

The vegetation characteristics of *Pinus taiwanensis* drive the changes in different components of soil respiration in Wuyi Mountain, Southeast China

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Abstract

Background and Aims

Many driving variables have been used to model different soil respiration components. However, large uncertainty exists in the annual fluxes of soil respiration related to vegetation characteristics and soil properties.

Methods

Here, five *Pinus taiwanensis* forests along different elevations in the Wuyi Mountain were used to explore how the annual fluxes of total soil respiration (R_S), autotrophic respiration (R_A), and heterotrophic respiration (R_H) were regulated by vegetation characteristics, including vegetation carbon sequestration (V_{CO_2}), 0-20 cm root biomass (W_R), litter production (P_L), leaf area index (LAI), and also soil properties, including soil temperature (ST), soil moisture (SM), fungal PLFAs and bacterial PLFAs.

Results

The results indicate that (1) the R_H was positively correlated with ST, P_L , W_R , and LAI, and negatively correlated with SM; and the R_A was positively related to the V_{CO_2} and LAI, and inversely correlated with fungal and bacterial PLFAs. (2) R_H is mainly determined by W_R , while R_A can be comprehensively predicted through the V_{CO_2} and LAI; besides, the redundancy analysis indicated that W_R , V_{CO_2} , and LAI together explained 83.06% of R_S , R_H , and R_A changes in different elevations.

Conclusion

Overall, our results suggested that vegetation characteristics attributes such as W_R , V_{CO_2} , and LAI rather than soil properties and microbial community composition, were more important for explaining the annual fluxes of soil respiration components variance in five *P. taiwanensis* forests. Thus, soil respiration depends more on the plant capacity to fix organic carbon as an initial source of organic matter sustaining overall soil respiration.

1. Introduction

The mountain usually became a hotspot area to study soil carbon (C) cycling in long-term climate change due to the altitudinal gradients causing climatic variations in short geographic distances. Generally, the soil heterotrophic respiration and autotrophic respiration decline with elevation mainly caused by the temperature decrease (Zimmermann et al., 2015; Nottingham et al., 2015; 2019a; Tang et al., 2020; Zeeshan et al., 2021; Okello et al., 2023). However, not only soil temperature, but also vegetation type, structure (Dong et al., 2020), and soil microbial community (Whitaker et al., 2014) are important environmental factors influencing soil respiration along the elevation gradient, but deciphering their relative contribution mechanisms is challenging.

From the perspective of global data, the total below-ground C allocation (TBCA) plays an important role in controlling soil autotrophic respiration (R_A), accounting for 50% of the variation in R_A changes across the globe (Tang et al., 2020). Prior investigations also suggest that root biomass should be considered a major factor controlling soil respiration in different altitude alpine grasslands on the Tibetan Plateau (Zhao et al., 2017). Apart from root biomass, other studies indicated that soil respiration was strongly correlated with canopy photosynthesis and productivity (Högberg et al., 2001; Jia et al., 2018; Ma et al., 2020). Furthermore, the capacity to modify leaf, stem, and root allocation in the function of environmental changes is also an important vegetation characteristic directly linked with soil respiration process (Metcalf et al., 2011; Han et al., 2014a; 2014b; Aubrey et al., 2018; Zhao et al., 2021). However, given that determining root types and production of roots is difficult, can explain because of there have not constant results of contribution in R_A to R_S in prior studies. For instance, the contribution of R_A to R_S varied from 31.8% (Wang et al., 2008) to 46% (Comeau et al., 2018) in the subtropical forest. On the one hand, the discrepancy might be due to the root system belonging to the different species and their functions are complex or to different litter production, that can either enhance or diminish the contribution of roots to total soil respiration (Raich & Tufekciogul, 2000). Although some studies have observed that root biomass and tree height of dominant species could change the soil respiration along the different elevation gradients (Dong et al., 2020; Badraghi et al., 2021). However, it is largely unknown the dominant species community's characteristics, soil properties, and their interactive effects on soil autotrophic respiration. Dominant tree species identity has great impact on soil autotrophic respiration, due to the plant functional traits that drive C assimilation, transfer and emission collaborate with root activity, litter production and climate conditions (De Deyn et al. 2008; Cassart et al., 2021). Accurate knowledge of the predictions of soil autotrophic respiration changes require the monodominant species of characteristics to quantify these relationships.

In the last 30 years, the proportion of heterotrophic respiration in total soil respiration has increased rapidly with global warming (Bond-Lamberty et al., 2018; Ogle, 2018). The temperature, litter production, precipitation, leaf area index (LAI), nematode density, and soil F:B ratio are the most critical factors that predict the heterotrophic respiration variations in the world (He et al., 2022). Besides, previous studies suggest that vegetation attributes, such as root biomass and litter production, apart from determine autotrophic soil respiration, and more than soil microbial community composition, should be crucially considered to understand the variance of heterotrophic soil respiration among the different subtropical forests (Jenkins & Adams, 2010; Wei et al., 2015). However, with increasing elevation gradients, the vegetation characteristics and soil properties change faster, and some studies have found conflicting results in terms of the relationship between soil respiration and environmental factors (Zimmermann et al., 2010; Luan et al., 2014; Tian et al., 2016). Thus, how soil properties, vegetation characteristics and microbial community structure along the elevation gradients affect the annual flux of autotrophic respiration and heterotrophic respiration is still unclear (Yu et al., 2017). The main reason for this uncertainty may be the complex composition of plant communities in previous studies. Therefore, it is reasonable to assume that the monodominant species characteristics, including photosynthetic

capability, root biomass, and litter production and their associated soil properties may play an essential role in driving the mechanism of soil respiration components changes.

The *P. taiwanensis* is a native and predominant species in mountain regions, across eastern and southern China. In the National Park of Wuyi Mountain, the *P. taiwanensis* is widely distributed from 1200 to 2000 m (a.s.l, above sea level). The uniformity of the *P. taiwanensis* distribution provides an opportunity to explore how the annual flux of soil respiration components responds to elevation change through vegetation characteristics and soil properties. We developed step regression analysis and redundancy analysis to test how the vegetation characteristics, including annual vegetation C sequestration, leaf area index, root biomass, and litter production, and also soil properties that include soil temperature, soil moisture, fungal PLFAs, bacterial PLFAs, and their interactions influences on the different annual flux of soil respiration components. The data were used to determine (1) how the elevational gradient affects the vegetation characteristics and the annual flux of soil respiration components, and (2) the main factors that drive the annual flux of total soil respiration (R_S), autotrophic respiration (R_A) and heterotrophic respiration (R_H) changes in different elevation environment.

