

1 **The vegetation traits of *Pinus taiwanensis* drive the changes in**  
2 **different components of soil respiration in Wuyi Mountain, Southeast**  
3 **China**

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23 **ABSTRACT**

24 Many driving variables used to model different soil respiration components include  
25 biotic and abiotic factors. However, large uncertainty exists in the soil respiration  
26 estimation by vegetation traits changes in different environments. Here, we investigated  
27 how the annual fluxes of soil respiration components and its proportion are regulated  
28 by vegetation trait along the elevation gradients. More than 20 months of soil respiration  
29 measurements from five *Pinus taiwanensis* forest along the different elevations in Wuyi  
30 Mountains were used to explore how the annual fluxes of total soil respiration ( $R_S$ ),  
31 autotrophic respiration ( $R_A$ ) and heterotrophic respiration ( $R_H$ ) are affected by  
32 vegetation traits, including the photosynthetic carbon sequestration, above- and  
33 belowground biomass and litter production. The data indicate that (1) the annual flux  
34 of total soil respiration ( $R_S$ ) and heterotrophic respiration ( $R_H$ ) both were positively  
35 correlated with litter production, total root biomass and 0-20 cm root biomass; the  $R_H$ :  
36  $R_S$  significantly increased with the increase of litter production ( $P_L$ ), and  $R_A$ :  $R_S$  was  
37 positively correlated with 0-20 cm root biomass, and (2) the annual photosynthetic  
38 carbon sequestration ( $W_{CO_2}$ ) was directly positively controlled by the annual flux of  
39 autotrophic respiration ( $R_A$ ) in different elevations with a standard total effect value of  
40 0.52, while  $R_H$  was directly influenced by litter production ( $P_L$ ) with a standard total  
41 effect value of 0.68. Our analyses highlight that the dominant vegetation trait regulating  
42 the annual flux of autotrophic respiration is the annual photosynthetic carbon  
43 sequestration from trees, but the annual flux of heterotrophic respiration is controlled  
44 by litter production. Thus, on a vegetation properties predict scale, these results indicate

45 different regulation mechanism of autotrophic respiration and heterotrophic respiration  
46 in *P. taiwanensis* forests along the different elevational gradients.

47 *Keywords:* annual flux; carbon sequestration; conifer forest; elevation gradient; root  
48 biomass

## 49 **1. Introduction**

50 The mountain usually became a hotspots area to study soil carbon cycling in long-term  
51 climate change due to the altitudinal gradients stretch across climatic variations in short  
52 geographic distances. Previous works along the altitude gradient led to many insights  
53 into how patterns of soil respiration ( $R_s$ ) components respond to nature climate gradient  
54 change (Rodeghiero & Cescatti, 2005; Zimmermann et al., 2010; Nottingham et al.,  
55 2015; 2019; Badraghi et al., 2021). Compared to the low-altitude area, the high-altitude  
56 area usually has lower rates of soil heterotrophic respiration but with a higher  
57 temperature sensitivity ( $Q_{10}$ ) (Zimmermann et al., 2015; Nottingham et al., 2019;  
58 Okello et al., 2023). The higher  $Q_{10}$  at the high-altitude area indicates carbon loose  
59 faster under warming climate conditions, which is caused by the higher content and  
60 activity of microbial biomass and soil organic carbon content. Similarly, global data  
61 analysis also shows that the annual flux of autotrophic respiration ( $R_A$ ) decreased  
62 significantly with the increase in altitudes (Tang et al., 2019; 2020), but the precipitation  
63 was the mainly climatic driver factors. Thus, the predicted rising of temperature  
64 globally during the 21st century would enhance the  $Q_{10}$ , and thus  $R_s$  will lead to positive  
65 feedback to the climate system at the highest elevations (Zeeshan et al., 2021). Besides,  
66 variations in soil temperature, plant composition, and soil microbial community both

67 are important components of environmental factors on soil respiration components  
68 along the elevation gradient, but deciphering their relative contribution mechanisms is  
69 challenging.

70 Prior investigations into below-ground biomass, such as root biomass considered  
71 a major factor controlling  $R_S$  in different altitude alpine grasslands on the Tibetan  
72 Plateau (Zhao et al., 2017). Indeed, the recent photosynthates and stored carbohydrates  
73 may play an important role in substrate supply to autotrophic respiration, thus affecting  
74 the total soil respiration on diel time scales (Carbone & Trumbore, 2007). Other studies  
75 also indicated that soil respiration was correlated with canopy photosynthesis and  
76 productivity (Högberg et al., 2001; Jia et al., 2018). However, given that determining  
77 root depth distribution and production of coarse and fine roots is difficult, there have  
78 not constant results of contribution in  $R_A$  to  $R_S$  in prior studies. For instance, the value  
79 of  $R_A: R_S$  in the subtropical forest changes from 31.8% (Wang et al., 2008) to 46%  
80 (Comeau et al., 2018). The discrepancy might be due to the different biomass allocation  
81 between fine root and coarse root under the ground. Besides, the photosynthate  
82 allocation ratio stem/root, the capacity of plants to genetical (homeostatic) and  
83 phenotypical flexibility/plasticity capacity to modify leaf, stem and root allocation in  
84 function of environmental changes is an important plant functional trait directly linked  
85 with soil respiration process (Metcalf et al., 2011; Han et al., 2014a; 2014b) . These  
86 results were also demonstrated by using allometric equation models of root biomass to  
87 distinguish the components of soil respiration in recent works (Zhao et al., 2021).  
88 However, with increasing the elevation gradients, the effect of vegetation traits on soil

89 autotrophic respiration is still not clear.

