast China was fitted with the multivariable linear regression equation. The Pearson correlation test was used to examine the relationships between  $Q_{10}$  and  $R_0$  and the measurement-period variables of temperature and respiration (i.e., minimum, maximum, and their difference) in R (R Development Core Team, version 1.1.419).

# 3 Results

A total of 154 available  $Q_{10}$  and  $R_0$  data were collected from forest ecosystems across northeast China. Temperature sensitivity of soil respiration was mainly studied in the Xiaoxing'an Mountains (N=66), Maor Mountains (N=43), Changbai Mountains (N=18), and Bingla Mountains (N=15), which together accounted for more than 90% of the data.  $Q_{10}$  and  $R_0$  from the van't Hoff equation and the related variables are summarized in Table 2. The means of  $Q_{10}$  from soil temperature at 5 cm depth and 10 cm depth were 2.63 and 2.90, ranging from 1.29 to 5.42 and 1.71 to 4.46, respectively. The large coefficients of variation (CVs) of 20–24% in  $Q_{10}$  values confirmed the high spatial variation of temperature sensitivity among forest ecosystems in northeast China. The mean of  $R_0$  was 0.8527 µmol m<sup>-2</sup> s<sup>-1</sup> in T<sub>5</sub>, ranging from 0.2615 to 1.9175 µmol m<sup>-2</sup> s<sup>-1</sup>, and 0.8069 µmol m<sup>-2</sup> s<sup>-1</sup> in T<sub>10</sub>, ranging from 0.1700 to 2.1194 µmol m<sup>-2</sup> s<sup>-1</sup>.

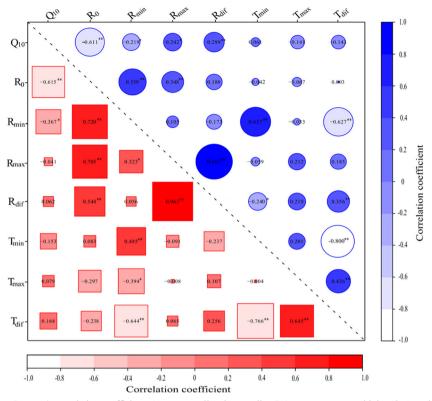
The correlation analyses in Fig. 1 were grouped into two parts with soil temperature at 5 cm depth (T<sub>5</sub>) and 10 cm depth (T<sub>10</sub>), from which Q<sub>10</sub> and R<sub>0</sub> were derived. There were significantly negative correlations between Q<sub>10</sub> and R<sub>0</sub>, both from soil temperature at 5 cm depth (r = -0.611, P < 0.01) and 10 cm depth (r = -0.615, P < 0.01). The relationships between Q<sub>10</sub> and R<sub>0</sub> could be best expressed with exponential decay equations, and  $R^2$  was 0.611 at 5 cm depth, 0.460 at 10 cm depth, and 0.502 at two depths (Fig. 2). This indicated that the forest ecosystems with lower soil carbon quality exhibited higher temperature sensitivity in northeast China. However, when the R<sub>0</sub> values were larger than ~1 µmol m<sup>-2</sup> s<sup>-1</sup>, the Q<sub>10</sub> values declined slowly and fluctuated between 1.29 and 3.06 (Fig. 2). The exponential decay models offer predictions about how the magnitude of basal respiration affects temperature sensitivity at a given site, and thus provide a biological interpretation for the differences of temperature sensitivity among sites. Additionally, the negative correlations (r = -0.219 in T<sub>5</sub> and r = -0.367 in T<sub>10</sub>) were found between Q<sub>10</sub> and the minimum soil respiration rates of measurement periods (R<sub>min</sub>), which may be attributed to the high correlations between R<sub>min</sub> and R<sub>0</sub> (r = 0.539 in T<sub>5</sub> and r = 0.720 in T<sub>10</sub>, see Fig. 1).