2. Materials and Methods

2.1. Study Site Description

The study site is located in the National Park of Wuyi Mountain (117°24'13"-117°59'19"E, 27°31'20"-27°55'49"N). It is located in the humid warm subtropics in the southeast of China and has a mean annual precipitation of 1684–1780 mm and a mean annual temperature of 17–19°C. The *P. taiwanensis* forests growing on Wuyi Mountain were selected for study because (1) this mountain is the highest peak in southeast mainland of China at 2160.8 m a.s.l and thus provided considerable climatic change along the elevational gradient, and (2) has the vertical zonation of *P. taiwanensis* forests along these elevational gradient ranges from 1200 m a.s.l to 2000 m a.s.l (Lyu et al., 2021). The major soil types of Wuyi Mountain are classified as Typic Haplohumults (300–500 m a.s.l), Typic Hapludults (500–900 m a.s.l), Typic Palehumults (900–1300 m a.s.l), Typic Dystrudepts (1300–1800 m a.s.l) and Histic Humuaquepts (1800–2100 m a.s.l.) (Chen, 2000).

2.2. Experiment design

Five *P. taiwanensis* forest sites were selected along an elevational gradient, located at intervals of 200 m from 1200 m a.s.l to 2000 m a.s.l, respectively. Three 20 m × 20 m plots were randomly established at each established level along the gradient. Forest canopy closure and stand density was calculated based on each forest plot. The stem diameter at breast height (DBH), and plant height (H) were measured from each trees (DBH ≥ 5 cm) in plot. Sample site information is shown in Table 1.

Table 1
The characteristics of *P. taiwanensis* sample sites along the Wuyi Mountain

Elevations	Soil type	Canopy closure (%)	Stand density (trees/ha)	Diameter of breast height (cm)	Height (m)	Mainly mixed species (<i>Pinus taiwanensis</i> : other)
1200 m	Typic Palehumults	86.67 ± 3.33a	575 ± 50b	28.02 ± 0.24a	19.42 ± 0.11a	<i>Schima superba</i> (1.62:1)
1400 m	Typic Dystrudepts	86.33 ± 3.18a	1525 ± 188a	17.57 ± 0.29b	18.10 ± 0.19b	<i>Cunninghamia lanceolata</i> (1.76:1)
1600 m	Typic Dystrudepts	90.33 ± 0.33a	1200 ± 288a	17.03 ± 0.33b	15.63 ± 0.17c	<i>Cunninghamia lanceolata</i> (5.07:1)
1800 m	Histic Humuaquepts	60.00 ± 5.77b	358 ± 102bc	17.20 ± 0.25b	7.07 ± 0.19d	<i>Rhododendron fortune</i> (2.23:1)
2000 m	Histic Humuaquepts	49.67 ± 0.33c	508 ± 154b	15.30 ± 0.35c	5.18 ± 0.20e	<i>Rhododendron fortune</i> (4.13:1)

2.3. Vegetation characteristic measurements

The total leaf biomass (W_L) of *P. taiwanensis* was calculated by using Eq. (1) (Hua et al., 2015), where the D and H are the diameters of tree breast height (DBH) and height per individual, respectively. Total leaf area per individual is calculated by the ratio of total leaf biomass per individual and leaf mass per area, i.e. $A_L = W_L / LMA$. The leaf area index (LAI) is the ratio between total leaf area of the sample plot and the sample plot area. Besides, three soil blocks (20cm depth and size 20cm×20cm) were randomly dug from each sample plot, and collected the fresh root. The *P. taiwanensis* root was identified, then put it into the ziplocked bag, and taken back to the laboratory, where it was washed and dried to obtain 0–20 cm root biomass (W_R).

$$W_L = \frac{0.04977D^{1.8394}H^{0.1207}}{1+1/(2.69418D^{-0.42942}H^{-0.22742})} \quad (1)$$

In July 2019 and December 2019, the Li-6800 (LICOR, Lincoln, Nebraska, USA) was used to measure the net photosynthetic rate (P_n , $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) of *P. taiwanensis* leaves at atmospheric temperature, and based 2 hours from 8:00 a.m. to 18:00. Three trees and total nine twigs have selected in each plot for the test. The light intensity was set to $2000 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, and the CO_2 concentration was set to 400

$\mu\text{mol}\cdot\text{mol}^{-1}$. Besides, the leaf dark respiration rates (R_d) were measured after half an hour of dark adaptation. Thus, the total assimilation amount per hour of a single leaf (A_i , $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was calculated based on photosynthesis rates through a simple integration method (Zhang et al., 2013) (2).

$$A_i = \sum_{i=1}^j (P_{i+1} + P_i) / 2 (T_{i+1} + T_i) \times 3600 / 1000 \quad (2)$$

Where 3600 and 1000 indicate that 1 hour contains 3600 seconds and conversion rates between μmol and mol , respectively. P_i was the initial photosynthetic rate ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and P_{i+1} was the next photosynthetic rate. T_i is the instantaneous time of the initial measurement point and T_{i+1} is the time of the next measurement point; j is the number of tests. To accurately study the annual vegetation carbon sequestration (V_{CO_2} , $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) of *P. taiwanensis*, we used the annual sunshine duration (A_{sh}) and instantaneous C utilization efficiency (ICUE) to estimate. The A_{sh} was 959 h in the local areas and $\text{ICUE} = P_n / (R_d + P_n) \times 100\%$ (Frantz & Bugbee et al., 2005). Finally, the annual vegetation carbon sequestration of *P. taiwanensis* was calculated by using Eq. (3).

$$V_{\text{CO}_2} = A_i \times 44 / 1000 \times A_L \times \text{SD} \times A_{\text{sh}} \times \text{ICUE} \quad (3)$$

Where A_L and SD indicate the total leaf area per individual and stand density in the sample site, respectively. The 44 is the molar mass of CO_2 .

Nine nylon net bags (80 cm×80 cm) were randomly set in each sample site to collect litter production (P_L) every month from March 2019 to January 2021. The litter of *P. taiwanensis* was taken back to the laboratory and weighting after air drying.

2.4. Soil respiration measurements

In August 2018, three subplots (size 80 cm×80 cm) of control treatment (CT) and three subplots of root removal (RR) treatments were randomly installed in each forest sample plot, respectively. Two layers of nylon mesh (size 0.01 mm) were used in the trench (size 80 cm×80 cm, depth 60 cm) to isolate fine roots as RR treatments. Then, a PVC collar with a diameter of 20 cm and height of 10 cm was installed in each treatment, embedded about 6 cm in the soil layer. The different components of soil respiration (i.e. R_S , R_A , and R_H) were monitored on clear days once every month between March 2019 and January 2021 using a LI-COR 8100 infrared gas analyzer (LICOR, Lincoln, Nebraska, USA), respectively. Annual respiration (R_s) was estimated by summing daily soil respiration calculated with the following Eq. (4) (Lavigne et al., 2003; Laganière et al., 2012).

$$R_s = \sum_{\text{daily}} e^{bt} 3600 \times (12 / 1000000) \quad (4)$$

Where α is the mean respiration rate, and t is the soil temperature at a depth of 5 cm. Where 3600 and (12/1000000) indicate that 1 hour contains 3600 seconds and convert C from micromoles to grams,

respectively.