90 Besides, according to the global data in the last 30 years, the proportion of  
91 heterotrophic respiration in total soil respiration is increasing rapidly with global  
92 warming, even causing total respiration to exceed the rate of carbon dioxide uptake by  
93 vegetation (Bond-Lamberty et al., 2018; Ogle, 2018). The temperature, litter production,  
94 precipitation, leaf area index (LAI), nematode density, and soil F:B ratio is the most  
95 crucial factors that predict the  $R_H$  variations in the world (He et al., 2022). The  
96 vegetation-related predictors (litter production and LAI) are the second-most influential  
97 factors (He et al., 2022) from the perspective of the overall effect. Likewise, previous  
98 studies indicate that the vegetation type influence  $R_H$  by producing different quality (C:  
99 N) of litter (Jenkins & Adams, 2010). So, the plant's physiological and ecological  
100 factors such as photosynthesis, fine root biomass, and litter production increasingly  
101 become important for predicting the process of different components of  $R_S$  (Han et al.,  
102 2014a). Thus, it is reasonable to assume that vegetation properties and their associated  
103 photosynthetic capability, above- and below-ground biomass allocation, and litter  
104 production may play an essential role in driving the mechanism of soil respiration  
105 changes. Although a large number of works have been carried out on the plant traits  
106 influencing soil respiration, the  $R_A$  and  $R_H$  effects by vegetations traits along the  
107 elevation gradients are still unclear (Zimmermann et al., 2010; Yu et al., 2017; Xu et  
108 al., 2019). The main reason for this uncertainty may be the complex composition of  
109 plant communities. In a species-rich subtropical forest, the community composition  
110 groups will affect the change of vegetation properties, thus increasing the uncertainty

111 of the soil respiration prediction process.

112 The *P. taiwanensis* is a native and predominant species in mountain regions, across  
113 eastern and southern China. In the National Park of Wuyi Mountains, the *P.*  
114 *taiwanensis* is widely distributed from 1200 to 2000 m (a.s.l, above sea level). The  
115 uniformity of the *P. taiwanensis* distribution provides an opportunity to explore how  
116 the annual fluxes of soil respiration components respond to elevation change through  
117 vegetation traits. To clarify the relationships between vegetation traits and components  
118 of soil respiration along the elevational gradient, we developed a structural equation  
119 modeling (SEM) to test how the vegetation traits that include the photosynthetic carbon  
120 sequestration, leaf area index, above- and belowground biomass affect the different  
121 annual fluxes of soil respiration components. The model and the data were used to  
122 determine (1) the relationships between vegetation traits and the annual flux of soil  
123 respiration components, and (2) how these traits drive the annual flux of total soil  
124 respiration ( $R_S$ ), autotrophic respiration ( $R_A$ ) and heterotrophic respiration ( $R_H$ ) in  
125 different elevation environment.

## 126 **2. Materials and Methods**

### 127 *2.1. Study Site Description*

128 The study site is located in the National Park of Wuyi Mountains (117°24'13"-  
129 117°59'19"E, 27°31'20"-27°55'49"N). It is located in the humid warm subtropics in the  
130 southeast of China and has a mean annual precipitation of 1684-1780 mm and a mean  
131 annual temperature of 17-19°C. The *P. taiwanensis* forests growing on Huanggang were  
132 selected for study because (1) this mountain is the highest peak in the National Park of

133 M.T. Wuyi at 2160.8 m a.s.l and thus provided considerable climatic change along the  
134 elevational gradients, and (2) has the vertical zonation of *P. taiwanensis* forests along  
135 these elevational gradients ranges from 1200 m a.s.l to 2000 m a.s.l (Lyu et al., 2021).  
136 The major soil types of Huanggang mountains are classified as mountain yellow-red  
137 soil (400-600 m a.s.l), mountain yellow soil (600-1300 m a.s.l.), mountain dark yellow-  
138 brown soil (1300-1900 m a.s.l.) and mountain meadow soil (above 1900 m a.s.l.) (Li et  
139 al., 2017).

## 140 2.2. Experiment design

141 Five *P. taiwanensis* forest sites were selected along an elevational gradient, located at  
142 intervals of 200 m from 1200 m a.s.l to 2000 m a.s.l, respectively. Three 20 m × 20 m  
143 plots were randomly established in each forest. Forest canopy closure, stand density,  
144 stem diameter at breast height (D), and plant height (H) were measured for woody  
145 species within each plot. Sample site information is showed in Table 1.