In this study, the start time of soil respiration measurements ranged from April to June, and the end time ranged from September to October, corresponding to large coefficients of variation (CVs) of 66–89% in minimum soil temperature (Table 2). Thus, variation in the temperature ranges ( $T_{dif}$ ) of measurement periods were mainly from variation of the minimum values at two depths (r = -0.800 in  $T_5$  and r = -0.766 in  $T_{10}$ ), and secondarily for the maximum temperature (r = 0.426 in  $T_5$  and r = 0.645 in  $T_{10}$ , see Fig. 1). Both  $R_{min}$  (57– 65%) and  $R_{max}$  (37–40%) showed large CVs; however, variation in the soil respiration ranges ( $R_{dif}$ ) resulted from differences in the maximum values (r = 0.961 in  $T_5$  and r = 0.963 in  $T_{10}$ , see Fig. 1). Positive correlation was observed between  $Q_{10}$  from soil temperature at 5 cm depth

	T <sub>5</sub>			T <sub>10</sub>				
	Min	Max	Mean	CV	Min	Max	Mean	CV
Q <sub>10</sub>	1.29	5.42	2.63	24.38%	1.71	4.46	2.90	20.20%
R <sub>0</sub>	0.2615	1.9175	0.8527	38.54%	0.17	2.1194	0.8069	44.07%
R <sub>min</sub>	0	3.95	1.16	56.82%	0.01	2.74	0.93	65.49%
R <sub>max</sub>	2.17	15.83	5.94	40.45%	2.37	10.92	6.12	36.67%
R <sub>dif</sub>	0.71	15.17	4.76	50.98%	2.06	9.87	5.19	40.96%
T <sub>min</sub>	0.20	15.41	4.46	65.83%	0	12.70	3.47	88.52%
T <sub>max</sub>	14.46	24.15	19.05	10.21%	13.69	27.22	19.03	13.57%
T <sub>dif</sub>	2.96	22.73	14.59	21.79%	6.02	24.84	15.56	25.85%

**Table 2** Summary statistics of temperature sensitivity ( $Q_{10}$ ), soil carbon quality ( $R_0$ , µmol m<sup>-2</sup> s<sup>-1</sup>), and the measurement-period variables of respiration and temperature during the growing seasons in forest ecosystems across northeast China, grouped into soil temperature at 5 cm depth ( $T_5$ ) and 10 cm depth ( $T_{10}$ )

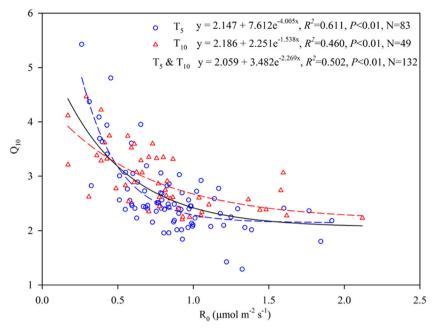
 $R_{min}$ ,  $R_{max}$ , and  $R_{dif}$ : minimum, maximum, and their difference in soil respiration rate (µmol m<sup>-2</sup> s<sup>-1</sup>),  $T_{min}$ ,  $T_{max}$ , and  $T_{dif}$ : minimum, maximum, and their difference in soil temperature (°C), CV: coefficient of variation



**Fig. 1** Pearson's correlation coefficients (*r*) among soil carbon quality ( $R_0$ ), temperature sensitivity ( $Q_{10}$ ), and the seasonal variables of respiration and temperature during the measurement periods in forest ecosystems across northeast China.  $R_0$  and  $Q_{10}$  from exponential soil respiration equations (Respiration =  $R_{0 e\beta T} \& Q_{10=e10\beta}$ ) based on soil temperature at the depth of 5 cm ( $T_5$ , blue circles) or 10 cm ( $T_{10}$ , red squares). The size of a circle or square is determined by the correlation coefficient. \* Indicates significance at P < 0.05 and \*\* at P < 0.01

and soil respiration range of measurement periods (r = 0.299, P < 0.01). However, no significant correlation was detected at 10 cm depth (r = 0.062).

