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Topographic controls on the variability of soil respiration in a humid subtropical forest

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Abstract Knowledge of the spatial and temporal variabilities of soil respiration is important in estimating the soil carbon budget and in understanding how soils may respond to global changes. In areas with complex terrain, the topography can modify the hydrological conditions and other biophysical variables, which complicates the spatial and temporal heterogeneity of soil respiration. Herein, we investigated soil respiration along topographic transects with ridge, middle slope, lower slope and valley positions in a humid subtropical mountain forest in China to assess the driving factors of the variations in soil respiration. Our results showed that there were substantial temporal and spatial variations in soil respiration. The temporal variation of soil respiration could be well explained by the dynamics of soil temperature and moisture. Soil respiration rates also showed clear topographic pattern and decreased significantly from the ridge to valley soils, with the mean rates equaled 3.43 ± 0.13, 2.64 ± 0.30, 2.13 ± 0.26 and 1.88 ± 0.24 μmol m^{-2} s^{-1} at the ridge, middle slope, lower slope, and valley, respectively. Correlation analyses revealed that the spatial variation of soil respiration could be explained by multiple variables (e.g., soil temperature, basal area of the trees, thickness of the forest floor, root biomass and stock of soil dissolved carbon, soil C/N and soil bulk density). Results from partial least squares path modeling suggested that the topography modified the fine root distribution and the lateral losses of light and dissolved organic materials that created areas of high carbon sources for soil respiration at the ridge. The topographically regulated processes further resulted in a high soil C/N at the ridge that favored SOC decomposition. The higher respiration rate for the ridge soil and its higher sensitivity to soil temperature and moisture changes suggested that the ridge position was a potential hot spot for future environmental changes. Future studies and management practices regarding the soil carbon efflux in forest ecosystems with topographical variations should take into account the topographic effects.

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Introduction

Soil respiration is an important component of the terrestrial carbon cycle. Knowledge about its spatial and temporal variabilities is important to carbon balance research. In areas with complex terrain, the landscape position can modify the hydrologic conditions and other biophysical variables within ecosystems (Lybrand and Rasmussen 2015; Mohammadi et al. 2015; Pontara et al. 2016), which complicates the spatial and temporal variations of soil respiration (Atkins et al. 2015; Fang et al. 1998; Konda et al. 2008; Pacific et al. 2011; Stegen et al. 2017; Takahashi et al. 2011; Wang et al. 2015).

Soil temperature and moisture are the well-known factors controlling the temporal variation of soil respiration, but the factors that control the spatial variation are uncertain. Along topographical gradient, soil temperature and moisture, vegetation cover, carbon sources and soil physico-chemical properties have all been found to affect soil respiration (Atkins et al. 2015; Brito et al. 2009; Stegen et al. 2017; Tamai 2010). Soil moisture can be mediated by the gravitational movement of soil water, and thus be a strong driver in the spatial variation of soil respiration (Pacific et al. 2008, 2011; Riveros-Iregui and McGlynn 2009; Sotta et al. 2006; Takahashi et al. 2011; Wiaux et al. 2014). Lower landscape positions with higher soil moisture were found to have higher soil CO_2 emission rates in subalpine watershed and semiarid Loess Plateaus (Pacific et al. 2011; Wang et al. 2017). However, in the tropical rain forests in French Guiana, increasing soil water in the moist bottomlands had lower soil respiration than in the well-drained plateau (Epron et al. 2006). Thus, depending on the drainage status of the research area, the topographic pattern of soil respiration might be variable. Compared to soil moisture, the effect of soil temperature on soil respiration is negligible due to the small fluctuations along the small-scale topographic gradient (Sotta et al. 2006; Wang et al. 2017). In a humid subtropical forest, how the topography regulates the soil water conditions and then affects the spatial variability of soil respiration is still not clear.

In addition to soil moisture, the vegetation distribution and abundance usually have strong patterns along topographic gradient (Olivas et al. 2011; Pontara et al. 2016; Werner and Homeier 2015), which then affects the soil carbon cycling through the carbon input and the modification of soil physico-chemical properties. Soil respiration along hillslopes was found to be significantly associated with vegetation-related variables such as basal area of trees, species composition, and stem density (Atkins et al. 2015; Stegen et al. 2017; Wang et al. 2015). Carbon sources, such as labile carbon or readily decomposable carbon, have also been demonstrated to be significantly associated with variations in soil respiration (Creed et al. 2013; Hursh et al. 2017; Konda et al. 2008). In addition, the soil physico-chemical properties such as soil C/N ratio, microbial biomass and activity, and soil porosity were all found to be important factors affecting soil respiration (Ohashi and Gyokusen 2007; Tamai 2010; Webster et al. 2008). In field conditions, these factors can further interact together to influence soil CO_2 efflux (Brito et al. 2009; Tamai 2010; Wiaux et al. 2014).

As a consequence of the joint influences of those interrelated factors, soil respiration rates were found to be decreasing from ridge to lower slope positions (Epron et al. 2006; Song et al. 2017) or increasing from hills to bottomlands in some cases (Pacific et al. 2008, 2011; Takahashi et al. 2011; Wang et al. 2017; Wiaux et al. 2014), while some other studies found no relationship between soil respiration and topography (Fang et al. 2009; Sotta et al. 2006). For accurate regional ecosystem carbon estimation, it is necessary to understand the interactions among topography, environmental variables, vegetation cover, carbon sources and soil physico-chemical properties, and to search for the controlling factors and mechanisms driving the spatial variation in soil respiration for given ecosystems.

Studies on the topographic variation in soil respiration have been well conducted in wet tropical forests or arid/semiarid sloping landscapes where vegetation and soil were significantly influenced by the redistribution of water sources, but were less documented in the humid and well-drained subtropical forests. The humid subtropical forests, which account for 10% of the total forest area in the world, are characterized as having sufficient water and heat sources, high productivity and complex topography (Pan et al. 2013; Wang et al. 2014; Yu et al. 2014). The average net ecosystem productivity of these forests was significantly higher than other forest ecosystems in Asia (Yu et al. 2014). Therefore, soil CO_2 emissions from these forests are expected to be huge. Quantifying the topography induced heterogeneity of soil respiration can improve our understanding of the variability of CO_2 emissions for similar forests in the world, and reduce the uncertainty in estimating the carbon losses for these forest landscapes.