## 146 2.3. Vegetation trait measurements

147 The DBH and tree height of *P. taiwanensis* were investigated once every three years  
148 from 2014 to 2020. The annual increase rates of stem cross-sectional area (BAI) were  
149 calculated based on stem diameter at breast height. The relative growth rate (RGR) of  
150 *P. taiwanensis* was calculated as  $RGR = (W_j - W_i) / T_{j-i} \times 100\%$ , where  $W$  and  $T$  indicate  
151 the individual biomass and the duration time,  $j$  and  $i$  mean the initial and last  
152 investigation time, respectively. The total leaf biomass ( $W_L$ ), total root biomass ( $W_R$ ),  
153 and per individual biomass ( $W_I$ ) of *P. taiwanensis* were calculated by using equation  
154 (1), equation (2), and equation (3), respectively (Hua et al., 2015). The D and H are the

155 diameters of tree breast height and height per individual, respectively. Total leaf area  
 156 per individual is calculated by the ratio of total leaf biomass per individual and leaf  
 157 mass per area, i.e.  $A_L = W_L / LMA$ . Leaf area index (LAI) = total leaf area of the sample  
 158 plot/plot area. Besides, three soil blocks (20cm depth and 20cm×20cm) were randomly  
 159 dug from each sample plot, and then collect the fresh root from the soil block. The root  
 160 was identified, then put into the ziplocked bag, and taken back to the laboratory, where  
 161 it was washed and dried to obtain 0-20 cm root biomass.

$$162 \quad W_L = \frac{0.04977D^{1.8394}H^{0.1207}}{1 + 1/(2.69418D^{-0.42942}H^{0.22742})} \quad (1)$$

$$163 \quad W_R = 0.03548D^{1.3587}H^{0.93684} \quad (2)$$

$$164 \quad W_I = 0.01978D^{1.2263}H^{1.4758} + 0.04977D^{1.8394}H^{0.1207} + 0.03548D^{1.3587}H^{0.93684} \quad (3)$$

165 In July 2019 and December 2019, the Li-6800 (LICOR, Lincoln, Nebraska, USA)  
 166 was used to measure the photosynthetic rate of *P. taiwanensis* leaves at atmospheric  
 167 temperature, and based 2 hours from 8:00 a.m. to 18:00. Three trees and total nine twigs  
 168 have selected in each plot for instantaneous photosynthetic rate and specific leaf mass  
 169 (LMA) (dry weight per unit leaf area) test. The light intensity was set to 2000  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ,  
 170 and the  $\text{CO}_2$  concentration was set to 400  $\mu\text{mol}\cdot\text{mol}^{-1}$ .  $P_i$  was measured as the initial  
 171 photosynthetic rate, and  $P_j$  was measured as the next photosynthetic rate.  $(P_i+P_j)/2$  was  
 172 taken as the annual photosynthetic rate ( $P_n$ ) of *P. taiwanensis*. Besides, the leaf dark  
 173 respiration rate ( $R_d$ ) was measured after half an hour of dark adaptation.

174 To accurately study the annual average carbon sequestration of *P. taiwanensis*, we  
 175 used the annual sunshine duration ( $A_{sh}$ ) and instantaneous carbon utilization efficiency



176 (ICUE) to estimate. The  $A_{sh}$  was 959 h in the local areas, and  $ICUE = P_n / (R_d + P_n) \times 100\%$   
177 (Frantz & Bugbee et al., 2005). Thus, the annual photosynthetic carbon sequestration  
178 amount of a single leaf ( $W_i$ ) was calculated based on  $P_n$  through a simple integration  
179 method (4).

$$180 \quad W_i = (P_n \times 3600 / 1000) \times A_{sh} \times ICUE \times 44 / 1000 \quad (4)$$

181 Where 3600 and 1000 indicate that 1 hour contains 3600 seconds and conversion  
182 rates between  $\mu\text{mol}$  and  $\text{mol}$ , respectively. The annual carbon sequestration ( $W_{CO_2}$ ) of  
183 *P. taiwanensis* forest was calculated by using equation (5). Where  $A_L$  and SD indicate  
184 that the total leaf area per individual and stand density in sample site, respectively.

$$185 \quad W_{CO_2} = W_i \times A_L \times SD \quad (5)$$

186 Nine nylon net bags (0.8 m×0.8 m) were randomly set in each sample site to collect  
187 litter production ( $P_L$ ) every month from March 2019 to January 2021. The litter of *P.*  
188 *taiwanensis* was taken back to the laboratory and weighting after air drying.

