



# Seasonal differences in soil respiration and methane uptake in rubber plantation and rainforest



Rong Lang<sup>a,b</sup>, Sergey Blagodatsky<sup>a,c,\*</sup>, Jianchu Xu<sup>d</sup>, Georg Cadisch<sup>a</sup>

<sup>a</sup> Institute of Agricultural Sciences in the Tropics (Hans-Ruthenberg-Institute), University of Hohenheim, Garbenstrasse 13, 70593 Stuttgart, Germany

<sup>b</sup> Center for Mountain Ecosystem Studies, Kunming Institute of Botany, Chinese Academy of Sciences, Lanhei Road 132, 650201 Kunming, PR China

<sup>c</sup> Institute of Physicochemical and Biological Problems in Soil Science, Russian Academy of Sciences, 142290 Pushchino, Russia

<sup>d</sup> World Agroforestry Centre, East and Central Asia, Lanhei Road 132, 650201 Kunming, PR China

## ARTICLE INFO

### Article history:

Received 6 September 2016

Received in revised form 21 February 2017

Accepted 22 February 2017

Available online xxx

### Keywords:

Greenhouse gases

Temperature sensitivity

Soil moisture

Land use change

Carbon emission

## ABSTRACT

Rubber plantations expanded remarkably in South-East Asia, while the impact of this land use change on soil carbon dynamics and greenhouse gases emissions has not been sufficiently understood. We measured monthly soil CO<sub>2</sub> fluxes during one year as well as CH<sub>4</sub> fluxes during the rainy season in secondary rainforest, 9 and 22 year-old rubber monoculture and 22-year-old rubber-tea intercropping in Xishuangbanna, Southwest China. Our aim was to assess the impact of the land use change on soil carbon fluxes and quantify the factors determining the difference in the carbon fluxes. A linear mixed effect model was used in studying the soil temperature and moisture variation and temperature sensitivity ( $Q_{10}$ ) of soil respiration.

The temporal pattern of soil respiration distinctly differed between sites during the rainy season: rainforest maintained a high soil respiration rate, while soil respiration became suppressed (by up to 69%) during the most moist period in rubber plantations. Rainforest soils thus emitted the highest amount of CO<sub>2</sub> with an annual cumulative flux of  $8.48 \pm 0.71 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ , compared to  $6.75 \pm 0.79$ ,  $5.98 \pm 0.42$  and  $5.09 \pm 0.47 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  for mature rubber, rubber-tea intercropping, and young rubber, respectively. Additionally, the soil CH<sub>4</sub> uptake was stronger in rainforest than in rubber plantations during the wet period. Soil temperature was the main factor explaining the overall seasonal variation of soil respiration. Adding a quadratic soil moisture term into the model accounted for moisture effects, identified moisture tipping points, and improved temperature sensitivity assessment when high soil moisture suppressed soil respiration under rubber. Temperature sensitivity of soil respiration was higher for rainforest soil compared to rubber plantations,  $Q_{10}$  values were 3.1 for rainforest and 1.7, 2.2 and 2.4 for mature rubber, rubber-tea intercropping and young rubber respectively.

Converting rainforest to rubber plantations tended to reduce soil CO<sub>2</sub> emissions and weakened CH<sub>4</sub> uptake especially during the very wet period. The altered condition of soil aeration under converted land appears to have a pronounced impact on processes of carbon fluxes from the soil and thus mitigates the positive feedback of climate change given the large area of cultivated rubber.

© 2017 Elsevier B.V. All rights reserved.