The objectives of this study were (1) to identify the topographic effects on the spatial and temporal variability of soil respiration; (2) to test the relative control of the soil temperature, soil moisture, vegetation cover, carbon sources, and soil physico-chemical properties to such respiration variations; and (3) to explore the possible mechanisms of how topography affect the soil respiration. To do this, we measured soil respiration rates along topographic transects with ridge, middle slope, lower slope and valley positions in a subtropical humid forest of China. Given the possible interactions among multiple factors, partial least squares path modeling was performed to analyze their effects on the soil respiration. We hypothesize that the topographic regulation of the carbon sources and soil physico-chemical properties are the major determinants of the spatial variation of soil respiration, and soil moisture had limited effects on the spatial variation of soil respiration since the forest is not water-limited.

Methods and materials

Site description

The study site is located in the Badagongshan National Nature Reserve, Hunan Province (29°46.04′N, 110°5.24′E), in the north of Wuling Mountain in the mid-subtropical zone of China. The climate is a subtropical mountain humid monsoon with a mean annual temperature of 10.7 °C. The mean annual precipitation is 2100 mm, of which 76% falls between May and September. The growing season is from May to October. The natural vegetation is dominated by evergreen and deciduous broad-leaved mixed forests. The dominant tree species include *Fagus lucida, Carpinus fargesii, Schima parviflora, Sassafras tzumu, Castanea seguinii, Cyclobalanopsis multinervis*, and *Cyclobalanopsis gracilis*.

Landscape characteristics

A typical headwater catchment in the reserve was chose. The topography is characterized by V-shaped valleys, steep slopes (up to 30°) and flat tops (Fig. 1). The slopes on the two sides of the valley were east and west facing slopes. The catchment elevation ranges from 1469 to 1508 m and encompasses 0.5 ha. The slopes and the valley are well drained and show no evidence of water logging condition.

In the catchment, five transects perpendicular to the valley were set up with 20 m distance apart. At each transect, 1 m × 1 m plots were set up at four topographic positions (ridge, middle slope, lower slope, and valley) at both east and west facing slopes (Fig. 1). Since the vegetation distribution, soil physico-chemical properties and CO_2 efflux rates showed no significant difference between the east and west facing slopes (Table S1 in the Online Resource 1), the effect of slope aspect was not considered. At last, we obtained ten ridge plots, ten middle slope plots, ten lower slope plots and five valley plots. The slope degree at the middle slope and lower slope positions (averagely 24°–29°) was significantly higher than at the ridge and valley positions (averagely 11°–14°).

Field measurements

At each plot, a PVC collar with a diameter of 20 cm and a height of 13 cm was inserted into the soil at a depth of approximately 10 cm in October 2015. For each collar, the height above the soil was measured along four directions and then the average value was used as the chamber offset. The live plants in the collars were manually removed. Soil respiration was measured in situ using an automated chamber system (model Li-8100, LI-COR, Nebraska, USA) from June to October in 2016. Each chamber was measured for 3 min and 15 s, including a 30 s pre-purge, a 45 s post-purge, and a 2 min observation period. Two days before each measurement, the regrown plants were clipped and the roots were left intact to minimize the disturbance to the belowground root respiration. Soil respiration was measured after at least three

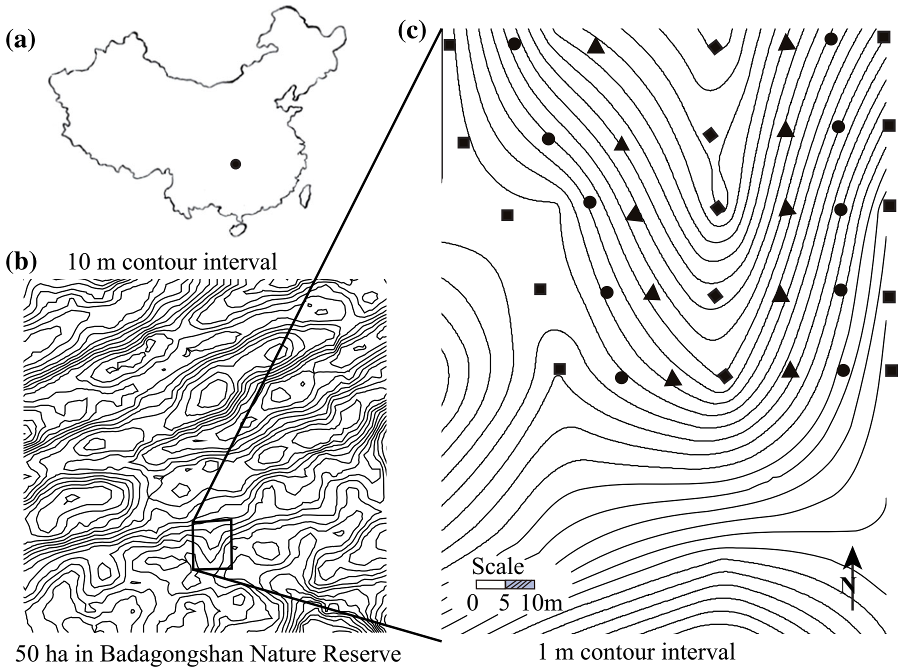

Fig. 1 Location and the topographic image of the study site in the Badagongshan National Nature Reserve (**a**, **b**), and the distribution of 35 plots across the catchment (**c**). In the vertical direction of the valley, five transects were set up. Each transect included plots from ridge (solid square), middle slope (solid cycle), lower slope (triangle) and valley (diamond) at both east and west facing slopes

continuous rain-free days to minimize the effect of precipitation events. Due to the frequent rain events in the growing season, soil respiration was measured four times in June, July, September and October. Soil temperature was measured with the temperature logger iButtons (DS1922 L, Maxin Integrated, CA, USA) at a depth of 10 cm from June 2016 to May 2017. The temperature averages were automatically logged every 2 h. Soil moisture was measured as the gravimetric water content after soil sampling. The soil moisture data showed that the soil was not under drought conditions during our CO_2 flux measurement. In addition, the annual precipitation and its monthly variation in 2016 were similar with other years, indicating that 2016 was a climatically typical year (Fig. S1 in the Online Resource 1).

All trees with a diameter at breast height ≥ 5 cm in the catchment were identified at the species level and measured in 2015. The tree number, the sum of the breast-height basal areas (basal area), and the Shannon index and Richness index of the tree species for the trees in a 5-m radius around the sampling plot were calculated. Above the 1 m × 1 m plot, a litter mesh-based collection device was used to collect the litterfall from September 2015 to August 2016. Leaves were taken back to the laboratory every month and dried at 105 °C for 1 h and then at 65 °C for 48 h to calculate the annual litterfall.