#### 189 2.4. Soil respiration measurements

190 The different components of soil respiration (i.e.  $R_S$ ,  $R_A$  and  $R_H$ ) were tested by  
191 manipulated plots in five *P. taiwanensis* forests from March 2019 to January 2021,  
192 respectively. In each 20 m × 20 m forest sample site, three 5 m × 5 m soil respiration  
193 plots were randomly installed in August 2018. A group of control treatment (CT) and  
194 root removal (RR) treatments were installed in each plot, with a total of nine replicates  
195 per treatment in each forest sample site. Two layers of nylon mesh (size 0.01 mm) were  
196 used in the trench to isolate fine roots. Then, a PVC pipe with a diameter of 20 cm and  
197 height of 10 cm was installed in each treatment, embedded about 6 cm in the soil layer.

198 2.5. Data Analysis

199 We compared the difference of *P. taiwanensis* sample site characteristics along the  
200 different elevations with one-way ANOVA ( $\alpha = 0.05$ ) and performed in SPSS19.0  
201 (SPASS Inc., Chicago, USA) software. We conducted a boxplot with "ggplot2" and  
202 "ggpubr" packages to test the variations of soil respiration components and vegetation  
203 traits of *P. taiwanensis* at different elevations on the R-4.0.0 software. The correlation  
204 matrix between the vegetation traits and soil respiration components analysis was  
205 performed on the R-4.0.0 software by using the "Corrplot" package with a significance  
206 level of 0.05.

207 Structural equation modeling (SEM) was used to analyze the process of soil  
208 respiration driven by vegetation traits and the standard total effect size of each trait on  
209 soil respiration. From the perspective of prior studies, the flux of carbon assimilations  
210 to roots is a critical driver of soil respiration (Högberg et al., 2001; Han et al., 2014a;  
211 Jia et al., 2018; Ma et al., 2020). Thus, we constructed an initial model for the expected  
212 that plants may drive the annual flux of soil respiration changes through annual  
213 photosynthetic carbon sequestration, leaf area index, leaf biomass, and root biomass.  
214 Then, the maximum likelihood method was used to fit the model. The chi-square test is  
215 used to determine the feasibility of the whole model. When the model's CMIN/DF (the  
216 Ratio of Chi-Square Test Value and Degrees of Freedom) changes from 0.0 to 2.0, GFI  
217 (Goodness of Fit Index) is  $\geq 0.90$ , RMSEA (Root Mean Square Error of Approximation)  
218  $< 0.08$ , the model is considered suitable in this study. SEM analysis was implemented  
219 in IBM SPASS Amos 20.0 software (Amos Development Company, Crawfordville,

220 Florida, USA).

### 221 3. Results

#### 222 3.1. The vegetation traits of *Pinus taiwanensis* in Wuyi Mountain

223 Statistical analyses show that there are significant differences in vegetation traits of *P.*  
224 *taiwanensis* along the elevational gradients. From 1200 m to 2000 m, the annual  
225 average carbon sequestration ( $W_{CO_2}$ ) of *P. taiwanensis* forest varied from 5.66 to 20.67  
226  $t \cdot hm^{-2} \cdot yr^{-1}$ , and the relative growth rate (RGR) ranged from 35.20 to 80.20  $g \cdot kg^{-1} \cdot yr^{-1}$ .  
227 The BAI varied from 7.10 to 14.91  $cm^2 \cdot yr^{-1}$ , and the leaf area index (LAI) varied from  
228 0.46 to 3.69  $m^2 \cdot m^{-2}$  (Figure 1). The annual carbon sequestration of *P. taiwanensis* ( $W_{CO_2}$ )  
229 and LAI of 1200 m, 1400 m, and 1600 m were significantly higher than those at 1800  
230 m and 2000 m, while the highest values of BAI and RGR occur at 1200 m and 1600 m  
231 ( $P < 0.05$ ), respectively.

232 The total leaf biomass ( $W_L$ ) of *P. taiwanensis* forests ranged from 1.45 to 6.24  
233  $t \cdot hm^{-2}$  across five elevations, the litter production ( $P_L$ ) ranged from 2.65 to 3.90  $t \cdot hm^{-2}$   
234  $\cdot yr^{-1}$ , and the total root biomass ( $W_R$ ) of *P. taiwanensis* ranged from 3.93 to 42.90  $t \cdot hm^{-2}$ .  
235 The 0-20 cm root biomass (0-20 cm  $W_R$ ) of the plots ranged from 1.19  $t \cdot hm^{-2}$  to 2.03  
236  $t \cdot hm^{-2}$  (Figure 2). The  $W_L$  and  $W_R$  at 1200 m, 1400 m and 1600 m were significantly  
237 higher than those at 1800 m and 2000 m, and the highest values of 0-20 cm  $W_R$  are  
238 mainly at 1200 m. The  $P_L$  was significantly highest at 1200 m and 1400 m ( $P < 0.05$ ).  
239 These results indicated that the leaf and root biomass of *P. taiwanensis* were  
240 significantly regulated by the elevations and its associated growing temperature.  
241 Together, the LAI,  $W_{CO_2}$ ,  $W_L$ ,  $W_R$ , 0-20 cm  $W_R$ , and  $P_L$  were significantly decreased

242 with increasing elevations.

