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# Litter and microclimate controls on soil heterotrophic respiration after converting seasonal rainforests to rubber plantations in tropical China

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#### ABSTRACT

Land-use changes can alter carbon cycling. Soil carbon loss resulting from the conversion of natural forests to rubber plantations (RP) may occur due to changes in litter inputs or in biotic and abiotic environmental conditions. In this study, we conducted a reciprocal soil and litter translocation mesocosm experiment for 15 months in a seasonal rainforest (SR) and RP to elucidate the effect of litter, soil and site conditions on heterotrophic respiration and its temperature sensitivity after land-use conversion. We found that rate of soil heterotrophic respiration ( $R_h$ ) was higher at RP site than at SR site or for SR litter than RP litter with significant interactions between forest site and litter type, and did not differ between SR and RP soils. The  $Q_{10}$  values of  $R_h$  did not differ between forest sites, soils, or litter types but were substantially lower when litter was absent and substantially higher when RP soil was incubated in SR site and vice versa. Removal of surface litters led to a reduction of  $R_h$  by 27-45%. Soil labile organic C pool and microbial biomass were not influenced by litter type and soil but differed between forest sites with higher moisture at RP site than SR site. Our results suggested that changes in physical environmental conditions, rather than changes in litter input or soil biochemical properties, attributed to the elevated soil heterotrophic respiration in RP, resulting in soil carbon loss following the tropical land-use changes.

# 1. Introduction

Deforestation is known as the second largest source of the elevated atmospheric carbon dioxide. Carbon loss through deforestation and degradation of tropical forests was estimated at 0.8 Pg to  $1.0 \text{ Pg C yr}^{-1}$  in the last decades (Bacciniet al., 2012; Harris et al., 2012). Southeast Asia is one of the global deforestation hot spots where almost 250,000 hectares of natural forest was converted to rubber plantation (RP) between 2005 and 2010 (Ahrends et al., 2015). Rubber and other economic crops have been the major land-use changes in this region. The area of RP in Southeast Asia reached 10.4 million ha by 2017, accounting for 89% of world total RP area (FAOSTAT, 2019). Since the first rubber establishment in the 1950s, the area of RPs has increased up to 24.2% of land cover by 2014 in Xishuangbanna, Southwest of China (Chen et al., 2016).

It is recognized that soil carbon sequestration ability in RPs is much

lower than that of natural forests (Jiang et al., 2017; Yang et al., 2016). This reduction in soil organic C may result from either reduced litter input or accelerated decomposition due to changed litter quality, microclimate, or soil activity. Litter production was reported to be lower in RP than in seasonal rain forest (SR) (Zhang and Zou, 2009; Zhang et al., 2013; Kotowska et al., 2016). Litter quality is lower in RP than in SR as indicated by a higher C/N ratio and aromatic carbon fractions (Zhang and Zou, 2009; Zhang et al., 2013). However, thinner floor layer in RP than SR (Zhang and Zou, 2009; Lan et al., 2020) suggests a cause of either reduced litter inputs or accelerated litter decomposition due to improved soil physical environment and soil activity, rather than litter decomposability in RP.

Soil is responsible for 60–90% of the carbon dioxide (CO<sub>2</sub>) released into the atmosphere in terrestrial ecosystems (Goulden et al., 1996). Soil CO<sub>2</sub> efflux is the outcome of the metabolic processes of plant roots (autotrophic respiration,  $R_a$ ) and microbial communities (heterotrophic

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Received 2 September 2020; Received in revised form 18 August 2021; Accepted 22 August 2021 Available online 17 September 2021 0168-1923/© 2021 Elsevier B.V. All rights reserved. respiration,  $R_h$ ). The  $R_a$  refers to CO<sub>2</sub> efflux derived from roots and the associated symbiotic organisms,  $R_h$  refers to microbial respiration of litter and root exudates as well as the transformed soil organic carbon (Sulaman et al., 2005; Kuzyakov, 2005). Because  $R_h$  could account for up to 70% of the total soil respiration ( $R_s$ ) in forest stands (Sulaman et al., 2005; Fernández-Alonso et al., 2018), it is therefore important to determine how  $R_h$  responds to land-use changes from native forests to monoculture agroforestry systems (Barba et al., 2016; Fernández-Alonso et al., 2018).