2.5. Soil microbial community measurements

In December 2019 and August 2020, the soil was sampled by using a 2.5 cm diameter stainless steel soil cylinder from each subplot, and then mixed based on forest sample sites, respectively. Samples were collected from depths 0–10 cm, and distance 20 cm from the edge of the PVC collar. A total of 15 samples were collected and measured from five forest sample sites, and then used the mean values of PLFAs concentrations in two experiments for data analysis. We performed phospholipid fatty acid analysis (PLFA) and this method described by Bossio and Scow (1998) to estimate bacterial and fungal biomass in soil. We used standard nomenclature to express the abundance of individual fatty acids and calculated the concentration of each PLFA based on 19:0 internal standard concentrations (Zhang et al., 2016a). Total bacterial PLFAs was the summary of i14:0, i15:0, a15:0, i16:0, i17:0, a17:0, 16:1 ω 9c, 16:1 ω 7c, cy17:0 ω 7c, 18:1 ω 7c, 18:1 ω 5c, cy19:0 ω 7c (Frostegård & Bååth, 1996). The fungal PLFAs were identified by 18:1 ω 9c, 18:2 ω 6, 9c, and 16:1 ω 5 (Nie et al., 2013).

2.6. Data Analysis

We compared the difference in vegetation characteristics along the different elevations with one-way ANOVA ($\alpha = 0.05$) and performed in R software (R Core Team, 2018). We conducted a boxplot with "ggplot2" and "ggpubr" packages to test the variations of soil respiration components (R_S , R_A , and R_H) and vegetation traits (V_{CO_2} , W_R , P_L , LAI,) of *P. taiwanensis* at different elevations on the R software (R Core Team, 2018). The correlation matrix between the vegetation traits and soil respiration components analysis was performed on the R software (R Core Team, 2018) using the "Corrplot" package with a significance level of 0.05. Step regression analysis and redundancy analysis were implemented in IBM SPASS software and CANOCO for Windows version 5.0 (Ter Braak & Šmilauer 2012), respectively.

3. Results

3.1. The vegetation characteristics and soil properties along the altitudinal gradients

Statistical analyses showed significant differences in vegetation characteristics of *P. taiwanensis* along the elevational gradient (Table 1, Fig. 1). From 1200 m to 2000 m, the annual vegetation C sequestration (V_{CO_2}) of *P. taiwanensis* forest ranged from 2.82 to 20.67 t C·ha·yr⁻¹, the leaf area index (LAI) ranged from 0.46 to 3.69 m²·m⁻², the 0–20 cm root biomass (W_R) of the *P. taiwanensis* forest ranged from 1.19 t·ha⁻¹ to 2.03 t·ha⁻¹, and the litter production (P_L) ranged from 2.65 to 3.90 t·ha⁻¹·yr⁻¹ (Fig. 1). The V_{CO_2} , W_R , and LAI at 1200 m, 1400 m, and 1600 m were significantly higher than those at 1800 m and 2000 m. The P_L was significantly highest at 1200 m and 1400 m ($P < 0.05$). Overall, the LAI, V_{CO_2} , W_R , and P_L significantly decreased with increasing elevations. The most variables linked to plant production capacity tends to decrease with altitude.

The bacterial PLFAs of CT treatments varied from 19.23 to 32.04 nmol·g dry soil⁻¹, and fungal PLFAs varied from 3.38 to 5.89 nmol·g dry soil⁻¹ along the elevational gradient. The bacterial PLFAs and fungal PLFAs of RR treatments varied from 17.36 to 32.77 nmol·g dry soil⁻¹, respectively. The bacterial PLFAs and fungal PLFAs were significantly different among the five elevations and highest at 2000 m (Fig. 2). The fungal PLFAs of RR treatments varied from 2.84 to 4.56 nmol·g dry soil⁻¹, and there are no significant differences between five elevations ($P = 0.064$) (Fig. 2).

3.2. The annual flux of soil respiration components

R_S ranged from 0.635 to 1.141 kg C m⁻²yr⁻¹, the R_H ranged from 0.44 to 0.873 kg C m⁻²yr⁻¹, and the R_A ranged from 0.147 to 0.397 kg C m⁻²yr⁻¹ across five elevations (Fig. 3). R_S and R_H decreased with increasing elevations and showed significant differences. While the R_A has no significant statistical difference among the five elevations (Fig. 3). The R_S and R_H showed the highest values occur at 1200 m, while the lowest values are mainly at 1800 m (Fig. 3).

3.3. Relationships between soil respiration vs. vegetation characteristics and soil properties

The R_S and R_H were positively correlated with V_{CO_2} , P_L , W_R , LAI, and soil temperature (ST), but inversely correlated with the fungal PLFAs, bacterial PLFAs, and soil moisture (SM) in *P. taiwanensis* forests across five elevations, respectively (Fig. 4). The R_A positively correlated with V_{CO_2} and LAI, but inversely correlated with the fungal PLFAs, and bacterial PLFAs (Fig. 4). The step regression analysis suggests that W_R and P_L provided adequate fit R_S changes in our data ($R^2 = 0.80$), and the V_{CO_2} and LAI explained 62% R_A changes along the different elevations (Table 1). All eight environmental factors (i.e., V_{CO_2} , W_R , LAI, P_L , fungal PLFAs, bacterial PLFAs, ST, SM) explained 83.10% of the total variability in the soil respiration components (Fig. 5). The W_R ($F = 20.8$, $p = 0.002$), P_L ($F = 3.3$, $p = 0.038$), and V_{CO_2} ($F = 3.2$, $p = 0.046$) were strongly correlated with variability of the soil respiration components along the Wuyi Mountain (Fig. 5).

4. Discussions

Different from the soil temperature and soil moisture, the vegetation characteristics of monodominant communities promote forest succession and development, which have stronger effects on soil respiration prediction. We demonstrated that the synergistic mechanism between the *P. taiwanensis* vegetation C sequestration of dominant species, litter production, root biomass, and soil properties can be seen as an effective way to explain the annual flux of soil respiration components changes along the different elevations in Wuyi Mountain.