### 243 3.2. The annual flux of soil respiration and its proportion in *Pinus taiwanensis* forest

244  $R_S$  ranged from 635 to 1141 g C m<sup>-2</sup>yr<sup>-1</sup>, the  $R_H$  ranged from 440 to 873 g C m<sup>-2</sup>yr<sup>-1</sup>, and  
245 the  $R_A$  ranged from 147 to 397 g C m<sup>-2</sup>yr<sup>-1</sup> across five elevations. The  $R_S$  and  $R_H$  showed  
246 the highest values occur at 1200 m, while the lowest values are mainly at 1800 m  
247 (Figure 3). There was no significant difference in  $R_A$  among the five elevations ( $P>0.05$ ).  
248 Besides, the  $R_H: R_S$  ranged from 0.58 to 0.82 and the  $R_A: R_S$  ranged from 0.18 to 0.42,  
249 and the  $R_A: R_H$  ranged from 0.24 to 0.71 across five elevations, respectively (Figure 3).  
250 The  $R_A: R_S$  and  $R_A: R_H$  show a significant difference between elevations ( $P<0.05$ , Figure  
251 3), and both decreased with increasing elevations. It indicates that the  $R_A$  and  $R_H$ ,  $R_H:$   
252  $R_S$ , and  $R_A: R_H$  variations along the elevational gradients are different.

### 253 3.3. The correlation of vegetation traits with annual flux of soil respiration components

254 The  $R_S$  was positively correlated with  $W_{CO_2}$ , BAI,  $P_L$ ,  $W_L$ ,  $W_R$ , 0-20 cm  $W_R$  and LAI,  
255 but negatively correlated with RGR in *P. taiwanensis* forests across five elevations,  
256 respectively (Figure 4). The annual fluxes of heterotrophic respiration ( $R_H$ ) was  
257 positively correlated with  $P_L$ , BAI,  $W_R$  and 0-20 cm  $W_R$ , and also negatively correlated  
258 with RGR (Figure 4). The annual fluxes of autotrophic respiration ( $R_A$ ) were positively  
259 correlated with RGR, and negatively correlated with BAI and 0-20 cm  $W_R$  (Figure 4).  
260 The  $R_H: R_S$  of *P. taiwanensis* forest significantly increased with the increasing  $P_L$ , BAI,  
261 and 0-20 cm  $W_R$ , but decreased with the increasing RGR. However,  $R_A: R_S$  was  
262 significantly decreased with the increasing  $P_L$ , BAI, and 0-20 cm  $W_R$ , and increased  
263 with the increasing RGR (Figure 4).

264 The final SEM predicting  $R_S$  and  $R_H$  provided an adequate fit to our data  
265 (CMIN/DF = 0.61 and 0.98, GFI = 0.90 and 0.85, and RMSEA < 0.08, respectively for  
266  $R_S$  and  $R_H$ ). The results demonstrate that  $W_L$  and LAI of *P. taiwanensis* could affect soil  
267 respiration components through the  $W_{CO_2}$ ,  $P_L$ ,  $W_R$  and 0-20 cm  $W_R$ . The total  
268 explanation was 89% for  $R_S$ , 73% for  $R_H$  and only 43% for  $R_A$ , respectively (Figure 5).  
269 Besides, for  $R_S$ ,  $W_{CO_2}$  may play the most important role with the standard total effect  
270 value of 0.74 (Figure 6). For  $R_H$ , the  $W_{CO_2}$  was significantly controlled by  $W_L$ , LAI,  $P_L$   
271 and 0-20 cm  $W_R$  with  $P_L$  having the highest standard total effect value (0.68) in the  
272 predicting process (Figure 6). The  $R_A$  was directly affected by  $W_{CO_2}$  with a path  
273 coefficient of 1.16 (Figure 5) and standard total effect value of 0.52 (Figure 6), which  
274 demonstrated that  $W_{CO_2}$  was the main driver in  $R_A$  measurements.

#### 275 4. Discussions

276 Different from the variable characteristics of elevational environment factors, i.e. soil  
277 temperature and soil moisture, the colonization characteristics of plants and  
278 communities promote forest succession and development, which also regularly affect  
279 soil carbon balance. In previous studies, photosynthesis in plants has been recognized  
280 (Högberg et al., 2001; Jia et al., 2018), its functional community composition (Jenkins  
281 & Adams, 2010; Han et al., 2014b), and aboveground and underground biomass (Geng  
282 et al., 2012; Gough et al., 2020) both are affected soil respiration rates. The diversity of  
283 vegetation types brought uncertainties to soil respiration, and it is unclear how the  
284 vegetation traits of dominant species predict the soil respiration changes. The findings  
285 of this study demonstrate that the synergistic mechanism between the carbon capture

286 capacity of dominant species, aboveground and underground biomass allocation can be  
287 seen as an effective way to explain the annual flux of soil respiration. The establishment  
288 of this mechanism offers a useful simplified model for complicated forest ecosystem  
289 carbon cycle models for different soil respiration components.