The conversion of native forest to monoculture RP may result in changes in plant litter input, soil biochemical properties such as microbial biomass and soil labile organic carbon, or in environmental conditions that include microclimate and soil water content (Liu et al., 2011; Meijide et al., 2018; Song et al., 2017; Lan et al., 2020), and consequently alter soil respiration and soil carbon stock. Temperature is the essential factor controlling soil metabolic activities; thus, the kinetics been of CO<sub>2</sub> efflux had modeled by various temperature-dependent functions. Many hypotheses were postulated to link the response of R<sub>h</sub> to soil temperature (Tuomi et al., 2008; Tremblay et al., 2018; Salazar et al., 2019). However, the temporal variability of *R*<sub>b</sub> observed in field experiments captures not only its dependence on soil temperature, but also reflects the influence on decomposition caused by seasonal changes in substrate quality and quantity, soil moisture and soil community (Gonzalez et al., 2001; Hou et al., 2005; Fernández-Alonso et al., 2018; Huang et al., 2020), as well as their interactions (Wall et al., 2008). Strong variations in seasonality of modeled soil R<sub>h</sub> was commonly observed, suggesting an apparent limitation to soil metabolic activity beyond that could be explained by temperature. Furthermore, homeostasis of native soil microbial community would suggest  $R_h$  dependency on soil organisms, which were also greatly constrained by soil water and temperature (Fernández-Alonso et al., 2018).

We conducted this study to elucidate the influence of aboveground litter input, forest soils and its organisms, and forest microclimate and water content on soil Rh and its temperature sensitivity following conversion of natural forest to RPs. A 15-month reciprocal soil and litter translocation mesocosm experiment were performed in Xishuangbanna of SW China. In the root-exclusion treatment it was assumed that  $R_a$  was completely suppressed and hence solely  $R_{\rm h}$  occurred that the CO<sub>2</sub> efflux derived from the microbial decomposition of soil organic matter and litter. We collected in-situ data on soil R<sub>h</sub>, litterfall, soil labile organic carbon, soil microbial biomass, and soil temperature and moisture from these mesocosms in SR and RP. We hypothesized that reduction of TOC in RPs was resulted from (1) reduced production of above-ground rubber litter, or (2) accelerated soil heterotrophic respiration and altered temperature sensitivity of TOC due to improved physical environmental conditions such as temperature and moisture or soil biochemical properties such as microbial biomass and soil labile organic carbon.

## 2. Materials and methods

## 2.1. Site description

Study sites were located in the Xishuangbanna Tropical Botanical Garden (XTBG, 21°54′N, 101°46′E), near the monitoring plots of the Chinese Ecological Research Network supported by the Chinese Academy of Sciences. The annual mean temperature in the region is 21.8°C and the annual mean precipitation is 1493 mm (Cao et al., 2006). This region is strongly influenced by the tropical monsoons that bring warm and humid air from the northeastern Indian Ocean during the months of May through October. Eighty-four percent of the annual precipitation occurs during this monsoon season. Heavy nocturnal fogs form frequently during the cool-dry season from November to next April (Lang et al., 2017).

This study was conducted in a native SR and a 25-year-old RP adjacent to the SR. The soil was a lateritic Oxisol developed from