Soil samples were collected near each plot in October 2015. The surface organic material was carefully removed after measuring its thickness (the thickness of the forest floor). 0–10 cm soil samples were then collected with a shovel. All soil samples were then immediately brought to the laboratory and passed through a 2 mm sieve. The roots and visible residues were picked out manually, and the roots were thoroughly washed with deionized water and dried at 65 °C for 48 h to calculate the root biomass. Part of the soils were stored in a refrigerator (= 4 °C, within 2 days) for lab analysis, and the other part of the soils were air-dried for further physico-chemical analysis. To determine the soil bulk density, 5 cm diameter and 5 cm deep stainless steel bulk density tubes were inserted into the soil at specified depths. The samples in the tubes were dried at 105 °C until the weight of the soil remained constant. To calculate the soil bulk density, the weight and volume of the rock fragments (> 2 mm) were subtracted from the total mass and volume in the tube. For the estimation of the rock fragment volume, the particle density is assumed to be 2.65 g cm^{-3}.

Laboratory analyses

Soil dissolved organic carbon (DOC) and inorganic nitrogen (NH_4^+ plus NO_3^-) were extracted once the soil samples were collected and sieved. To measure soil DOC, 10 g of fresh soil was extracted with 50 mL of deionized water. The mixed paste was shaken for 0.5 h at 250 rpm at 25 °C and centrifuged for 10 min at 4000 rpm. Next, the supernatant liquid was filtered through a 0.45 mm filterable membrane. The concentrations of the DOC were measured by a TOC Analyzer (Vario TOC, Elemental, Germany). To measure soil NH_4^+ and NO_3^-, 10 g of fresh soil were extracted with 100 mL of 2 mol L^{-1} KCl. The concentrations of NH_4^+ and NO_3^- were measured using a discrete autoanalyzer (EasyChem, Systea Scientific Inc., Italy).

Soil organic carbon (SOC) and total nitrogen (TN) were then determined using an elemental analyzer (Thermo Fisher Flash 2000, USA). Before the carbon and nitrogen analysis, the soil samples were tested for the presence of carbonate, and no carbonate was found. Soil texture was determined using a laser particle size analyzer (Mastersizer 3000, Malvern, UK). Soil available phosphorous was extracted using 0.03 mol L^{-1} NH_4F, and the absorbance was detected using a spectrophotometer at 700 nm. Soil pH was measured with a calomel electrode using a 1:2.5 (weight: volume) paste of air-dried soil and deionized water.

The stocks of SOC/DOC for the 0–10 cm depth profile were calculated as follows:

$$\text{SOC stock} = d \times SOC \times BD \times (1 - R) \quad (1)$$

$$\text{DOC stock} = d \times DOC \times BD \times (1 - R) \quad (2)$$

where *SOC stock* (kg m^{-2}) and *DOC stock* (g m^{-2}) are the stocks of these fractions at 0–10 cm depth. *d* (m) is the thickness of the soil layer. *SOC* (mg g^{-1}) and *DOC* (μg g^{-1}) are the total organic carbon concentration and dissolved organic carbon concentration, respectively; *BD* (g cm^{-3}) is the soil bulk density; and *R* is the mass proportion of rock fragments (> 2 mm).

Statistical analyses

The data were checked for normal distribution and homoscedasticity of variances using the Kolmogorov–Smirnov test and the Levené test using SPSS 16.0 for Windows (IBM Corporation, USA), and the data were log-transformed when necessary (Levené 1960; Lilliefors 1967). The comparisons of slope degree, properties of vegetation cover, annual litterfall, thickness of the forest floor, root biomass, stocks of SOC/DOC, and other soil physico-chemical properties at the four landscape positions were performed using one-way analyses of variance (ANOVA) with Tukey's HSD as post hoc. The changes in soil respiration, soil temperature and moisture for the four measurements at different times were determined using a repeated measurements analysis of variance. Coefficients of variation (CVs) were calculated to quantify the temporal and spatial variability of soil respiration and other predictor variables.

To explore the main factors controlling the temporal variability in respiration, correlation and regression analyses were used to determine the relationships of soil respiration with soil temperature and moisture over the measurement period. Different linear regressions among the four landscape positions were compared using the analysis of covariance. To explore the main factors controlling the spatial variability in respiration, Pearson correlation analysis was used to examine the relationship between soil respiration and the predictor factors. The average respiration data of September and October were used for the analysis of the spatial variability since the soil samples were collected in 1st October. Principal component analysis (PCA) and Pearson correlation analysis were performed among the predictor variables to examine their correlations. The analysis of variance and covariance were conducted using SPSS 16.0 for Windows, and each test was carried out at an α-level of 0.05. The correlation and regression analyses were performed in R version 3.3.2 using the stats and psych packages. The PCA was executed in R version 3.3.2 using the vegan package.

Partial least squares (PLS) path modeling was further performed to evaluate the possible mechanisms of how the predictor variables affect soil respiration (Sanchez 2013; Tenenhaus et al. 2005). Five latent variables (including topographic traits, environmental conditions, vegetation cover, carbon sources and soil physico-chemical properties) were summarized for the PLS path modeling. Each latent variable included one or more manifest variables. The topographic traits included landscape position and slope degree. The environmental conditions included soil temperature and moisture. The vegetation cover included tree number, basal area of the trees, and diversity index of the tree species. The carbon sources included annual litterfall, thickness of the forest floor, root biomass, and SOC/DOC stocks. Other soil properties were grouped as the soil physico-chemical properties. The path coefficients (representing the direction and strength of the linear relationships between the latent variables) and the explained variability (R^2) were estimated in the models. The total effect (direct plus indirect effect) of each latent variable on soil respiration was calculated. The direct effects are given by the path coefficients, and the indirect effect are obtained as the product of the path coefficients by taking an indirect path. The goodness of fit (GOF) was used to evaluate the overall predictive power of the model. PLS path modeling was conducted in R version 3.3.2 using the plspm package. The raw data and R code for this manuscript are given in the Online Resources 2 and 3.

Results

Temporal and spatial variations in soil respiration

Soil respiration rates peaked in July, and then gradually decreased in September and October (Fig. 2). The average CV for this temporal variation of soil respiration was 33.3 ± 2.0%. Soil respiration also exhibited large spatial heterogeneity with a mean CV that equaled 40.7 ± 2.1%. The respiration rates significantly decreased from the ridge to valley positions ($p < 0.01$). This spatial pattern of soil respiration remained comparatively consistent throughout the measurement campaigns. The mean soil respiration rates were 3.43 ± 0.13, 2.64 ± 0.30, 2.13 ± 0.26 and 1.88 ± 0.24 µmol m^{-2} s^{-1} at the ridge, middle slope, lower slope and valley, respectively.