#### 290 4.1. Relationships between vegetation traits and soil respiration components and its 291 proportion

292 Differences among vegetation traits in physiology may play critical roles in  
293 determining soil carbon cycling. Correlation matrix analysis indicated that  $R_S$  of *P.*  
294 *taiwanensis* forest was significantly positively correlated with  $W_{CO_2}$ , BAI,  $P_L$ ,  $W_R$ ,  $W_L$ ,  
295 0-20 cm  $W_R$ , and LAI (Figure 4), respectively. In line with our results, Högberg et al.  
296 (2001) and Bahn et al. (2009) found that photosynthates significantly affected soil  
297 respiration variations. On a daily time scale, soil respiration is closely coupled with the  
298 diurnal variation of photosynthesis, although this relationship is time-delayed (Jia et al.,  
299 2018). Besides, LAI is regarded as one of the key indicators that affect the soil CO<sub>2</sub>  
300 efflux and is positively correlated with soil CO<sub>2</sub> efflux (Bond-Lamberty & Thomson,  
301 2010). We observed that  $R_S$  linearly increased with increasing LAI. We also identified  
302 the critical role of BAI on soil CO<sub>2</sub> efflux, which has, based on the vegetation traits  
303 scale, generally been ignored when estimating soil carbon decomposition in the past  
304 (Jenkins & Adams, 2010; Wang et al., 2015; Yao et al., 2021; He et al., 2022). In  
305 addition, the carbon allocation proxies ( $P_L$ ,  $W_R$ , and  $W_L$ ) showed close correlations with  
306  $R_S$  (Figure 4). That is to say, carbon allocation plays an important role in *P. taiwanensis*  
307 forest ecosystem along the different elevations. Most of the vegetation properties

308 including  $W_{CO_2}$ ,  $P_L$ ,  $W_R$ ,  $W_L$ , 0-20 cm  $W_R$  and LAI decreased significantly with  
309 increasing elevations ( $P < 0.05$ ), which is also indicating that the growth of *P.*  
310 *taiwanensis* in Mt. Wuyi was limited by temperature (Lyu et al., 2020).

311 However, there is still a lack of measured data to explain how soil respiration  
312 component proportion (i.e.  $R_H: R_S$ ,  $R_A: R_S$ , and  $R_A: R_H$ ) changes with vegetation  
313 properties. This study fills a such gap. For instance, our results show that the  $R_H: R_S$   
314 positively lies with BAI and 0-20 cm  $W_R$ , but negatively lies with  $R_A: R_S$  (Figure 4).  
315 Our results are consistent with previous works that found that the mean  $R_H$  was  
316 significantly higher in the 49-year plantation than in 12-, 24-, and 34-year plantations  
317 in southwest China, indicating that  $R_S$  in old-growth stands dominated by  $R_H$  (Gao et  
318 al., 2019). In this study, the highest BAI and 0-20 cm  $W_R$  were found at 1200 m (Figure  
319 1 and Figure 2), suggesting that forests with higher gross primary production rates have  
320 higher detritus inputs and thus have a greater contribution to  $R_H$  in  $R_S$  (Bond-Lamberty  
321 et al., 2018). On the other hand, with an increase of 0-20 cm  $W_R$ , indicating that dead  
322 roots might have increased by the trenching method, thus increasing the uncertainty in  
323 separating  $R_A$  and  $R_H$ , causing an underestimation of the  $R_A: R_S$  ratio (Savage et al 2013,  
324 2018). However, it is worth noting that previous studies indicated that the climatic  
325 factor controlled the proportions of  $R_S$  components variations in terrestrial ecosystems  
326 (Zhu et al., 2023). By contrast, the  $R_H: R_S$  and  $R_A: R_S$  varied with different vegetation  
327 traits in this study could provide an evidence from plant perspective on controlling soil  
328 C release under the different elevational gradient.

329 4.2 Difference regulation mechanism of  $R_H$  and  $R_A$  by vegetation traits