arenaceous shale sediments (Zhang et al., 2013). The dominant tree species of SR are *Pometia tomentosa, Terminalia myriocarpa, Gironniera subaequalis*, and *Garuga floribunda*. SR has an average canopy height of approximately 40 m and canopy closure of 90% (Cao and Zhang, 1996; Ren, et al., 1999; Zhu, et al., 2006). Rubber plantations were established on terraces, with wide-narrow row distance and tree spacing of 3.1and 2.5 m. It has an average canopy height of approximately 20 m, density of 370 specie per ha and canopy closure of 65% (Ren, et al., 1999; Zhu, et al., 2006). The area was selectively logged in the 1960's and was cleared for slash-and-burn agriculture before rubber planting. The plantation was fertilized with a composite fertilizer (N, P, and K) at a rate of approximately 60 kg N ha<sup>-1</sup> yr<sup>-1</sup>. Fertilizers were point-applied in March and August at a dose of about 0.15 kg N per tree hole per year. Latex of the rubber trees was harvested starting at age 8-years old from March to November with a mean yield of 2.6 Mg dry latex ha<sup>-1</sup> yr<sup>-1</sup>.

# The reciprocal translocation experiment

Five  $4 \times 4$  m plots were established at 20-50 m spacing in both the RP and SR. Six soil mesocosms of  $50 \times 50 \times 10$  cm (depth) were buried randomly in each plot in August. Soils used in the mesocosms were collected from the 0-10 cm layer in SR and RP and passed through a 1cm mesh to remove plant roots, rocks and large soil animals. Two layers of 53 µm nylon mesh were placed underneath the soil to separate it from the local soil. Litters were collected (square baskets with side length of 50 cm were placed 30cm above each soil mesocosm with litter removal) and put in the corresponding soil mesocosms every 10 days. There were six treatments in each plot: 1) Soil derived from SR, without litter cover  $(S_{SR} + NL)$ , 2) Soil derived from RP, without litter cover  $(S_{RP} + NL)$ , 3) Soil origination from SR, with aboveground litter of SR ( $S_{SR} + L_{SR}$ ), 4) Soil derived from RP, with above round litter of SR ( $S_{RP} + L_{SR}$ ), 5) Soil derived from SR, with above ground litter of RP (S $_{\rm SR}$  +  $L_{\rm RP}$ ), 6) Soil derived from RP, with above round litter of RP ( $S_{RP} + L_{RP}$ ). After 15 months of field incubation, soils in these six treatments and the nearby control soil that was not disturbed were sampled to a depth of 5 cm for chemical analyses. Three soil cores (5 cm diameter) from each mesocosm were bulked into one composite sample. Samples were then passed through a 2 mm sieve and plant materials were removed by hand. A subset of the sieved soil samples was air-dried and grounded for the analyses of soil C and N content. Five conical baskets of 50 cm in diameter were randomly placed adjacent to each plot and plant litter was collected 2-3 times per month from each basket. Litters were oven dried at 60 °C to obtain dry weight.

#### 2.2. Soil heterotrophic respiration (R<sub>h</sub>)

Since plant roots were excluded from the mesocosms and litter was removed when measuring soil CO<sub>2</sub> efflux, we attribute the respiration measured within the collars mostly to microbial decomposition of soil organic matter in the non-rhizosphere. Soil respiration was measured using an infrared gas analyzer (IRGA, LI-COR 820, LI-COR, Lincoln, NE, USA) in November and February, April, and August of the next year. A PVC soil chamber (inner diameter 20.3 cm) was installed on soil surface and the total volume of the chamber was 5700 cm<sup>3</sup>. The chamber was pressed slightly into the soil to keep gas tight. An integrated pump circulated the headspace air from the chamber to the analyzer in which CO<sub>2</sub> concentration was recorded. Soil respirations of all plots were measured within 4 hours from 8:00 to 12:00 am. Soil temperature (C) was measured using a thermometer (TM-150, Custom, Tokyo, Japan), and soil moisture (v/w) was measured with a time domain reflectometry sensor (TDR; TRIME-FM, IMKO, Ettlingen, Germany), both at 5 cm depth.

#### 2.3. Laboratory processing

Soil microbial biomass carbon (MBC) was determined by the difference in soil CO<sub>2</sub>-C evolved from the control and fumigated samples following the procedures of Jenkinson and Powlson (1976). We used a sequential fumigation-incubation (SFI) procedure (Zou et al., 2005) to estimate soil labile organic carbon (LOC). The fumigated samples for microbial biomass carbon (MBC) were subject to five additional fumigation-incubation cycles. Total  $CO_2$  evolved from the fumigated soils during six incubation cycles (10 days for each cycle) was used to estimate LOC. Total organic C and N in soils were determined using an Elementar Vario Max CN combustion analyzer (Hanau, Germany).