Temporal and spatial variations in soil temperature and moisture

Soil temperature throughout the measurement period varied between 13.3 and 19.1 °C, the lowest value being observed in October and the highest in July (Fig. 3a). The average CV for this temporal variation of soil temperature was 14.7 ± 0.2%. In contrast, the spatial variation of soil temperature among the 35 sites was much smaller, with CV averagely equaled to 2.1 ± 0.3%. Whereas, we still observed significant difference for soil temperature among the four landscape positions in September and October, but not in June and July ($p > 0.05$). In September and October, soil temperature at the ridge was significantly higher than other positions.

Soil moisture throughout the measurement period varied between 1.06 and 1.31 g g^{-1} dry soil (Fig. 3b). Soil moisture was the lowest in October, and the highest in July which corresponded to the rainfall that peaked in July. The average CV for this temporal variation of soil moisture was 11.5 ± 1.3%. In addition, we also observed a considerable spatial variation of soil moisture among the 35 sites, with average CV equaled to 13.9 ± 1.1%. Whereas, we did not observed significant difference for soil moisture among the four landscape positions at the four measurements, except in June ($p > 0.05$). In June, soil moisture at the ridge was significantly lower than at the lower slope and valley positions.

Topographic heterogeneity of the predictor variables

The vegetation-related factors exhibited large spatial heterogeneity (Table 1). The CVs for the tree number, basal area of the trees, and the Shannon index and Richness index of the trees were 42.3, 70.1, 27.7 and 39.5, respectively. The tree number and basal area of the trees significantly decreased from the ridge to the valley ($p < 0.05$), but the diversity and richness of the trees showed no differences among the four landscape positions. Meanwhile, the variables related to carbon sources also showed high spatial heterogeneity, with CVs ranged from 19.9 to 61.3%. The thickness of the forest floor, the root biomass and the DOC stock decreased significantly from the ridge to the valley ($p < 0.05$), but the annual litterfall and SOC stock showed no differences among the four landscape

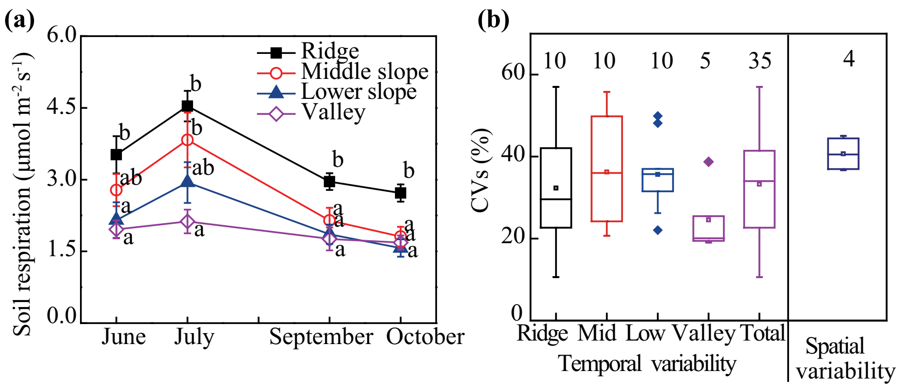

Fig. 2 Soil respiration rates at the four landscape positions (**a**) and the spatiotemporal variability of soil respiration (**b**). Results in the chart (**a**) were means ± standard errors for n = 10 at the ridge, middle slope, lower slope, and n = 5 at the valley. The same letter indicated no significant differences at different landscape positions at the same measurement time. Coefficients of temporal variation (CVs) among the four measurements at the four positions were showed in the left part of the boxplot. Coefficients of spatial variation among the 35 sites during the four measurements in time were showed in the right part of the boxplot. The numbers above each box were the n value for the boxplot

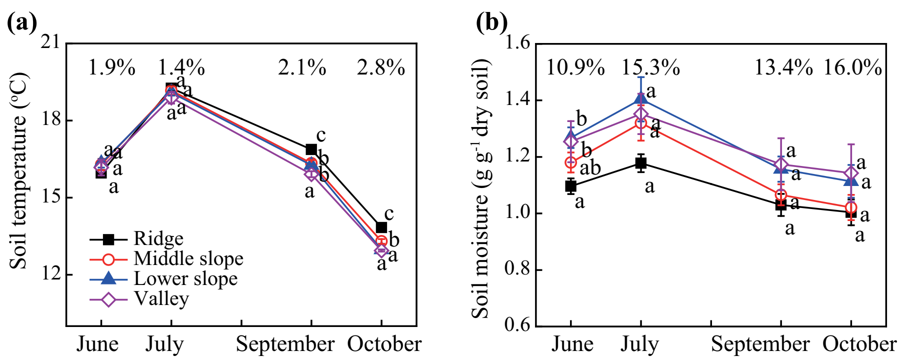

Fig. 3 Soil temperature (**a**), soil moisture (**b**) at the four landscape positions over the measurement period. Results were means ± standard errors for n = 10 at the ridge, middle slope, lower slope, and n = 5 at the valley. The same letter indicated no significant differences at different landscape positions at the same measurement time. The numbers above the points were the coefficients of spatial variation among the 35 sites

positions. The CVs of the variables related to soil physic-chemical properties ranged from 5.7 to 48.5%. We only found that soil C/N significantly differed among the four landscape positions ($p < 0.05$), with the soil at the ridge having a significantly higher C/N ratio. Other properties, such as the concentration of soil inorganic nitrogen, soil available phosphorus, pH, soil texture and soil bulk density, had no significant differences among the four landscape positions.