4.1. Vegetation characteristics and soil respiration components change along the elevational gradient

Previous studies suggested that leaf C capture capacity at high altitudes was mainly limited by low temperatures and UV damage to leaf cell metabolism and gas exchange (Zhou et al., 2023). Consistent with our previous results, we found the C use efficiency of *P. taiwanensis* decreased with increasing elevations in Mt. Wuyi (Lyu et al., 2021). The decrease in vegetation C capture capacity may have caused the C storage decrease in the soil-plant system. Indeed, the vegetation characteristics of *P. taiwanensis*, including V_{CO_2} , P_L , W_R and LAI decreased significantly with increasing elevations ($P < 0.05$) (Fig. 1), which indicates that the growth of *P. taiwanensis* in Mt. Wuyi mainly limited by low temperature (Lyu et al., 2021), thus probably increase in root/shoot ratio to increase nutrient uptake. Besides, we found the R_S and R_H decreased with elevations (Fig. 3). Soil respiration rates of the four types of forest exhibited a similar trend with our result along the elevation in Shennongjia, Hubei (Ma et al., 2019). These results indicated that soil respiration was highly sensitive to elevation changes in subtropical forests. One possible reason is the effect of soil temperature and moisture on soil respiration along the mountain forest due to these factors can account for most of the variation in soil CO_2 efflux (Zimmermann et al., 2015; Zhao et al., 2017; Ma et al., 2019; Tang et al., 2020; Zeeshan et al., 2021; Okello et al., 2023). Compared with the R_S and R_H , R_A showed an increase at first and then decreased from 1200 m to 2000 m but with no statistical difference between the five elevations (Fig. 3). We speculate that due to the canopy closure of *P. taiwanensis* was highest at 1600 m with a higher supply of carbohydrates (Table 1). Given the plant C supply provides the main substrates in driving root metabolism (Li et al., 2010), thus, we found that V_{CO_2} and LAI have positively correlated with R_A , respectively (Fig. 4). The altitude environments may influence *P. taiwanensis* growth characteristics through the soil temperature and moisture, thus further modifying R_S , R_H , and R_A changes in Wuyi Mountain.

4.2. Relationships between vegetation characteristics and total soil respiration

Differences among vegetation characteristics in physiology may play critical roles in determining soil C cycling. Consistent with our results, Högberg et al. (2001) and Bahn et al. (2009) both found that photosynthates significantly affected soil respiration variations. In this study, although we indicated that V_{CO_2} strongly correlated with R_S (Fig. 4), the W_R and P_L have been considered as key predicting factors for R_S dynamics in different elevational gradients (Table 1). A potential cause for such a result is the biome type. The *P. taiwanensis* forest community composition in the current study is relatively simple, and the variation of V_{CO_2} is close (Table 1, Fig. 1). These results might reduce the sensitivity of R_S response to changes in the photosynthesis capacity of *P. taiwanensis* forest along the different elevations.

Previous studies also suggest that root biomass and litter production can be related to total soil respiration changes (Wang et al., 2015; Zhao et al., 2021; He et al., 2022). In line with our results, we also identified the positive relationships of R_S vs. W_R and R_S vs. P_L (Fig. 4), and indeed W_R and P_L were chosen as the best predictors of modeling ($R^2 = 0.80$) the R_S changes (Table 2). Root traits, i.e., root biomass, may be temporally and spatially dynamic along the different elevations. We found the W_R highest at 1200 m, with no significant difference between other sample sites (Fig. 2). Previous studies also observed that the

diameter at breast height was positively correlated with fine root production (Cai et al., 2019). Therefore, we suggest that the W_R changes along Mt. Wuyi may be ascribed to the DBH of *P. taiwanensis* forest. Because, we found the DBH showed the highest at 1200 m and parallel the trend of W_R changes (Table 1, Fig. 1). In addition, similar to W_R , litter-derived respiration is part of the total soil respiration, and R_S generally be reported as linearly increased with litter production (Zhang et al., 2016b). This may be due, at least in part, to the litter production strongly influences soil C sources and regulates microbial activities in the forest ecosystem (Zhang et al., 2016b; Zhu et al., 2023).

Table 2
Stepwise regression analysis between soil respiration components and *P. taiwanensis* vegetation characteristics

Project	Formula	Standardized coefficients		R^2	F	p
R_S	$y = 1.25 + 2.72 W_R + 1.20 P_L$	W_R	0.54	0.80	28.74	0.006
		P_L	0.46			0.017
R_H	$y = 1.47 W_R + 3.15$	W_R	0.81	0.62	24.17	0.001
R_A	$y = 1.71 + 0.19 V_{CO_2} - 0.97 LAI$	V_{CO_2}	2.23	0.62	12.35	0.001
		LAI	-1.72			0.006

Besides, LAI is usually regarded as one of the key indicators that affect soil CO_2 efflux (Reichstein et al., 2003; Bond-Lamberty & Thomson, 2010; Li et al., 2010; Bolat & Öztürk, 2017; Yao et al., 2021). Consistent with prior studies, we observed that R_S linearly increased with increasing LAI. Theoretically, the LAI can be viewed as an indicator through the C assimilation and vegetation productivity capacity, directly or indirectly affecting the soil CO_2 efflux. On the other hand, it should be noted that LAI has a closely associated with soil temperature and soil moisture, and thus indirectly influences the R_S changes (Bolat & Öztürk, 2017). However, the relationships between soil respiration and LAI are not as stable. For instance, Reichstein et al. (2003) found that LAI strongly linear correlated with the standardized soil respiration rates, while other studies showed the LAI has a peaked relationship with total belowground C flux (TBCF) (Berryman et al., 2016). In any case, our results strongly suggested the importance of LAI for predicting R_S changes among the five *P. taiwanensis* forests along the different elevational gradients.

4.3. Relationships between soil properties and total soil respiration

It is not only our goal to review the biomass allocation (i.e., root biomass and litter production) by which vegetation characteristics can modify soil respiration, but also other soil properties (i.e., soil temperature, soil moisture, soil microbial community structure) are important. In the present work, we found positive correlations between R_S and soil temperature and negative correlations between R_S and soil moisture (Fig. 4). That is to say, soil temperature and moisture conditions significantly influence R_S in different

elevations. Generally, soil temperature has a considerable effect on soil respiration and is the dominant driver of R_S in mountain forests (Zimmermann et al., 2015; Tang et al., 2020; Zeeshan et al., 2021; Okello et al., 2023). In this study, soil temperature showed a higher degree of correlation with R_S ($R^2 = 0.84$) (Fig. 4). Several potential mechanisms may be suggested to account for this. Firstly, although soil temperature decreases with increasing elevation, it is still controlled by other environmental factors. For instance, previous studies suggest that LAI can influence soil temperature by reducing solar radiation (Yan et al. 2013; Bolat & Öztürk, 2017). Secondly, some prior studies indicated that soil respiration includes a temperature-dependent model and a temperature-independent model (Vargas & Allen 2008; Geng et al., 2012). Moreover, the amount of C source input potentially varies with plant productivity rather than being limited by soil temperature, thus strongly affecting the soil CO_2 emitted to the atmosphere. Hence, our results suggest that to incorporate vegetation characteristics should be a vital dimension driver of R_S modeling efforts in the forest ecosystem.