The ranges of soil temperature at 5 cm and 10 cm depths were 0–15 °C in minimum ( $T_{min}$ ), 14–27 °C in maximum ( $T_{max}$ ) and 3–25 °C in their differences during measurement periods (Table 2), which were not significantly correlated with  $R_0$  and  $Q_{10}$  (Fig. 1). However, we found there were significant relationships of  $R_0$  with the minimum soil respiration rates of measurement periods ( $R_{min}$ ) and the soil respiration rates corresponding with minimum soil temperature ( $R_{Tmin}$ ), as seen in Fig. 3. For  $R_0$  from soil temperature at 10 cm depth ( $T_{10}$ ), the correlation was better with  $R_{Tmin}$  ( $R^2 = 0.760$ ) than with  $R_{min}$  ( $R^2 = 0.518$ ). For  $R_0$  from soil temperature at 5 cm depth ( $T_5$ ), the correlation coefficients were similar with  $R_{Tmin}$  ( $R^2 = 0.282$ ) and with  $R_{min}$  ( $R^2 = 0.291$ ).  $R_0$  is soil respiration rate at a reference temperature of 0 °C; thus, the linear basal respiration models with minimum soil temperature is taken at 5 cm depth or 10 cm depth, Eqs. 2 and 5, with the minimum soil temperature and their corresponding soil respiration rates, were the best and could explain 69.6% or 85.7% of the variation in  $R_0$ , respectively.



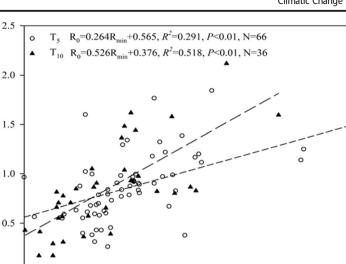
**Fig. 2** The exponential decay relationships between soil carbon quality ( $R_0$ ) and temperature sensitivity ( $Q_{10}$ ) in forest ecosystems across northeast China, with soil temperature grouped into 5 cm depth ( $T_5$ , blue circle and dashed line) and 10 cm depth ( $T_{10}$ , red triangle and dashed line)

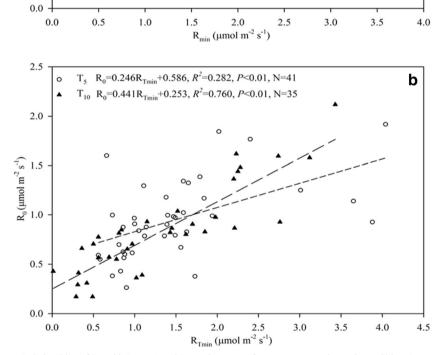
## 4 Discussion

The spatial characteristics in the temperature sensitivity of soil respiration have been reviewed at the national and global scales; however, only small sample sizes (N = 16 - 31) were included from northeastern China (Table 1). Moreover, they only focused on key forest ecosystems in northeastern China, most of which were the same among the large-scale syntheses. In this study, 154 available Q<sub>10</sub> values were collected from forest ecosystems across northeast China and varied from 1.29 to 5.42, which was similar to China's forest ecosystems (1.09-5.53) and in the mid-lower range of global forest ecosystems (0.98–8.90). The sensitivity of soil respiration to temperature is highly dependent on soil temperature measurement depth (Peng et al. 2009). We analyzed the  $Q_{10}$  and  $R_0$  values inferred from soil temperature at 5 cm and 10 cm depths, upon which most soil respiration models were based (Wang et al. 2010b; Song et al. 2014; Xu et al. 2015). The means of  $Q_{10}$  from soil temperature at 5 cm depth and 10 cm depth were 2.63 and 2.90 in this study, which was in the range of 2.28-2.70 (T<sub>5</sub>) and 2.74-3.31 $(T_{10})$  reported in Chinese and global forest ecosystems (Table 1). Other studies also found  $Q_{10}$ values generally increased with the depth of soil temperature observation point because soil temperature fluctuates less in deeper soil (Xu and Qi 2001; Peng et al. 2009; Wang et al. 2010a). Given the great variation in the  $Q_{10}$  values, the assumed constant  $Q_{10}$  of 2 in many biogeochemical models (e.g., Cox et al. 2000; Friedlingstein et al. 2006; Sampson et al. 2007) will influence the accuracy of the quantitative prediction of carbon balance between ecosystem carbon fixation and decomposition in a warmer world, especially for boreal forests (Townsend et al. 1992).