330 According to the fitting results of the stepwise regression linear model, the  $R_S$  can  
331 be accounted for 81% by the 0-20 cm  $W_R$  and  $W_{CO_2}$  (Table 2), thus confirming the initial  
332 model hypothesis. Our result demonstrates that photosynthesis capability and  
333 belowground biomass both account for the soil respiration variations along the different  
334 elevational *P. taiwanensis* forests. However, the soil heterotrophic respiration and  
335 autotrophic respiration have different responses to the growth traits of *P. taiwanensis*.  
336 For instance,  $R_H$  is mainly determined by 0-20 cm  $W_R$ , while  $R_A$  can be comprehensively  
337 predicted through the  $W_{CO_2}$ , BAI, and  $W_L$ . Both vegetation traits of *P. taiwanensis*  
338 account for 67% and 60% of  $R_H$  and  $R_A$ , respectively. The results of our dataset indicate  
339 that the 0-20 cm  $W_R$  have a greater contribution to  $R_H$  may be due to the large number  
340 of dead roots generated after root isolation, and the decomposition of dead roots  
341 provides available carbon sources for microbial activities (Kuzyakov & Bol, 2006;  
342 Savage et al 2018). In addition, prior studies have pointed out that ectomycorrhizal  
343 biomass in coniferous forests will be significantly increased (Awad et al., 2019), and  
344 the presence of ectomycorrhizal biomass may significantly increase the soil  
345 heterotrophic respiration (Högberg & Högberg, 2002; Heinemeyer et al., 2007; Tomé  
346 et al., 2016). From LAI contribution to  $R_S$  and  $R_H$  positive effect, the increase of LAI  
347 means that the increase of canopy density, which might prompt the ectotrophic  
348 mycorrhiza hyphae of existence to improve the heterotrophic respiration rate, the  
349 findings echo the fungal biomass can predict litter soil respiration under different  
350 processing characteristics in the variation of  $CO_2$  efflux (Figure 5). The LAI has a  
351 greater effect on  $R_H$  than  $R_S$ , but a negative effect on  $R_A$  (Figure 6). Although the



352 relationships among the leaf area index, heterotrophic respiration, and fungal biomass  
353 have not been measured in the current study, it is reasonable to suppose that it provides  
354 evidence for  $R_H$  and  $R_A$  influenced by vegetation traits.

355 Previous studies generally concluded that photosynthesis provides an important  
356 and immediate C source. Thus, for  $R_A$ , diurnal photosynthesis significantly enhances  
357 autotrophic respiration when carbohydrates reach the roots (Högberg et al., 2001; Han  
358 et al., 2014a; Jia et al., 2018; Ma et al., 2020). In addition, it was also affected by the  
359 growth rate of total leaf biomass and DBH (Figure 4), but interestingly,  $W_R$  was found  
360 to have a negative standard effect on  $R_A$  (Figure 5 and Figure 6). On the one hand, these  
361 results may be caused by the widespread existence of ectomycorrhizas. On the other  
362 hand, this also can be supported by the fact that as greater are total root biomass it has  
363 most proportion of structural-low-active tissues. Together, these facts indicate that the  
364 annual fluxes of autotrophic respiration components are more controlled by the  
365 productivity of the aboveground and root-associated microorganisms than the root  
366 biomass. In present work, the value of  $R_A$  changed by approximately 17.6%-41.6%, and  
367 there is no significant statistical difference among the five elevations. By contrast, our  
368 results were highly independent of previous studies suggesting that autotrophic  
369 respiration can account for 40%-60% of total respiration variations across-latitude  
370 climate zones (Ryan et al., 1997). With the decrease in annual average temperature,  
371 plant root turnover and regeneration in soil are slower, which may increase the  
372 accumulation of soil C, and reduce autotrophic respiration rate (McGroddy & Silver,  
373 2000). Generally, under colder climates, the lower temperature limits the microbial

374 activity for soil organic matter decomposition and result in a decreased supply of  
375 nutrients such as nitrogen and phosphorus. Thus, plants usually invest more in fine root  
376 biomass for maintaining the growth (Reich et al., 2014) rather than metabolism (e.g.,  
377 respiration). Indeed, our results show clear patterns of  $W_R$  has a negative standard effect  
378 on  $R_A$  (Figure 6). These results indicate that the positive correlation between root  
379 biomass and autotrophic respiration weakened to adapt to the heterogeneity of the  
380 altitude environment.

381 To further demonstrate how the above-ground growth characteristics of *P.*  
382 *taiwanensis* affect the underground root biomass and then soil respiration variations,  
383 we established a structural equation modeling based on a simple hypothesis. Our results  
384 show that  $R_S$  and  $R_A$  are significantly regulated by  $W_{CO_2}$ , with path coefficients of 0.61  
385 and 1.16 (Figure 5), but had no direct effect on  $R_H$  (Figure 5). These results indicated  
386 that the photosynthetic pathways of *P. taiwanensis* forest may have different effects on  
387 different soil respiration components. Another important result was that the  
388 interpretation of  $R_S$  is significantly better than that of  $R_H$  and  $R_A$  in terms of the fitting  
389 effect of the model, and the goodness-of-fit index (GFI) was 0.90, 0.85, and 0.81,  
390 respectively. Therefore, the  $W_{CO_2}$  controlled the  $R_S$  by significantly affecting the 0-20  
391 cm  $W_R$  and regulating the  $W_L$  and LAI in the *P. taiwanensis* forest. This was consistent  
392 with previous studies that seasonal changes in vegetation activity play a dominant role  
393 in the sensitivity of soil respiration components, which highlights the important  
394 ecological linkages between plant physiological processes and soil processes (Wang et  
395 al., 2010; Cassart et al., 2021).