## 1. Introduction

Soil respiration, emitting greenhouse gas CO<sub>2</sub> into the atmosphere from roots, microbes, and soil fauna, is the second largest terrestrial carbon flux between the ecosystem and atmosphere (Reichstein et al., 2003). Estimates of the annual global soil

respiration in 2008 were  $98 \pm 12 \text{ Pg C}$  (Bond-Lamberty and Thomson, 2010), which was around 10 times that of emissions from fossil fuel combustion and industry with a current CO<sub>2</sub> emission rate of  $9.8 \pm 0.5 \text{ Pg C yr}^{-1}$  (Le Quéré et al., 2015). Methane (CH<sub>4</sub>), with 28–32 times the CO<sub>2</sub> global warming potential (GWP) in a 100-year time horizon (Myhre et al., 2013; Neubauer and Magonigal, 2015) is responsible for about 18% of human-induced radiative forcing. The estimated global emissions of anthropogenic CH<sub>4</sub> was 335 (273–409) Tg CH<sub>4</sub> yr<sup>-1</sup> during 2000–2009, while the soil consumed 32 (26–42) Tg CH<sub>4</sub> yr<sup>-1</sup> during the same period (Ciais et al., 2013). Small changes in the soil carbon flux pathways

\* Corresponding author.

E-mail addresses: [langrong@mail.kib.ac.cn](mailto:langrong@mail.kib.ac.cn) (R. Lang),

[Sergey.Blagodatskiy@uni-hohenheim.de](mailto:Sergey.Blagodatskiy@uni-hohenheim.de) (S. Blagodatsky), [J.Xu@cgiar.org](mailto:J.Xu@cgiar.org) (J. Xu), [Georg.Cadisch@uni-hohenheim.de](mailto:Georg.Cadisch@uni-hohenheim.de) (G. Cadisch).

thus may have a profound impact on the carbon budget and feedback to climate change.

Land use change is the second largest source of human induced greenhouse gas emissions, mainly from deforestation and degradation of forests in the tropics and subtropics (Don et al., 2011). The carbon loss through deforestation and degradation of rainforests was estimated at 0.8 Pg to 1.0 Pg C yr<sup>-1</sup> in the last decades (Baccini et al., 2012; Harris et al., 2012). Southeast Asia is one of the global deforestation hot spots where rubber (*Hevea brasiliensis*) and oil palm (*Elaeis guineensis*) plantations expanded substantially in the past several decades, at the expense of natural forests and shifting agriculture (Kou et al., 2015; Li and Fox, 2012; Wicke et al., 2011). Though 72% of current rubber plantation areas are already located in environmentally marginal zones with low yield (Ahrends et al., 2015), this land use conversion trend is likely to continue with projected increasing demand of natural rubber and oil palm (Warren-Thomas et al., 2015). Xishuangbanna prefecture, Southwestern China is a typical case for rapid rubber expansion in the upper Mekong. Since the first rubber establishment on state farms in the 1950s, the area of rubber plantations has increased from 4.5% of total land area in 1992 to 8.0% in 2002, 22.2% in 2010, and reached 24.2% in 2014 (Chen et al., 2016; Li et al., 2007; Wu et al., 2001; Xu et al., 2014).

Impacts of converting forests into rubber plantations generally leads to carbon losses from decreased living biomass carbon and soil organic carbon (Blagodatsky et al., 2016; de Blécourt et al., 2013; Guillaume et al., 2015; Li et al., 2008). Measuring soil respiration, especially with determination of respiration components, helps understanding how land use change affects the underlying processes and the carbon budgets (Sheng et al., 2010). The impact of land use change on soil respiration and CH<sub>4</sub> exchange has often been assessed by comparing soil carbon fluxes under different land uses (space substitutes time) (Hassler et al., 2015; Sheng et al., 2010). There are some studies measured soil respiration in either rubber plantations or rainforest in the region, but only a few considered both land uses using the same methodology and measuring devices (Fang and Sha, 2006; Hassler et al., 2015; Ishizuka et al., 2002; Lu et al., 2009; Werner et al., 2006). Due to differences in methodology, considerable spatial heterogeneity, strong seasonality and lacking of long term measurements, previous studies showed large discrepancies in soil greenhouse gas (GHG) fluxes under forest and converted plantations.