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**Fig. 3** Relationships of  $R_0$  with  $R_{min}$  (a) and  $R_{Tmin}$  (b) among forest ecosystems in northeast China.  $R_0$  are soil respiration rates at a reference temperature of 0 °C from exponential soil respiration functions based on soil temperature at the depth of 5 cm (T<sub>5</sub>, circles) or 10 cm (T<sub>10</sub>, triangles).  $R_{min}$  and  $R_{Tmin}$  denote the minimum soil respiration rates of measurement periods in the growing seasons and the soil respiration rates corresponding with the minimum soil temperature, respectively

The  $Q_{10}$  is calculated from the seasonal changes in soil respiration relative to the changes in temperature; thus, the more pronounced seasonal increase of soil respiration could explain the larger seasonal  $Q_{10}$  over a similar temperature range. Yuste et al. (2004) found the  $Q_{10}$  values depended on not only the amplitude of the seasonal changes in soil respiration but also the different seasonal patterns of plant activity. In this study, the seasonal differences of soil

R<sub>0</sub> (µmol m<sup>-2</sup> s<sup>-1</sup>)

<b>Table 3</b> Multiple linear regressions of basal respiration ( $R_0$ , $\mu$ mol m <sup>-2</sup> s <sup>-1</sup> ) with the minimum soil respiration and
temperature during the measurement periods in forest ecosystems across northeast China, with soil temperature
grouped into 5 cm depth (Eqs. 1–3) and 10 cm depth (Eqs. 4–6)

No.	Equation	$R^2$	Sig.	Ν
1	$R_0 = 0.923 + 0.482 R_{min} - 0.095 T_{Rmin}$	0.606	P<0.01	40
2	$R_0 = 0.751 + 0.462 R_{Tmin} - 0.090 T_{min}$	0.696	P<0.01	41
3	$R_0 = 0.711 + 0.494 R_{min} - 0.084 T_{min}$	0.570	P<0.01	62
4	$R_0 = 0.492 + 0.601 R_{min} - 0.040 T_{Rmin}$	0.597	P<0.01	35
5	$R_0 = 0.314 + 0.523 R_{Tmin} - 0.050 T_{min}$	0.857	P<0.01	35
6	$R_0 = 0.413 + 0.660 R_{min} - 0.049 T_{min}$	0.615	P<0.01	35

 $R_{min}$  and  $T_{Rmin}$ : minimum soil respiration rates (µmol m<sup>-2</sup> s<sup>-1</sup>) and their corresponding soil temperature (°C),  $T_{min}$  and  $R_{Tmin}$ : minimum soil temperature (°C) and their corresponding soil respiration rates (µmol m<sup>-2</sup> s<sup>-1</sup>)

respiration ( $R_{dif}$ ) were significantly correlated with changes of soil temperature ( $T_{dif}$ ) at 5 cm depth (r = 0.356) but not at 10 cm depth (r = 0.256, see Fig. 1). Therefore, it was not surprising that there was a positive correlation between the variation ranges of soil respiration and  $Q_{10}$  from soil temperature at 5 cm depth (r = 0.299, P < 0.01). However, no significant correlation was detected at 10 cm depth.