Factors controlling the temporal variability of soil respiration

The temporal variation of soil respiration was similar to the changes in soil temperature and moisture (Figs. 2, 3). Soil respiration exponentially increased with temperature for all four positions (Fig. 4a), and the regression slopes and intercepts were significantly different for the four positions (Table 2). The response of the respiration to soil temperature at the middle slope was significantly ($p < 0.05$) larger than that of the valley. The Q10 values of respiration were 2.56, 3.93, 2.89 and 1.49 at the ridge, middle slope, lower slope and valley, respectively. Soil respiration linearly

Table 1 Study site description and soil properties at the four landscape positions

Properties	Ridge	Middle slope	Lower slope	Valley	CVs (%)
Site description					
Slope degree (°)	11 ± 2a	24 ± 3b	29 ± 3b	14 ± 4a	53.1
Vegetation cover					
Tree number (ha^{-1})	5400 ± 300a	3840 ± 573b	3120 ± 331b	2320 ± 344b	42.3
Basal area (cm^2 m^{-2})	33.2 ± 5.1a	18.4 ± 2.5b	12.9 ± 2.5b	8.5 ± 2.1b	70.1
Shannon index	1.90 ± 0.09a	1.64 ± 0.17a	1.62 ± 0.15a	1.40 ± 0.20a	27.7
Richness index	8.0 ± 0.7a	6.4 ± 0.9a	5.8 ± 0.8a	5.2 ± 1.2a	39.5
Carbon sources					
Litterfall (g m^{-2})	349 ± 43a	268 ± 32a	316 ± 26a	305 ± 57a	35.8
Forest floor (cm)	7 ± 1a	4 ± 1b	4 ± 1b	3 ± 1b	42.3
Root biomass (kg m^{-3})	0.44 ± 0.05a	0.32 ± 0.03b	0.15 ± 0.03c	0.14 ± 0.04c	61.3
SOC stock (kg m^{-2})	9.85 ± 0.47a	9.82 ± 0.79a	9.26 ± 0.46a	8.48 ± 0.69a	19.9
DOC stock (g m^{-2})	1.98 ± 0.31a	1.53 ± 0.23ab	1.11 ± 0.07b	1.04 ± 0.20b	46.5
Soil properties					
C/N	14.5 ± 0.5a	12.0 ± 0.2ab	11.1 ± 0.3b	10.8 ± 0.5b	14.6
$NH_4^+ + NO_3^-$ (μg g^{-1})	17.3 ± 1.6a	21.1 ± 2.8a	24.0 ± 2.0a	24.7 ± 6.3a	39.2
Soil available P (μg g^{-1})	2.3 ± 0.2a	2.0 ± 0.1a	2.4 ± 0.3a	1.5 ± 0.4a	48.5
pH	4.5 ± 0.1a	4.6 ± 0.1a	4.7 ± 0.0a	4.9 ± 0.2a	5.7
Clay (%)	11.4 ± 1.0a	11.4 ± 0.6a	12.1 ± 0.8a	14.1 ± 1.3a	22.1
Silt (%)	67.7 ± 2.0a	68.7 ± 1.6a	70.1 ± 1.6a	66.9 ± 2.2a	7.8
Sand (%)	20.9 ± 1.1a	19.9 ± 1.4a	17.8 ± 0.8a	19.1 ± 1.5a	18.5
Bulk density (g cm^{-3})	0.52 ± 0.02a	0.58 ± 0.03a	0.54 ± 0.03a	0.51 ± 0.05a	20.4

The properties of vegetation cover were calculated for the trees in a 5-m radius around the sampling plot. Basal area was the sum of the breast-height basal area for the trees. Root biomass was calculated for the fine root within 0–10 cm depth profile. The stocks of SOC and DOC were the sum of 0–10 cm depth profile. Soil available P was soil available phosphorus. Soil texture was represented as % soil volume of clay (< 2 μm), silt (< 2–20 μm) and sand (20–2000 μm). CVs were the coefficients of variation of the variables among the 35 sites. The error term represented standard error for n = 10 in the ridge, middle slope, lower slope, and n = 5 in the valley. Different letters within each row indicated significant differences ($p < 0.05$)

increased with soil moisture for all four positions (Fig. 4b). The regression slopes and intercepts had significant differences among the four positions (Table 2), and the response of soil respiration to moisture significantly decreased from the ridge to the valley ($p < 0.01$).

Factors controlling the spatial variability of soil respiration

When considering the spatial variability, soil respiration rate was positively correlated with soil temperature, the basal area of the trees, the thickness of the forest floor, the root biomass, the DOC stock and the soil C/N and negatively correlated with the soil bulk density (Table 3).

PCA was used to analyze the relationships among the predictor variables (Fig. 5 and Table S2 in the Online Resource 1). The first two axes of the PCA explained approximately 47% of the variation among the predictor variables. Soil temperature was positively correlated with the parameters associated with the vegetation cover (tree number, basal area and diversity index of the trees), the parameters associated with carbon sources (root biomass, thickness of the forest floor, and DOC stock), and the soil C/N ratio. Soil moisture was positively correlated with the concentration of soil inorganic nitrogen. Soil C/N ratio was positively correlated with the parameters

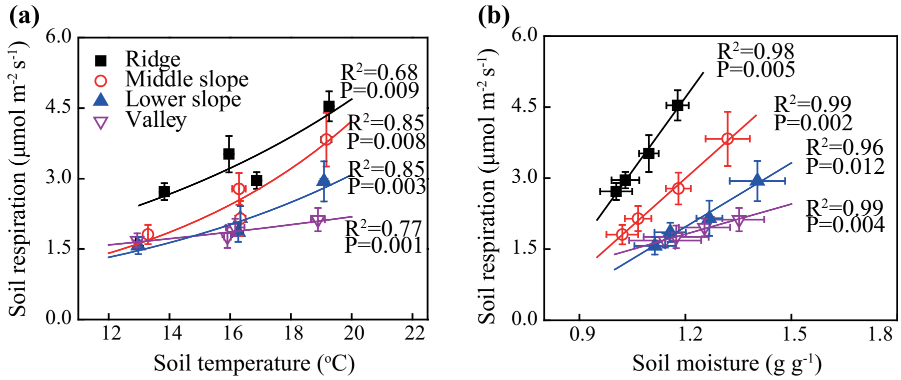

Fig. 4 Relationships between soil respiration and soil temperature (**a**), soil moisture (**b**) over the measurement period. Each point was a mean value for the corresponding position at one measurement time. Lines were exponential regressions for soil temperature and linear regressions for moisture with $p < 0.05$. R^2 and p value values were given in the figure, and the coefficients of the regressions were given in Table 2

Table 2 Coefficients of the regressions between soil respiration and soil temperature, and soil moisture for soils from the four positions

Positions	Respiration × temperature[a]		Respiration × moisture	
	Line slope	Intercept	Line slope	Intercept
Ridge	0.094ab	− 0.328a	10.34a	− 7.71a
Middle slope	0.137b	− 1.309b	6.65b	− 4.98b
Lower slope	0.106ab	− 0.994a	4.50c	− 3.42c
Valley	0.040a	− 0.020a	2.12d	− 0.73c

[a]The exponential regressions between soil respiration and soil temperature were natural log transformed to linear regressions for the covariance analysis. The covariance analysis was performed to evaluate the differences among the regressions. Different letters within each column indicated significant differences ($p < 0.05$) of the slope or intercept of the regressions

associated with carbon sources. The concentration of soil inorganic nitrogen was negatively correlated with the basal area of the trees. The basal area of the trees was positively correlated with the thickness of the forest floor, but was not correlated with the parameters that are associated with the carbon sources.