#### 2.4. Statistical analysis

An exponential growth equation combined with a Gaussian function for soil moisture were used to calculate the temperature (T) sensitivity  $(Q_{10})$  in relation with soil moisture (M).

$$R_h = a e^{bT - 0.5 \left(\frac{M - M_0}{c}\right)^2}$$
(1)

$$Q_{10} = e^{10b}$$
 (2)

where a, b, c and  $M_0$  are fitted parameters. Soil respirations were Gaussian correlated with soil moisture under different litter and environment treatment.

All data presented here are means ( $\pm$  SD) of five plot replicates and statistical analyses were performed with Stat View 8.0 (SAS Institute, Cary, NC, USA). The mixed-model ANOVA was used to examine the effects of litter, soil and forest site (independent variables) on  $Q_{10}$ , and three-way repeated measures ANOVA for soil  $R_{\rm h}$ , total organic carbon (TOC), total nitrogen (TN), MBC and LOC contents (dependent variables). Pearson correlations analyses were conducted to show relationships between two variables. The Nonlinear regression and coefficient of determination were used to identify the relationship between respiration and soil temperature and moisture. All data were tested for homogeneity variance (Levene's test, p > 0.05). Fisher's least significant difference (LSD) was used for estimation of differences between treatments. All significance level was set at alpha = 0.05

# 3. Results

#### 3.1. Controls on heterotrophic respiration

Soil respiration rates varied greatly, ranging from 1.8  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> to 14.3  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> at the SR site and from 3.6 to 28.1  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> at the RP site. Soil respiration rate without litters was on average about 68% of that with litters. Annual  $R_h$  was apparently greater in RP than SR sites, and in treatment with litter than without litter inputs, suggesting that physical environment and the presence of litter had significant influences on annual  $R_h$  (Fig. 1). The average  $R_h$  of soils incubated at the RP site were 90% greater than that at the SR site in dry season and 30% greater in rainy seasons, regardless of litter inputs and soil origins (Table 1). Annual  $R_h$  was not affected by soil origin (SR versus RP) or litter type. There was a significant interaction between litter type and forest site, but there were no interactions among forest site, litter type, and soil origin, or between forest site and soil origin, or between litter type and soil origin (Fig. 1).

#### 3.2. R<sub>h</sub> Sensitivity to soil temperature and moisture

Temperature sensitivity of  $R_h$  ( $Q_{10}$ ) was lower in litter removal treatments than those with litter (Fig. 2, Table 2). Soil origin, litter type or forest site did not significantly affect  $Q_{10}$  values of soil  $R_h$ . There was a significant interaction between soil origin and forest site where soil  $Q_{10}$  values appeared to be higher in foreign site than that in native sites. All other interactions were not significant.



**Fig. 1.** Means ( $\pm$ SD) of annual soil respiration rates ( $R_h$ ) as affected by forest site, litter input, soil origin, and their interactions by the repeated measure ANOVA.

Note: Black bars represent Soil  $_{SR}$  (Soil derived from SR); Grey bars represent Soil $_{RP}$  (Soil derived from RP); Site $_{SR}$  indicates incubation in SR; Site $_{RP}$  indicates incubation in RP; NL means no litter;  $L_{SR}$  means litter from SR;  $L_{RP}$  means litter from RP.

# Table 1

Means ( $\pm$ SD) of soil  $R_h$  in a rubber plantation (site<sub>RP</sub>) and a seasonal forest (site<sub>SR</sub>) during rainy and dry seasons.