Regardless of the considerable amount of literature describing the controlling factors of soil respiration, the impact of land use change on soil CO<sub>2</sub> flux has not been well understood particularly in tropical ecosystems (Adachi et al., 2006; Sheng et al., 2010; Veldkamp et al., 2008). Soil CO<sub>2</sub> flux is regulated by factors such as photosynthetic activity or vegetation productivity (Tang et al., 2005), soil properties including substrate quantity and quality (Wan and Luo, 2003), soil temperature and water status (Bolstad and Vose, 2005; Geng et al., 2012; Suseela et al., 2012; Werner et al., 2006), while only soil temperature was extensively used as controlling factor to explain the seasonal variation of soil respiration (Jia et al., 2013; Lloyd and Taylor, 1994; Raich and Schlesinger, 1992; Wood et al., 2013; Zhou et al., 2013). Their relationship is often assessed with temperature sensitivity, expressed as  $Q_{10}$ , a parameter reflecting the respiration rate response to a temperature increase of 10 °C. The Lloyd and Taylor equation (Lloyd and Taylor, 1994) was frequently used in soil respiration studies because of the unbiased estimation across a wide range of ecosystems. Considering the joint effect of soil moisture and temperature on respiration rate, more recent studies are trying to separate these two effects, either by building mathematical functions based on field measurements (Ali et al., 2015; Demyan et al., 2016; Qi and Xu, 2001; Tan et al., 2013; Qi and Xu, 2001; Tan et al., 2013), or manipulating temperature and

moisture in controlled experiments (Jiang et al., 2013; Zimmermann et al., 2015). To our knowledge, no studies on soil respiration under rubber investigated its temperature sensitivity with separating the moisture effect. Therefore, for the SE Asia region, like in Xishuangbanna, China where both temperature and moisture are either high or low during wet versus dry period, analyzing the temperature sensitivity under two land uses helps understanding the response of soil CO<sub>2</sub> flux to land use and climate change.

Upland soils are normally a net sink for atmospheric CH<sub>4</sub>, but current understanding of CH<sub>4</sub> fluxes in upland systems especially in tropical forests is incomplete (Megonigal and Guenther, 2008). Studies on the combined effect of land use change and rubber cultivation on soil CH<sub>4</sub> flux are scarce, compared to soil respiration studies. It is known that the production or consumption of CH<sub>4</sub> depends on the soil water content, soil gas diffusivity and oxygen availability in the soil profile. Whether a soil acts as CH<sub>4</sub> source or sink depends on the balance between methane production and oxidation (Megonigal and Guenther, 2008; Smith et al., 2003; Wood and Silver, 2012). Ammonium fertilizers in cultivated soils can serve as competitive inhibitors for CH<sub>4</sub> oxidation decreasing the methane uptake (Nesbit and Breitenbeck, 1992). Compared to tropical forests, converted plantations showed a reduced CH<sub>4</sub> uptake by soil to a different extent (Hassler et al., 2015; Verchot et al., 2000), being sometimes comparable with uptake in forest (Ishizuka et al., 2005).