The bacterial PLFAs and fungal PLFAs were inversely correlated with R_S along the different elevations (Fig. 4). It is likely due to the drop of microbial activity with altitude probably been mainly due to an increase of temperature limitation of biological activity, as observed in previous studies (Nottingham et al., 2019b). Consistent with our results, the fungal biomass of *Cunninghamia lanceolata* forests increased with increasing elevations at different altitudes in Wuyishan National Park (Xiong et al., 2022). But interestingly, our results indicated that R_S decreased with an increase in fungal PLFAs and bacterial PLFAs along the elevational gradient. We postulate that this pattern may be mainly offset by plant growth and soil organic matter input decreased along the elevational gradients. Thus, the microbial biomass-independent of the soil respiration was principally determined by substrate supply and very probably by the decrease of microbial community activity capacity under low temperature rather than by the pool size of microbial biomass content, as shown in previous cases (Wang et al., 2003; Birgé et al., 2015).

4.4 Difference regulation mechanism of R_H and R_A by vegetation characteristics

Our result demonstrates that vegetation characteristics and soil properties both account for 83.10% of R_S , R_H , and R_A variations along the different elevational *P. taiwanensis* forests (Fig. 5). However, R_H and R_A have different responses to the vegetation characteristics of *P. taiwanensis*. For instance, R_H is mainly determined by W_R , while R_A can be comprehensively predicted through the V_{CO_2} and LAI (Table 2). The results of our dataset indicate that the W_R has a greater contribution to R_H may be due to the large number of dead roots generated after root isolation, and the decomposition of these dead roots or root exudates potentially provides an available and sustainable substrate for microbial activities (Kuzyakov & Bol, 2006; Savage et al., 2018). From LAI and P_L related to higher R_S and R_H , the increase of LAI means the increase of canopy closure and litter production, which might prompt the ectotrophic mycorrhiza hyphae of existence to improve the heterotrophic respiration rate. Thus, the findings suggested that the fungal biomass can predict R_H under different elevational gradients (Fig. 4). Nevertheless, future studies

should also consider the mycorrhizal types associated with species and the role of mycorrhizal biomass in soil respiration.

In the present work, the value of R_A changed by approximately 17.6%-41.6%, and there is no significant statistical difference among the five elevations. However, with the increase in elevations, plant root turnover and regeneration in soil are slower, which may increase the accumulation of soil C, and reduce the autotrophic respiration rate (McGroddy & Silver, 2000). Therefore, it is reasonable to believe that lower temperatures limited the root production and activity in *P. taiwanensis* forest, and finally caused an insignificant correlation between R_A and W_R . These results indicate that the vegetation characteristics controlled the R_A by significantly regulating the V_{CO_2} and LAI in the function of temperature in the *P. taiwanensis* forest across the altitudinal gradient. It was consistent with previous studies that seasonal changes in vegetation activity play a dominant role in the sensitivity of soil respiration component and highlights the critical ecological linkages between plant physiological processes and soil C cycling processes (Wang et al., 2010; Cassart et al., 2021).

The results of this study clearly showed that above-ground C sequestration, soil C source, and below-ground biomass allocation of *P. taiwanensis* forest were strongly related to annual soil respiration. However, the different components of soil respiration are difficult to quantify through the vegetation characteristics with the present facilities. To gain a precise understanding of the underlying mechanisms and the extent of soil respiration changes in this region, it is essential to conduct further research that focuses on analyzing shifts in microbial community species composition and explores the interactions with plant production and temperature variations.

5. Conclusions

We found that the altitude environment strongly affects the regulations of vegetation characteristics and soil respiration components in the *P. taiwanensis* forest. More than soil traits, plant related traits such as V_{CO_2} , P_L , and W_R were be-well to predict the soil respiration component variations in different elevational gradients. This implies a general rule of the plant C fixation and allocation's role in soil respiration prediction processes.

Besides, the most critical driving factor that predicts the R_H is W_R , but V_{CO_2} and LAI directly control the R_A , respectively. Given the different mechanisms of R_H and R_A driven by vegetation characteristics, our findings highlighted that the soil respiration types (R_H and R_A) both depend on the system's capacity to produce more, with the logical and simple difference that the most direct variables are below-ground biomass and above-ground carbon capture capacity, respectively.

The results of this work offer a useful simplified model based on vegetation characteristics for predicting the complicated forest ecosystem C cycle models for different soil respiration components. We simply expect that under global change in this region, the shift of soil respiration would depend primarily on the effects on plant C fixation and allocation, and the feedback effect can be more or less neutral.

Nevertheless, it is crucial for future research to clarify the impact of the overall microbial community on annual soil respiration fluxes, especially in light of the possibility that an increase in microbial biomass could potentially diminish its overall activity.