Treatments	Dry	Rainy
site <sub>sr</sub> site <sub>rp</sub>	$\begin{array}{c} 2.94 \pm 0.14a \\ 5.61 \pm 0.30b \end{array}$	$\begin{array}{l} 6.74 \pm 0.54 \text{ a} \\ 8.88 \pm 0.94 \text{ ab} \end{array}$



**Fig. 2.** Means ( $\pm$ SD) of the  $Q_{I0}$  of  $R_h$  as affected by forest site, litter input and soil origin by the mixed functions of ANOVA.

Note: Black bars represent Soil<sub>SR</sub> (Soil derived from the SR); Grey bars represent Soil<sub>RP</sub> (Soil derived from RP); Site<sub>SR</sub> indicates incubation in SR; Site<sub>RP</sub> indicates incubation in RP; NL means no litter; L<sub>SR</sub> means litter from SR; L<sub>RP</sub> means litter from RP;  $Q_{10}$  value was calculated using Eq. (2):  $Q_{10} = e^{10b}$ .

#### 3.3. Soil environment and carbon pools

Soil temperature at the depth of 5 cm was 0.45 °C higher in the rainy season (May through November) in the RP site than in SR site (Table 3).

#### Table 2

Parameters of fitted equations with soil respiration rate (Eq. (1):  $R_h = bT - 0.5 \left(\frac{M - M_0}{r}\right)^2$ 

Site	Parameter name	Treatments						
		NL Soil <sub>sr</sub>	Soil <sub>RP</sub>	Litter <sub>sR</sub> Soil <sub>sR</sub>	Soil <sub>RP</sub>	Litter <sub>RP</sub> Soil <sub>SR</sub>	Soil <sub>RP</sub>	
SR	Intercept a	1.36	0.98	0.63	0.18	0.65	0.07	
	Soil temperature (T) b	0.06	0.08	0.14	0.18	0.09	0.20	
	Soil moisture (M) M <sub>0</sub>	31.21	29.16	31.53	30.49	26.73	23.49	
	Soil moisture (M) c	13.43	9.40	6.95	8.01	22.22	13.91	
	$R^2$	0.40	0.74	0.65	0.72	0.30	0.67	
RP	Intercept a	0.45	2.18	0.19	1.32	0.19	0.73	
	Soil temperature (T) b	0.13	0.07	0.18	0.09	0.18	0.16	
	Soil moisture (M) Mo	29.94	28.62	28.92	30.77	30.73	32.20	
	Soil moisture (M) c	10.55	9.57	11.11	12.49	10.94	6.92	
	$R^2$	0.59	0.44	0.63	0.45	0.65	0.51	

Soil moisture was also 3.3% greater in the RP site than in the SR site for both the dry and wet seasons or for the entire year (Table 3). Furthermore, soil moisture was greater with SR litter than RP litter in the rainy season, and in the SR soil than the RP soil for both dry and rainy seasons.

#### Table 3 Average temperature and moisture in soil mesocosms in rainy and dry seasons

Litter input increased soil moisture compared with treatment without litter input. There was higher annual litterfall mass in SR ( $8.4\pm0.9$  t ha<sup>-1</sup> a<sup>-1</sup>) than RP ( $7.6\pm0.4$  kg ha<sup>-1</sup> a<sup>-1</sup>) with apparent more canopy opening in the latter. Canopy opening was further enhanced in January and February in RP (Fig. 3) when rubber trees senescence their leaves, which would lead to higher soil temperature in RP than SR sites during the dry season.

Soils derived from SR (Soil<sub>SR</sub>) still had higher C and N contents and microbial biomass than those from RP (Soil<sub>RP</sub>) under the same treatments (Fig. 4). TOC, LOC and MBC ranged from 17.09 to 28.97 g kg<sup>-1</sup>, 0.83 to 2.20 g kg<sup>-1</sup>, and 0.34 to 0.70 g kg<sup>-1</sup> in SR soil; and from 14.96 to 20.65 g kg<sup>-1</sup>, 0.57 to 1.37 g kg<sup>-1</sup>, and 0.26 to 0.63 g kg<sup>-1</sup> in RP soil, respectively. Soils without litter cover had lower TOC contents than those with litter. There was no significant difference in soil TOC content between treatments of L<sub>SR</sub> and L<sub>RP</sub>. Soil respiration rate was positively correlated with soil temperature and moisture, rather than soil C pools in dry seasons (Table 4). No correlations were found between  $Q_{10}$  and soil carbon pools.