To evaluate the influences of the predictor factors on soil respiration, PLS path modeling was implemented to identify the key factors and to reveal the possible pathways. Five groups of factors (topographic traits, environmental conditions, vegetation cover, carbon sources and soil physico-chemical properties) were included in the model. This modeling analysis provided the best fit to our data according to the respective indices of the model fit (GOF = 0.64). The PLS path modeling explained 63% of the variance in the soil respiration (Fig. 6). The topographic traits had a significant direct influence on the environmental conditions and carbon sources. In addition, the topography indirectly influenced the vegetation cover and soil physico-chemical properties through its effects on the environmental conditions and carbon sources. The total effect of topography on the environmental conditions, vegetation cover, carbon sources and soil physico-chemical properties were 0.87, 0.70, 0.77 and 0.73, respectively. The soil physico-chemical properties significantly influenced soil respiration directly and the carbon sources significantly influenced soil respiration directly or indirectly by their effects on soil physico-chemical properties. There was no significant direct effect of environmental conditions on soil respiration. The total effects of the topographic traits, environmental conditions, vegetation cover, carbon sources and soil physico-chemical properties on the spatial variation of soil respiration were 0.59, 0.12, 0.05, and 0.55, respectively. Together, these results

Table 3 Pearson correlations between soil respiration and predictor variables (including environmental factors, vegetation variables and soil variables)

Properties	Pearson correlation	
	r	*p*
Temperature	**0.580**	**<0.001**
Moisture	– 0.166	0.278
Tree number	0.278	0.106
Basal area	**0.333**	**0.050**
Shannon index	– 0.024	0.891
Richness index	– 0.071	0.686
Litterfall	0.257	0.137
Forest floor	**0.524**	**0.001**
Root biomass	**0.697**	**<0.001**
SOC stock	0.133	0.447
DOC stock	**0.380**	**0.030**
C/N	**0.672**	**<0.001**
$NH_4^+ + NO_3^-$	– 0.316	0.064
Soil available P	– 0.036	0.838
Clay	– 0.238	0.169
Density	– **0.474**	**0.004**

Numbers in bold indicate significant correlations with $p < 0.05$

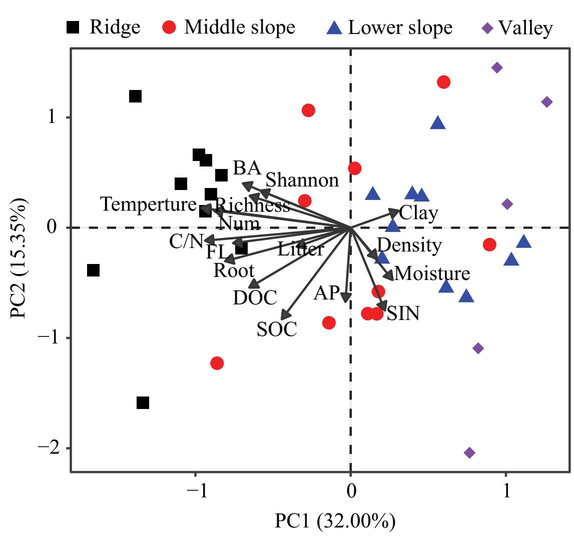

Fig. 5 Principal component analysis (PCA) of the predictor variables. *Num* tree number, *BA* the breast-height basal area of the trees, *Root* root biomass of 0–10 cm depth profile, *Litterfall* annual amount of litterfall, *Forest floor* the thickness of the forest floor, *SOC/DOC* the stocks of SOC/DOC of 0–10 cm depth profile, *AP* soil available phosphorus, *SIN* the concentration of soil NH_4^+ plus NO_3^-, *density* soil bulk density

suggested that topography exerted indirect effects on soil respiration mainly through direct or indirect effects on the carbon sources and soil physico-chemical properties.

Discussion

Temporal variations in soil respiration

At each landscape position, both soil temperature and soil moisture showed significant strong positive relationships with soil respiration (Fig. 4), suggesting that they are the dominant factors controlling the temporal variation of soil respiration in our subtropical forest. However, these results were different from some wet tropical forests where the effects of soil temperature on CO_2 efflux are constrained by soil water availability (Goodrick et al. 2016; Hanpattanakit et al. 2015; Sotta et al. 2004), or in some cases the surface soil moisture alone largely explained the temporal variation of soil respiration (Rubio and Detto 2017). The reason might be that soil temperature and soil moisture co-vary across the seasons due to the effect of the East Asian summer monsoon in the study area.

The relationship between soil respiration and moisture can be linear, logarithmic, quadratic, or parabolic (Hanpattanakit et al. 2015; Luo et al. 2012; Rubio and Detto 2017). In this study, linear relationships were found at all four positions (Fig. 4b). This was because the range of soil moisture was proper for soil respiration with no suppression due to the plentiful rainfall and well-drained terrain. Furthermore, soil respiration rates were detected for at least three continuing rain-free days, and thus the effect of precipitation events was minimized (Kishimoto-Mo et al. 2015; Zhang et al. 2013). Interestingly, the response of soil respiration to the moisture change was different among the four positions (Table 2). This might be due to the higher water content for lower slope and valley soils (near the optimum water-holding capacity) that limited the positive effect of soil moisture, thereby causing the responses of soil respiration to moisture change to be weaker than those of the ridge and middle slope soils.