Declarations

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Figures

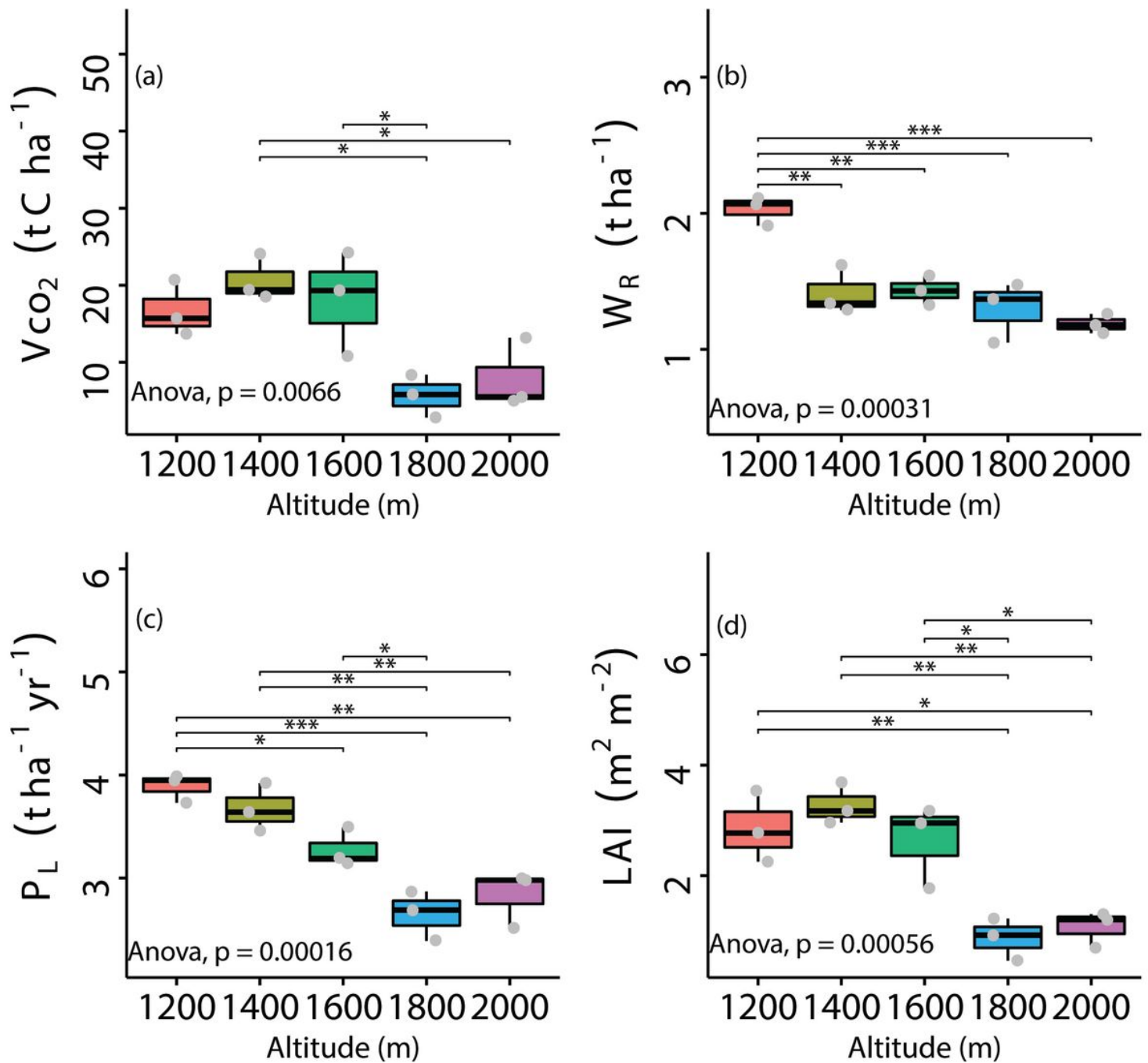


Figure 1

The vegetation characteristics of annual vegetation carbon sequestration (V_{CO_2}), 0-20 cm root biomass (W_R), litter production (P_L), and leaf area index (LAI) for *P. taiwanensis* forest along the different elevation gradients in Wuyi Mountain.

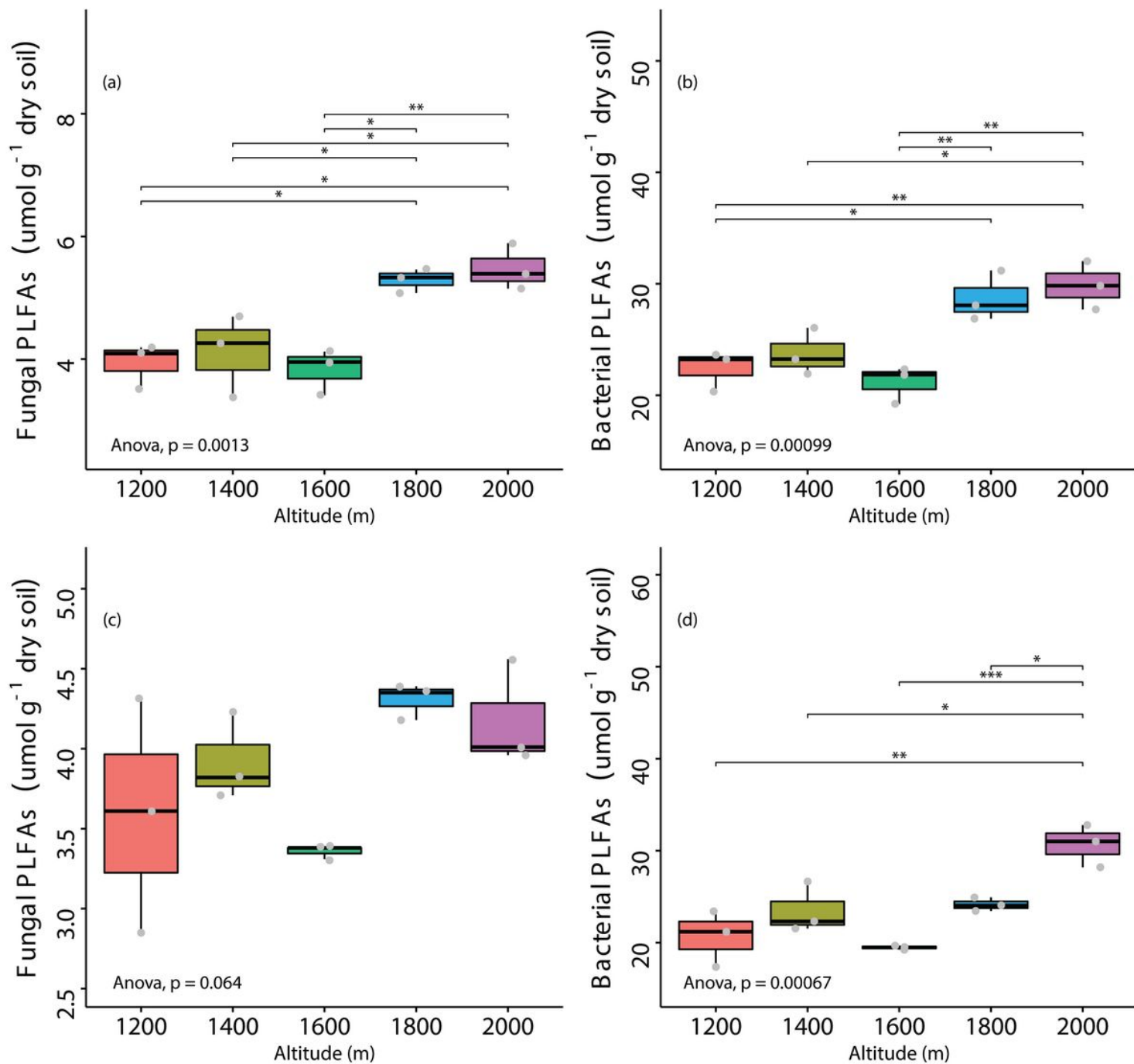


Figure 2

The characteristics of **a** Fungal PLFAs for Control Treatments, **b** Bacterial PLFAs for Control Treatments, **c** Fungal PLFAs for Root Removal Treatments and **d** Bacterial PLFAs for Root Removal Treatments for *P. taiwanensis* forest along the different elevation gradients in Wuyi Mountain..