# 4. Discussion

Reduction in TOC following conversion from SR to RP may have resulted from one or more of these factors: improved physical environment for decomposition, improved quality of organic C for decomposition, reduced litter input, and increased biotic activity in decomposition. In this study, soil  $R_h$  in RP site was overall higher than that in SR site, whereas aboveground litter input and soil origin had no significant

Treatments	Temperature (°C)			Moisture (v/w)			
	Dry	Rainy	Annual	Dry	Rainy	Annual	
site <sub>SR</sub>	$21.52{\pm}0.20$	25.43±0.04	$23.58 {\pm} 0.16$	$21.49{\pm}0.58$	42.38±0.48	$27.02{\pm}0.98$	
site <sub>RP</sub>	$21.12{\pm}0.20$	$25.88 {\pm} 0.04$	$23.40{\pm}0.16$	$24.63 {\pm} 0.58$	47.6±0.48	$30.37 {\pm} 0.98$	
	<i>p</i> =0.1651	p < <b>0.001</b>	<i>p</i> >0.05	p = <b>0.001</b>	p < <b>0.001</b>	p = <b>0.016</b>	
NL	$21.17{\pm}0.24$	$25.70 \pm 0.05$	$23.39{\pm}0.19$	$22.17{\pm}0.70$	43.16±0.60	27.42±1.19	
litter <sub>sR</sub>	$21.36{\pm}0.24$	$25.62{\pm}0.05$	$23.51 {\pm} 0.19$	$23.51 {\pm} 0.70$	$45.64 \pm 0.60$	29.05±1.19	
litter <sub>RP</sub>	$21.43 {\pm} 0.24$	$25.65 {\pm} 0.05$	$23.57{\pm}0.19$	$24.12{\pm}0.70$	44.24±0.60	29.63±1.19	
	<i>p</i> >0.05	<i>p</i> >0.05	<i>p</i> >0.05	<i>p</i> =0.1401	p = <b>0.0016</b>	p=0.4020	
Soil <sub>SR</sub>	$21.37{\pm}0.20$	$25.63 \pm 0.04$	$23.52{\pm}0.16$	24.33±0.58	45.74±0.48	29.68±0.98	
Soil <sub>RP</sub>	$21.26{\pm}0.20$	$25.68{\pm}0.04$	$23.46{\pm}0.16$	$22.21 {\pm} 0.58$	$44.23 {\pm} 0.48$	$27.71 {\pm} 0.98$	
	<i>p</i> >0.05	<i>p</i> >0.05	<i>p</i> >0.05	p = <b>0.0103</b>	p = <b>0.0324</b>	p=0.1571	



Fig. 3. Seasonal litterfall rate in the seasonal rain forest (SR) and rubber plantation (RP).



Fig. 4. Effects of site, litter type and soil source on means (SD) of (A) soil total organic carbon (TOC), (B) nitrogen (TN), (C) microbial biomass carbon (MBC) and (D). labile organic carbon (LOC).

Notes: Results of three-way ANOVA are showed in the figures, with absence of interactions among the three factors. \* and \*\* Indicate significant difference between RP and SR soils for each litter treatment and incubation site at 0.01 and <math>p < 0.01, respectively.

# Table 4 Correlation coefficient (r) between soil respiration and soil environment conditions and properties

Season	Temperature	Moisture	TOC	TN	C/N	LOC	MBC
Rainy	ns	-0.29*	ns	-0.31*	0.26*	Ns	-0.27*
Dry	0.38**	0.52**	ns	ns	ns	Ns	ns

Note: TOC indicates soil total organic carbon; TN for soil total nitrogen; LOC for labile organic carbon; MBC for soil microbial biomass carbon; C/N is the ratio of TOC to TN; and ns indicates no significant difference.