Basal respiration rate is usually used as an index of soil carbon quality, between which the significantly positive correlations were found (Luan et al. 2011; He and Yu 2016). Higher temperature sensitivity of soil samples with lower carbon quality was observed from laboratory microcosm experiments in the tundra (0-14 °C, Mikan et al. 2002), wetlands (10-30 °C, Inglett et al. 2012), and cropland and grasslands (10-30 °C, Fierer et al. 2005; 5-25 °C, Leifeld and Fuhrer 2005; 25–35 °C, Conant et al. 2008; 10–35 °C, Xu et al. 2012). Our current understanding of the inverse relationship, however, is based primarily on microbial decomposition in laboratory incubations at a series of controlled temperatures (i.e., at the fixed temperature intervals of 2 °C, 5 °C or 10 °C), which may not accurately reflect in situ respiration dynamics. In this study, the "carbon quality-temperature" hypothesis was tested with field soil respiration measurements (including root and microbial respiration) at a wider temperature range of 0–27 °C in forest ecosystems across northeast China (Table 2). We found that the temperature sensitivity decreased exponentially with increasing soil carbon quality, consistent with the thermodynamic hypothesis that the decomposition of low-quality substrates should have stronger temperature dependence than that of high-quality substrates (Bosatta and Ågren 1999). Additionally, the negative correlation only occurred when the  $R_0$  values were smaller than  $\sim 1 \mu mol m^{-2} s^{-1}$  (Fig. 2). As another component of soil respiration, root respiration and its response pattern should be considered in the future. Our results are only compared with in situ experiments without root exclusion methods, and not with laboratory incubation results nor in situ experiments with root exclusion methods.

On the other hand, Luan et al. (2018) revealed that higher tree species diversity leads to lower  $Q_{10}$ . Karhu et al. (2010) showed that the temperature sensitivity increased remarkably from the younger soil organic carbon fraction (i.e., annually cycling,  $Q_{10} < 2$ ) to the older one (i.e., decennial cycling,  $Q_{10} = 4.2-6.9$ ), but decreased again in the oldest one (i.e., centennially cycling,  $Q_{10} = 2.4-2.8$ ) in boreal forest soil. Malcolm et al. (2009) found greater temperature sensitivity in the humus layer than in the litter or fermentation layer between 5 °C and 17 °C, and they concluded that it was presumably from the more recalcitrant forms of carbon in the humus layer. Knorr et al. (2005) also conclude that stable soil organic carbon pools are more sensitive to temperature than labile pools. In general, recalcitrant reactants have higher

activation energies and hence higher temperature sensitivity (Davidson and Janssens 2006). However, similar temperature sensitivity was reported between labile and resistant soil organic matter pools (Fang et al. 2005), between decades-old and younger (< 10 year) carbon (Hopkins et al. 2012), and among different soil depths of 0–90 cm (Hicks Pries et al. 2017). The related mechanisms are still unclear and require further study.

## 5 Conclusions

The key parameters of soil respiration, temperature sensitivity ( $Q_{10}$ ) and basal respiration rate at 0 °C ( $R_0$ ), were studied in forest ecosystems across northeast China.  $Q_{10}$  and  $R_0$  from the commonly used exponential equations (Respiration =  $R_0 e^{\beta T} \& Q_{10} = e^{10\beta}$ ) fitted with in situ soil respiration measurements during the growing seasons (April–October), were highly variable from 1.29 to 5.42 and from 0.1700 to 2.1194 µmol m<sup>-2</sup> s<sup>-1</sup>, respectively. The relationships between  $Q_{10}$  and  $R_0$  could be best fitted with exponential decay equations for soil temperature at 5 cm depth ( $R^2 = 0.611$ , P < 0.01, N = 83), 10 cm depth ( $R^2 = 0.460$ , P < 0.01, N = 49), or both ( $R^2 = 0.502$ , P < 0.01, N = 132). Our results provided large-scale field evidence that the temperature sensitivity decreased with increasing the soil carbon quality, and tended to level off when the  $R_0$  values were larger than ~1 µmol m<sup>-2</sup> s<sup>-1</sup>. The seasonal  $R_0$ values can be more accurately deduced using a bivariate linear model that incorporates both minimum soil temperatures and their corresponding soil respiration rates during the growing season.

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