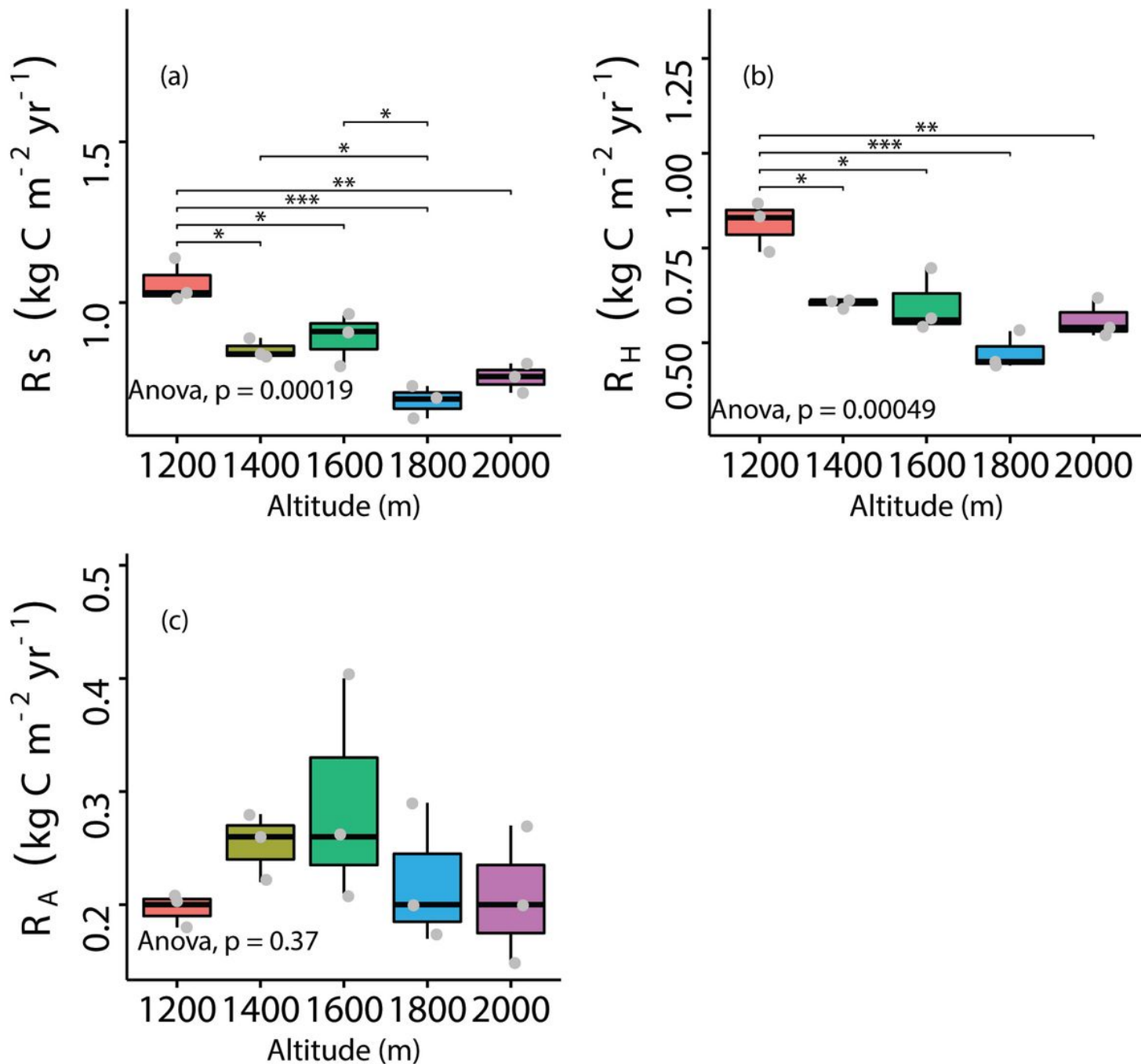


Figure 3

Characteristics of annual fluxes of **a** total soil respiration (R_S), **b** heterotrophic respiration (R_H), **c** autotrophic respiration (R_A) a changes in *P. taiwanensis* forest along the different elevations in Wuyi Mountain.