\* and \*\* Indicate significant difference between treatments at 0.01 and <math>p < 0.01, respectively.

influences on  $R_h$ . Higher C/N ratio (Zhang et al., 2013) of RP litter (42.5±1.0) than SR (27.6 ± 4.1) and lower RP litter production did not appear to influence soil  $R_h$ . Furthermore, there were no differences in soil MBC, and LOC between treatments of RP and SR litter or incubation sites. Our data suggested that physical environment became the main control for the increased soil  $R_h$  following conversion from SR to RP, rather than changes in aboveground litter mass, litter decomposability and soil biochemical properties, and consequently reduced TOC in RP.

Compared with SR, higher soil temperature and moisture were usually found in RPs (Zhu et al., 2018; Lang et al., 2020). Soil moistures in various treatments at RP sites were higher than those at SR, but soil temperature was not significantly different between RP and SR sites except in the rainy season when RP soil was 0.45 °C warmer than the SR soil, likely due to the increased light level following the peak litterfall near the end of dry season. First, conversion of SR to RP resulted in less vegetation and reduced canopy cover. Canopy openness is recognized as a key driver of below-canopy microclimate following the conversion from SR to RP, which were found positively related to air temperature and soil temperature (Meijide et al., 2018). Second, conversion from SR to RP changed multi-layered canopy into single-layered canopy induced decreased canopy cover, increased throughfall water and reduced water transpiration, consequently increased soil water content (Zhu et al., 2018).

Either with or without litter present, both the RP and SR soils delivered at least 30% more  $CO_2$  efflux when they were incubated at the RP site than at the SR site in the dry season. The elevated soil moisture and temperature were likely a key factor regulating soil respiration in RP. Hawakes et al., (2017) found the sensitivity of soil respiration to

moisture increased with increasing rainfall and litter mass, resulting in greater C loss in historically wetter soils than historically drier soils. In tropical regions, soil respiration is more sensitive to moisture than to temperature (Fernández-Alonso, et al., 2018), resulting in more rapid soil C loss in the tropical soils than in the temperate soils due to land-use changes. Lang et al. (2017) reported similar results that soil moisture was 40% higher in August in a RP than in a natural forest in Xish-uangbannan, SW China. In our study,  $R_h$  responded more sensitively to changes in soil moisture with an exponent power of 2 than to temperature with an exponent power of 1. Soil respiration became suppressed during the rainy season even with higher soil temperature in the RP than the SR site, likely due to over-saturation that might inhibit the decomposition and/or alter CO<sub>2</sub> pathways through dissolution into soil solution (Lang et al., 2017).

Theoretically, increase of  $R_h$  in RP can be caused by changes in soil biochemical properties. However, we found that soil microbial biomass, soil labile organic carbon, soil total organic carbon and soil total nitrogen were not affected by forest site or by litter type, but were affected only by the origin of soils with no interactions with other factors, suggesting that the elevated R<sub>h</sub> in RP was not caused by changes of soil biochemical properties. However, invasion of soil animals occurs often after land-use changes. Exotic Pontoscolex corethrurus became a dominant earthworm in RPs of Xishuangbanna with an average population density of 182 $\pm$ 29 ind m<sup>-2</sup> compared with only 89 ind.m<sup>-2</sup> in SR, dominated by native species (Yu, 2007). Our earlier study with 20-months field incubation showed that Pontoscolex corethrurus invasion induced a decrease of 6% total TOC and increased the turnover rate of soil labile organic carbon in the surface soil layer of RPs (Zhang et al., 2010). A global meta-analysis shows that earthworm density correlated linearly with litter mass loss and TOC decay (Huang et al., 2020). Earthworms can increase soil respiration primarily by increasing the proportion of bacteria or lowering fungi-to-bacteria ratio, because bacteria have a higher turnover rate and lower carbon assimilation efficiency than fungi. In contrast, P. corethrurus was reported to have no effect on soil respiration through stabilizing organic carbon to form large macro-aggregates (Wu et al., 2017). Because we rarely saw earthworms present in our soil mesocosms that were constructed with 53 µm nylon mesh to prevent the entry of earthworms, the difference in soil respiration between SR and RP sites were unlikely caused by earthworms in this study.