The relationship between soil temperature and respiration is usually described using an exponential equation (Davidson et al. 1998). Here, the exponential temperature-based model could explain the temporal

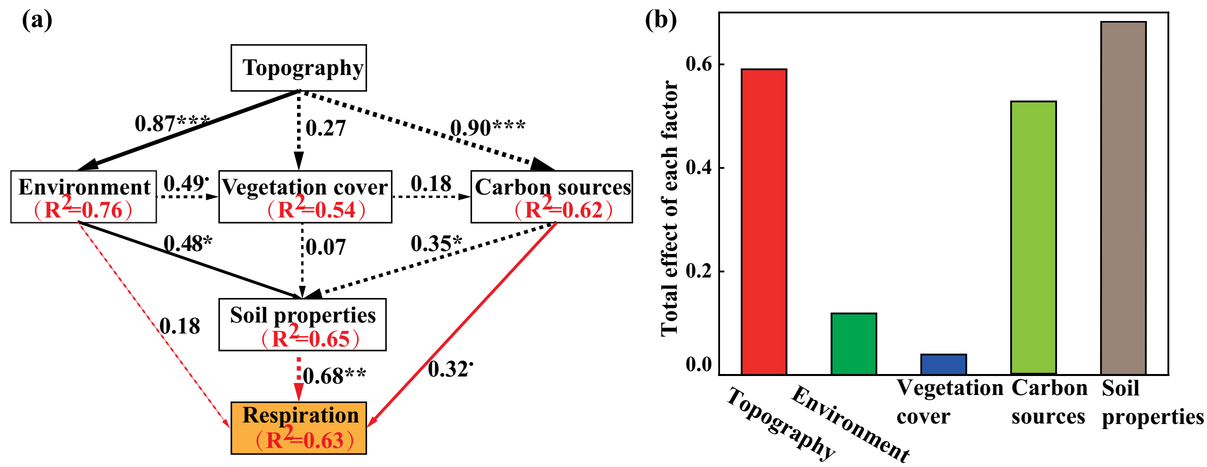

Fig. 6 Path analysis diagrams (**a**) and total effects (**b**) of each factor on spatial variation in soil respiration (The partial least squares path modeling analysis of CO_2 efflux). Topography included variables of landscape position and slope degree; environment included variables of soil temperature and moisture; vegetation cover included variables of tree number, basal area and the richness index of the trees; carbon sources included variables of the thickness of the forest floor, root biomass and DOC stock; soil properties included variables of soil C/N, soil inorganic nitrogen content and soil bulk density. The goodness of the fit equaled 0.64. The arrows represented the direction of effects. The numbers in lines showed the loadings coefficient between variables. Solid and dashed arrows represent the positive and negative effects in a fitted structural equation model, respectively. Widths of the arrows indicate the strength of the causal relationship. Percentages (R^2) indicated the variance explained by other factors. A significant relationship at ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, and a relationship at $\cdot p < 0.1$. The total effect of each factor equaled the direct effect plus the indirect effect

variation of soil respiration very well at each position (Fig. 4a). The Q10 values ranged from 1.49 to 3.93, which was within the range of the reported Q10 in other subtropical forests (Bondlamberty and Thomson 2010; Zhou and Shi 2011). Interestingly, the valley soil had the lowest Q10 value among the four landscape positions (Table 2). Q10 was reported to be positively related to the substrate availability (Fissore et al. 2013; Luan et al. 2013). The low Q10 value of the valley soil might be explained by the low substrate availability that was revealed by the low content of soil labile carbon sources (DOC stock in Table 1).

Spatial variation in soil respiration and its controlling factors

We observed a significant topographic effect on soil respiration with the ridge soil having the highest respiration rate among the four positions. The topography can spatially modify soil temperature and soil water content and consequently impose organized heterogeneity on the vegetation cover, carbon sources and soil physico-chemical properties (Lybrand and Rasmussen 2015; Mohammadi et al. 2015; Pontara et al. 2016). Here, soil respiration was significantly correlated with multiple parameters that were associated with the environmental conditions, vegetation cover, carbon sources and soil physico-chemical properties (Table 3), indicating that there were multiple processes that controlled the CO_2 efflux together.

Soil physico-chemical properties (e.g., soil C/N, soil inorganic nitrogen and soil bulk density) contributed the largest portion of the variance in respiration (Fig. 6) (Martin and Bolstad 2009; Ngao et al. 2012; Tamai 2010). The effect of the soil C/N was ambiguous in previous studies. Some researchers found that a high soil C/N constrained decomposition due to the limited availability of nitrogen for microbial assimilation (Mande et al. 2015; Xu et al. 2016). In contrast, some other researchers found that a low soil C/N constrained microbial activity and decomposition due to the refractory carbon sources since a low C/N indicated that SOC was more decomposed by microorganisms (Ngao et al. 2012; Webster et al. 2008). Thus, our positive relationship between the soil C/N and soil respiration probably reflects better carbon consumption with an increasing C/N under non-limiting nitrogen conditions. Similarly, we also found that the soil inorganic nitrogen content was slightly negatively related to soil respiration. In contrast with our results, the soil available nitrogen was found to be positively correlated with soil respiration due to its positive effect on the root biomass and consequently higher respiration rates (Scott-Denton et al. 2003; Wang et al. 2015). However, this effect was not observed here with no relationship being found between the soil inorganic nitrogen and root biomass. The negative relationship between the soil inorganic nitrogen and the basal area of trees (Fig. 5) suggested that the higher accumulation of the soil inorganic nitrogen at the valley was probably caused by the lower uptake by plants. In addition, the bulk density here was negatively correlated with soil respiration. Commonly, a lower soil bulk density contributes to higher soil porosity, thus resulting in higher soil O_2 availability, which facilitates microbial activities and higher CO_2 diffusion, and at last leads to the increase in soil respiration (Brito et al. 2009; Ngao et al. 2012; Ohashi and Gyokusen 2007).

Substrate supply (including the carbon sources that are allocated to microbes through roots and its exudation, litterfall, and soil carbon) also contributed a large portion of the variance observed in soil respiration (Hursh et al. 2017). Among the parameters that are associated with carbon sources, soil respiration was most correlated with the fine root biomass. Fine roots lead to variations in the root-derived autotrophic respiration and provide substrates to microbes through the root residue and its exudation, which jointly influence the total soil respiration (Hanpattanakit et al. 2015; Huang et al. 2014; Zhou et al. 2013). In consequence, the higher root biomass at the ridge resulted in higher CO_2 fluxes than at the other lower slope positions. Litter was an important carbon source for microbes from aboveground (Webster et al. 2008; Zhou et al. 2013). The forest floor contains plenty of decomposed and half-decomposed residual carbon from the litterfall, thus contributed to the variation of soil respiration (Table 3). The importance of the forest floor carbon to the soil respiration was also demonstrated by some previous studies (Rayment and Jarvis 2000; Takahashi et al. 2011). Despite a relatively homogenous annual litterfall among the four positions (Table 1), the significant higher accumulation of the forest floor at the flat ridge and the lower accumulation at the steep slope and valley positions suggested that there was an intensive lateral transport of these free and light fractions with water or gravity along the sloping landscape. It's notable that V-shaped Valley in steepland could accumulate surface runoffs from both slopes, resulting a stronger water force and consequently a more intensive lateral transport of light organic materials.