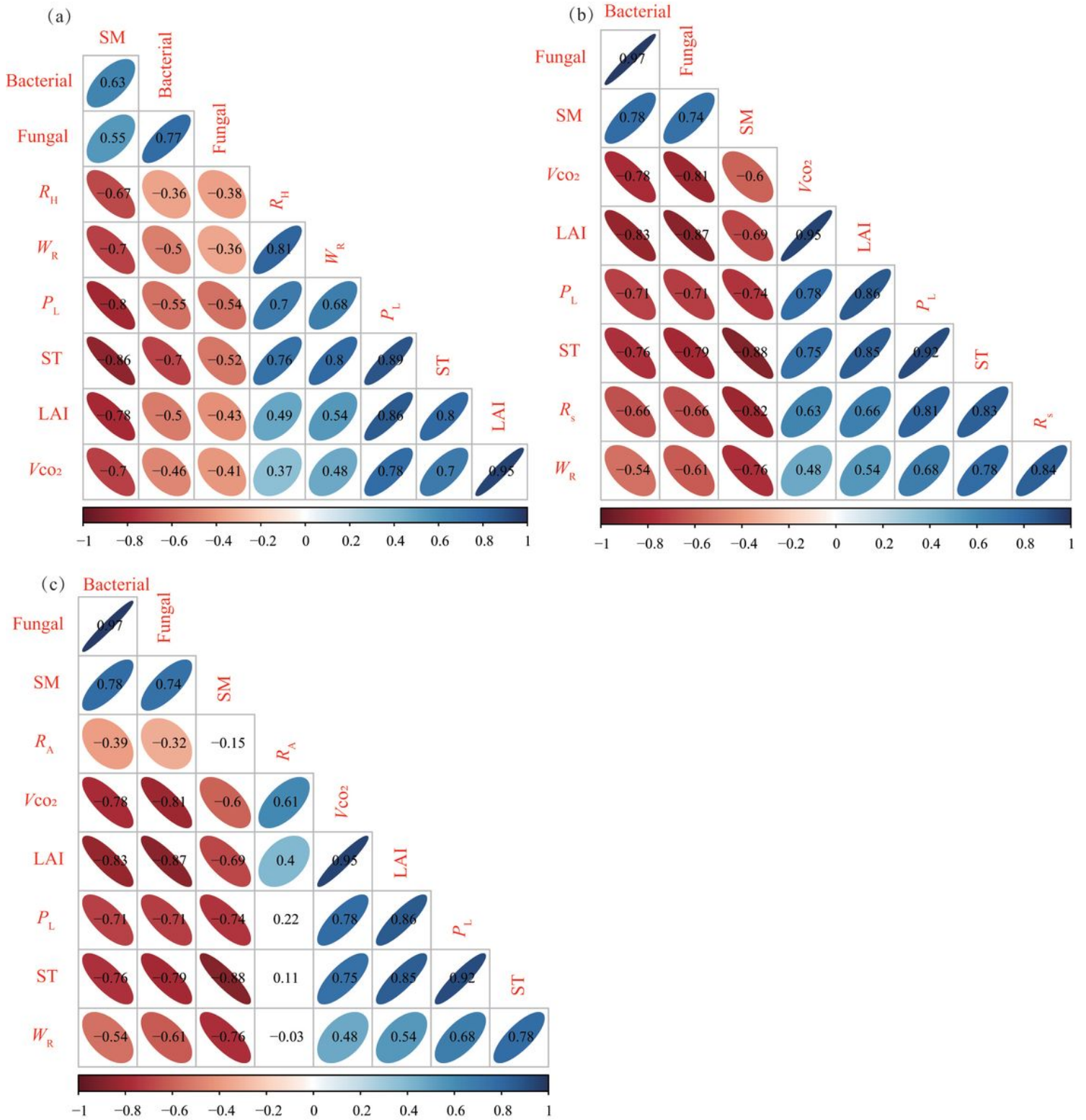


Figure 4

Correlation plots between the annual flux of **a** total soil respiration (R_S), **b** heterotrophic respiration (R_H), **c** autotrophic respiration (R_A) versus vegetation characteristics, soil properties and soil microbial characteristics of *P. taiwanensis* forest along the Wuyi Mountain ($n=15$). Note: Spearman's correlation coefficient is printed in each circle, and darker blue circles are traits that are more positively correlated with one another while darker red circles represent traits that are more negatively correlated with one

another. Boxes with no circle were indicated that not significantly correlated ($P > 0.05$). The vegetation carbon sequestration (V_{CO_2}), leaf area index (LAI), 0-20 cm root biomass (W_R), litter production (P_L), soil temperature (ST), soil moisture (SM).

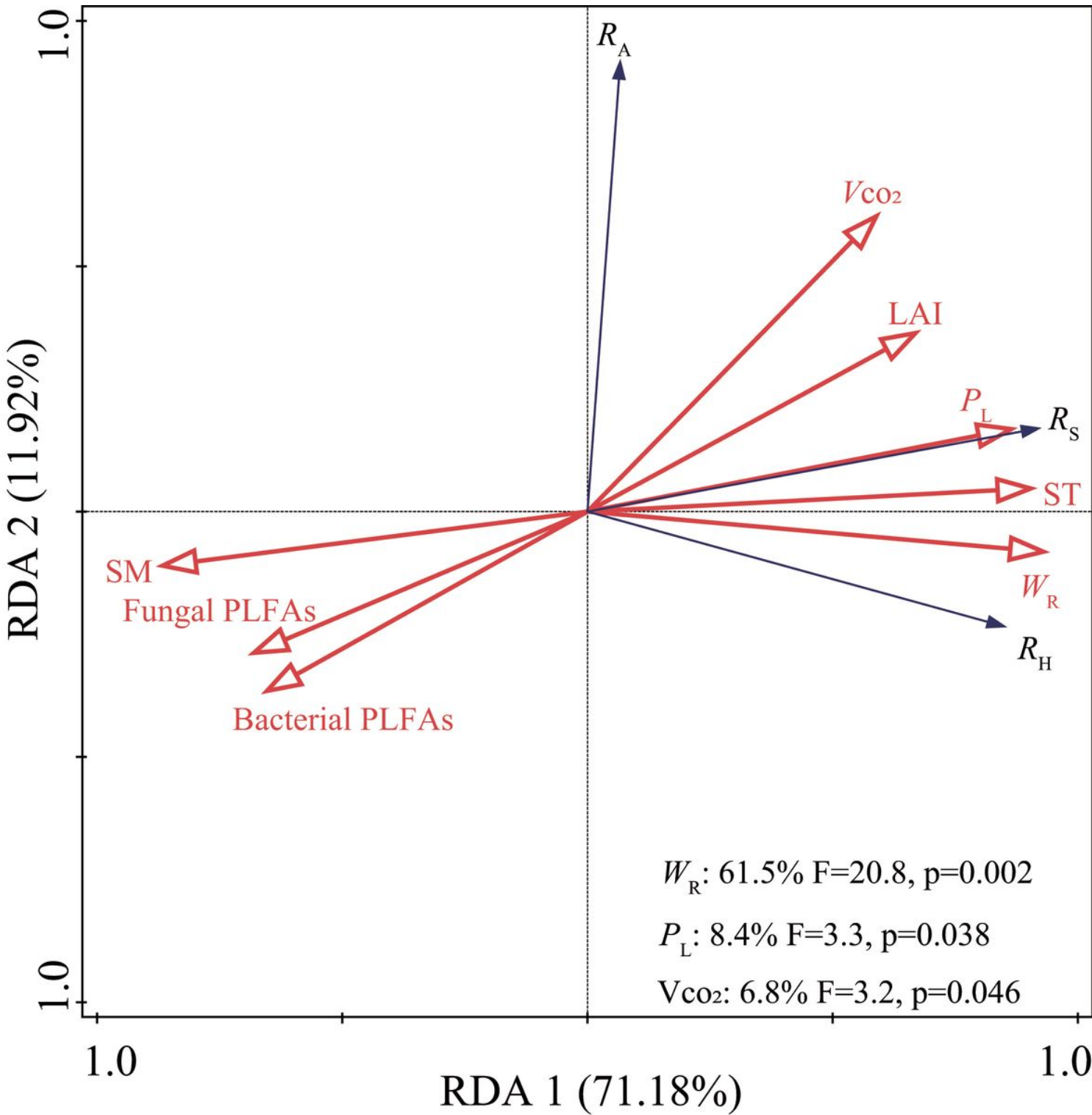


Figure 5

Redundancy analysis between annual fluxes of soil respiration components and vegetation characteristics, soil properties and soil microbial characteristics of *P. taiwanensis* forest along the Wuyi

Mountain ($n=15$). Note: The vegetation carbon sequestration (V_{CO_2}), leaf area index (LAI), 0-20 cm root biomass (W_R), litter production (P_L), soil temperature (ST), soil moisture (SM), the annual flux of a heterotrophic respiration (R_H), autotrophic respiration (R_A) and total soil respiration (R_S).