396 Future studies should also consider the mycorrhizal types associated with species  
397 and the role of mycorrhizal biomass in soil respiration. This requires the use of isotope  
398 techniques at different scales and putting the plant trait into models of soil respiration.

## 399 **5. Conclusions**

400 In summary, we found that the altitude environment has a strong effect on the  
401 regulations of vegetation traits in the *P. taiwanensis* forest: the  $W_{CO_2}$ ,  $P_L$ ,  $W_R$ ,  $W_L$ , 0-20  
402 cm  $W_R$ , and LAI decreased with increasing elevations.  $R_S$  and  $R_H$  were positively  
403 correlated with  $P_L$ ,  $W_R$ , and 0-20 cm  $W_R$ , but  $R_A$  was negatively correlated with BAI  
404 and 0-20 cm  $W_R$ . This implies a general rule of the plant carbon fixation's role in  
405 different soil respiration components prediction, although the forests along the different  
406 elevational environments. Besides, the structural equation modeling demonstrates that  
407  $W_{CO_2}$  affects the  $W_L$ , LAI, and 0-20 cm  $W_R$ , thus determining the changes in  $R_S$ ,  $R_H$ , and  
408  $R_A$ . However, the most critical driving factor that predicts the  $R_H$  is  $P_L$ , and  $W_{CO_2}$   
409 directly controls the  $R_A$ , respectively. In an overall view, both soil respiration systems  
410 ( $R_H$  and  $R_A$ ) both depend on the system's capacity to produce more, with the logical and  
411 simple difference that the most direct variables are litter production and root biomass,  
412 respectively. We simply expect that under global change in this region, the shift of soil  
413 respiration would depend primarily on the effects on carbon fixation, and thus the  
414 feedback effect can be more or less neutral.

## 415 **Declaration of Competing Interest**

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

418 **Data availability**

419 Data will be made available on request.

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

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587 Table 2 Stepwise regression analysis between soil respiration components and *P. taiwanensis*  
588 vegetation traits

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614 Figure 1 The growth characteristics of **a** annual carbon sequestration ( $W_{CO_2}$ ), **b** stem cross-section  
615 of tree (BAI), **c** relative growth rate (RGR), and **d** leaf area index (LAI) for *P. taiwanensis* along  
616 the different elevation gradients.

617

618 Figure 2 The characteristics of **a** total leaf biomass ( $W_L$ ), **b** litter production ( $P_L$ ), **c** 0-20 cm root  
619 biomass (0-20 cm  $W_R$ ) and **d** total root biomass ( $W_R$ ) for *P. taiwanensis* along the different elevation  
620 gradients.

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622 Figure 3 Characteristics of annual fluxes of **a** total soil respiration ( $R_S$ ), **b** heterotrophic respiration  
623 ( $R_H$ ), **c** autotrophic respiration ( $R_A$ ) and **d**, **e**, **f** the proportion between soil respiration components  
624 in *P. taiwanensis* forest along the different elevations in Wuyi Mountain.

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626 Figure 4 Correlation plots between the annual flux of soil respiration components and its proportion  
627 versus growth traits of *P. taiwanensis* in Wuyi Mountain

628 Note: The photosynthetic carbon sequestration ( $W_{CO_2}$ ), the relative growth rate of tree (RGR), leaf  
629 area index (LAI), total leaf biomass ( $W_L$ ), litter production ( $P_L$ ), 0-20 cm root biomass (0-20 cm  
630  $W_R$ ), total root biomass ( $W_R$ ), total annual soil respiration ( $R_S$ ), annual heterotrophic respiration  
631 ( $R_H$ ), annual autotrophic respiration ( $R_A$ ).

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634 Figure 5 Structural equation model analysis of the annual flux characteristics of different soil  
635 respiration components driven by the growth of *P. taiwanensis*

636 Note: **a**, **b**, and **c** indicate total annual soil respiration ( $R_S$ ), annual heterotrophic respiration ( $R_H$ ),  
637 annual autotrophic respiration ( $R_A$ ), respectively. The photosynthetic carbon sequestration ( $W_{CO_2}$ ),  
638 leaf area index (LAI), total leaf biomass ( $W_L$ ), litter production ( $P_L$ ), 0-20 cm root biomass (0-20  
639 cm  $W_R$ ), total root biomass ( $W_R$ ).

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642 Figure 6 Structural equation model analysis of the standard total effect size of different *P.*

643 *taiwanensis* community traits on soil respiration

644 Note: **a**, **b**, and **c** indicate the standard total effect size to total annual soil respiration ( $R_S$ ), annual

645 heterotrophic respiration ( $R_H$ ), annual autotrophic respiration ( $R_A$ ), respectively. The photosynthetic

646 carbon sequestration ( $W_{CO_2}$ ), leaf area index (LAI), total leaf biomass ( $W_L$ ), litter production ( $P_L$ ),

647 0-20 cm root biomass (0-20 cm  $W_R$ ), total root biomass ( $W_R$ ).