Soil carbon pool has also been widely demonstrated to affect soil respiration (Lecki and Creed 2016; Mande et al. 2015; Søe and Buchmann 2005; Zhou et al. 2013). However, here we observed a significant positive correlation between soil respiration and soil DOC stock, but not with the SOC (Table 3). DOC is thought to be the primary substrate for the microbial soil CO_2 efflux because it is labile and can be readily utilized by microbes (Creed et al. 2013). With steep land, the distribution of the DOC might be further affected by the topography due to its high mobility (Creed et al. 2013; Sun et al. 2015). We had data showing that the DOC concentration in the surface water was higher than that in the soil (Wang, unpublished data), which suggests that there was lateral transportation of DOC with water along the sloping landscape. This topographic regulated process resulted in higher DOC stock at the flat ridge and lower DOC stock at the steep slope and valley positions. Overall, as decomposable carbon sources, the root biomass, forest floor and DOC stock could positively influence soil respiration. Furthermore, sufficient carbon sources could also lead to a high soil C/N ratio (Fig. 5), which indirectly favors soil respiration.

A positive correlation between soil respiration and vegetation cover parameter (basal area of trees) was observed here. Previous studies have found significant effects of the plant compositions, the mean diameter at breast height of trees, the stem density and the distance to the nearest tree on the spatial variation of soil respiration (Katayama et al. 2009; Luan et al. 2012; Stegen et al. 2017). However, the diversity of trees here had no correlation with soil respiration. Thus, compared to the qualitative characteristic (diversity of trees) of the vegetation cover, the quantitative characteristic (basal area of trees) better explained the variation of soil respiration. This broadly strong link between the vegetation cover and soil CO_2 fluxes suggests an opportunity to use the vegetation cover to characterize the spatial pattern of the soil respiration (Katayama et al. 2009; Søe and Buchmann 2005; Stegen et al. 2017).

Vegetation cover has been found to affect soil respiration through its close links with roots and litterfall, which control the distribution of the carbon sources (ArchMiller and Samuelson 2016; Raich and Tufekciogul 2000). Here, we actually found that the tree number significantly affected the root biomass (p = 0.012) and soil DOC stock (p = 0.049). However, the basal area of trees only had a certain correlation with the thickness of the forest floor (p = 0.004), but had no effect on the distribution of the root biomass and soil DOC stock. This was because the topography could redistribute the free and light labile carbon sources (as mentioned above) and weaken the influence of the vegetation cover on the carbon sources. At last, the total effect of the vegetation cover on the variance of soil respiration was much smaller than other factors (Fig. 6).

Soil temperature and moisture have been widely reported to explain the spatial variance of soil respiration (Davidson et al. 1998; Hursh et al. 2017; Mande et al. 2015). In tropical forests or arid/semiarid sloping landscapes, soil moisture was further recognized as the most important factor controlling the topographic variation of soil respiration (Pacific et al. 2008, 2011; Riveros-Iregui and McGlynn 2009; Sotta et al. 2006; Takahashi et al. 2011; Wiaux et al. 2014). However, soil moisture had no significant effect on the spatial variance of soil respiration in this subtropical forest. This might be caused by the following two reasons. First, our study site was humid and well-drained with no drought or flooding, thus the effect of water redistribution was small along the sloping landscape. Second, soil respiration was measured after at least three continuous rain-free days, and this sampling scheme might also weaken the difference of soil moisture among the four positions, and consequently obfuscated the effect of soil moisture (Fig. 3). Since soil respiration was measured after three rain-free days, the results of soil respiration were largely an indication of the baseline CO_2 effluxes. Having the measurements closer or further to rain events would give us a better understanding of how much precipitation and soil moisture contribute to CO_2 effluxes. However, our sampling scheme did not fully consider this uncertainty and the associated effects of topography. As a result, this uncertainty could potentially limit the generalizability of our results. Future studies are needed to be designed to consider the effects of precipitation and topography on soil respiration rates, which may yield more information on the temporal and spatial variations of soil respiration in this complex terrain.

In contrast, we found a significant correlation between soil temperature and respiration. This result suggested that the spatial variation of soil respiration in this ecosystem was more affected by soil temperature than soil moisture. It is notable that soil temperature also co-varied with many other parameters (Fig. 5 and Table S2 in the Online Resource 1), suggesting that soil temperature did not work alone, but interacted with other parameters. The results of the path analysis further demonstrated that soil temperature (environmental traits) could indirectly influence soil respiration through its effect on the vegetation cover and soil physico-chemical properties, and the direct effect of soil temperature on respiration rate was small (Fig. 6).

From the above analysis, the environmental conditions, vegetation cover, carbon sources and soil physico-chemical properties all affected the spatial variation of soil respiration. According to the total effects of each factor, the carbon sources and soil physico-chemical properties explained higher fractions of the variance in respiration than the environment and vegetation cover (Fig. 6). This result was consistent with our hypothesis that the topography controlled the heterogeneity of soil respiration mainly through its effects on the carbon sources and soil physico-chemical properties, and soil moisture had minimal effect. Some previous studies have also demonstrated that carbon sources and soil physico-chemical properties primarily determined the spatial variation of soil respiration, while soil temperature and moisture played much weaker roles (Xu and Qi 2001; Zhou et al. 2013). First, the topography resulted in the fine root distribution through the vegetation cover that created areas of higher soil CO_2 efflux at the ridge and resulted in the lateral losses of light materials at sloping and valley positions that created areas of lower decomposable carbon sources for soil respiration. Second, the topography indirectly regulated the soil C/N due to its effects on soil temperature and carbon sources, and resulted in the faster decomposition of the ridge SOC.

Conclusion

Soil respiration in this humid and well-drained subtropical mountain forest had strong temporal and spatial variations. Both soil temperature and soil moisture could well explain the temporal variation of the soil respiration. The spatial variation of soil respiration could be explained by multiple parameters associated with soil temperature, vegetation cover, carbon sources and soil physico-chemical properties. The topography controlled the heterogeneity of soil respiration mainly through its effects on the carbon sources and soil physico-chemical properties, but not soil moisture. Overall, the ridge position was a hot spot of respiration because it had the optimal soil C/N for microbial decomposition and large pools of carbon sources, particularly root biomass and DOC stock. Moreover, compared to other positions, the soil at the ridge had higher sensitivity to the changes in temperature and moisture, indicating that the feedback of the soil carbon cycling to climate change would be different based on the landscape positions. These results suggested that soil respiration of the sloping landscape was affected by geomorphological, biogeochemical and hydrological processes, and future studies on the soil carbon efflux should take into account the topographic effects.

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Compliance with ethical standards

Conflict of interest The authors declare no potential conflicts of interest.

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