Changes in litter input following land-use conversion can also be an important factor altering soil  $R_{\rm h}$ . The presence of either SR or RP litter elevated soil  $R_{\rm h}$  as expected. However, soil with RP litter decomposed faster (higher  $R_{\rm h}$ ) in RP site than SR site, whereas soil with SR litter decomposed invariantly between the SR and RP sites (Fig. 1), suggesting a possible "home-court" advantage for RP litter decomposition in which plant litter decompose faster in its home site compared with "exotic" sites (Rodríguez-Calcerrada et al., 2019). This "home-court" advantage might be compensated by the accelerated decomposition in RP site for the SR litter. Regardless of reduced litter input,  $R_{\rm h}$  is still greater in the RP site than in the SR site, suggesting combustion of existing organic carbon in the RP site. The improved microclimate conditions and a possible "home-court" advantage effect together might attribute to the elevated  $R_{\rm h}$  in the RP sites.

We found that  $Q_{10}$  of  $R_h$  was negatively related to temperature and positively to moisture, consistent with previous results (Suseela et al., 2012). Furthermore,  $Q_{10}$  increased when soils were transplanted to a foreign forest site in this study. Bai et al. (2017) suggested a tightly coupled relationship between  $Q_{10}$  and microbial trophic guilds: the copiotrophic prokaryotes responded positively to high  $Q_{10}$  values, while the oligotrophs showed a negative response. Salazar et al. (2019) suggested that the response of  $R_h$  to temperature was stronger when soil contains more active microbes. Higher  $Q_{10}$  in foreign forest site may be caused by the dominance of copiotrophic strategists. In this study we showed that  $Q_{10}$  increased when nutrient-rich plant litter was added to soils, suggesting a dominance of copiotrophic strategists with litter addition treatment. Although  $Q_{10}$  of  $R_h$  was not affected after converting SR to RP, itwas increased when soils were placed in exotic sites with altered environmental conditions. This might also attribute to the reduction of TOC in RP immediately following the land-use conversion since there appeared to have an "exotic-court" advantage in  $Q_{10}$  of  $R_h$ .

The microbial community in rainforest is dominated by fungi that can decompose cellulose and lignin in litter (Schneider et al. 2012). Removal of forest litter might decrease the fungi to bacteria (F/B) ratio in the soil. Since most fungi have a higher C use efficiency than bacteria (Keiblinger et al. 2010), a shift in the F-B ratio is likely to affect soil CO<sub>2</sub> emissions. Previous studies found that aboveground litter does not influence microbial community composition of mineral soils in long term (Creamer et al., 2015; Leitner, et al., 2016). Removal of above-ground litter results in removal of young carbon that may result in alteration of microbial community. Lan (2020) found conversion from SR to RP resulted in shifts in soil bacterial composition (from the Proteobacteria to Chloroflexi), Archaeal composition (from Thaumarchaeota to Bathyarchaeota), and fungal composition (from Basidiomycota to Ascomycota). Compared with that in SR, the RP leaf litter is poorer in N and lignin. This would favor Ascomycota at the expense of Basidiomycota which contain many lignin decomposers and other specialists on recalcitrant substrates. The more sunlight would benefit chloroflexi in RP.

In conclusion, our study clearly suggested that the increase of soil  $R_h$  in RP was resulted from an elevated soil moisture condition. Both  $R_h$  and its temperature sensitivity were substantially lower when litter was absent. Although temperature sensitivity of  $R_h$  was not influenced by litter type, soil origin, and forest site, it was elevated when soils were incubated in foreign forest site, suggesting likely an "exotic-court" advantage effect. Converting SR to RP can lead to decrease in soil organic carbon stock through accelerating soil heterotrophic respiration and elevating its temperature sensitivity following tropical land-use changes.

# **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.

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