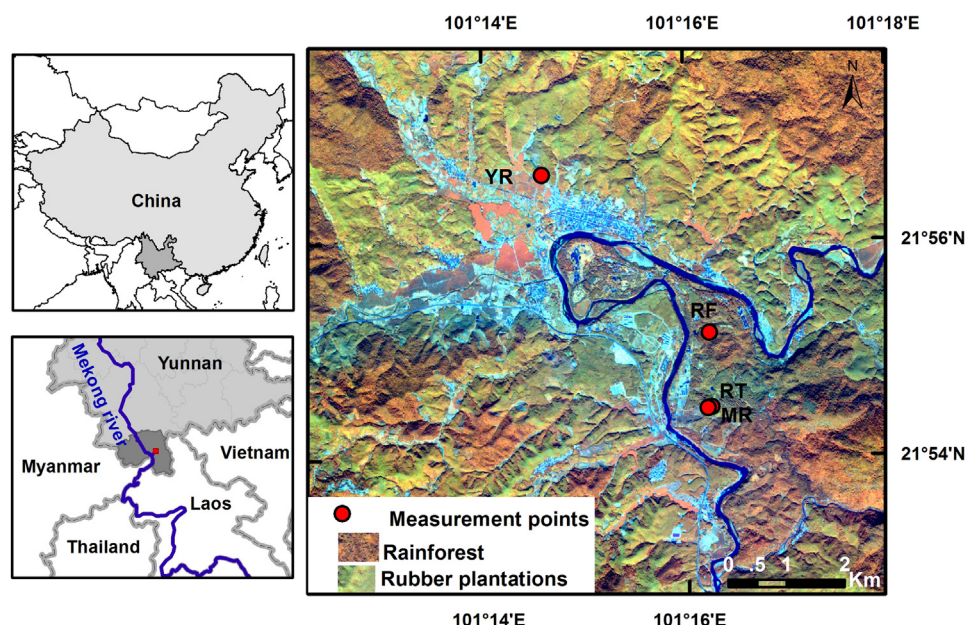
Therefore, this study focused on (1) the temporal dynamics of soil CO<sub>2</sub> fluxes under rainforest and rubber plantations, and CH<sub>4</sub> fluxes estimated during the wet period of the rainy season when the largest differences in CO<sub>2</sub> flux between rainforest and rubber plantations was observed; (2) separating the soil temperature and moisture impact on soil respiration using a linear mixed model; and (3) reviewing of available soil CO<sub>2</sub> and CH<sub>4</sub> fluxes data obtained in rubber plantations and rainforests in Southeast Asia. By comparing both soil CO<sub>2</sub> and CH<sub>4</sub> fluxes under different land uses and corresponding relationships with controlling factors, we aimed to assess the impact of land use change from rainforest to rubber plantation on soil gaseous carbon fluxes.

## 2. Methods

### 2.1. Study sites

The study was carried out in Xishuangbanna prefecture, Yunnan province, SW China. Xishuangbanna is a Dai Ethnic nationality autonomous prefecture, located between 99.94°E – 101.84°E and 21.14°N – 22.59°N, known as the Upper Mekong region (Fig. 1). The prevailing monsoon climate is characterized by strong seasonality, i.e. the tropical southwest monsoon from the Indian Ocean delivers about 80% of annual rainfall from May to October (rainy season), whereas dry, cold air from subtropical regions in the east dominates from November till April (dry season) (Cao et al., 2006). The average annual temperature was 22.26 ± 0.55 °C, and average annual precipitation was 1166 ± 165 mm, of which 987 mm (85%) occurred during May to October (data are from the Jinghong meteorological station, located in 50 km from study sites at altitude 582 m, averaged from 1957 to 2012). Laterite soil, lateritic red soil, and limestone derived soil are the three main soil types in Xishuangbanna, and natural vegetation is dominated by five main types of tropical rainforest according to the formation, community structure and habitat (Zhu, 2006).

We chose four nearby sites along the Luosuo river, a tributary of the Mekong river to conduct soil carbon flux measurements, including tropical rainforest (RF), 22-year-old rubber monoculture (MR) and 22-year-old rubber-tea intercropping (RT) within Xishuangbanna Tropical Botanical Garden, and 9-year-old rubber monoculture (YR) near Menglun town. The rainforest site was



**Fig. 1.** Location of the study sites. Measured sites are rainforest (RF), 22-year-old rubber monoculture (MR), 22-year-old rubber-tea intercropping (RT), and 9-year-old rubber monoculture (YR).

located in a typical habitat for tropical seasonal rainforest covering moist valleys or low hills with altitudes lower than 900 m. Current vegetation was the regrowth from disturbance caused by policy reforms in the 1950s and 1960s (Sayer and Sun, 2003; Xu et al., 2009). The selected tropical seasonal rainforest was dominated by *Terminalia myriocarpa* and *Pometia tomentosa*, characterized by an uneven canopy structure and with a diverse species composition in different layers (Zhang and Cao, 1995). Rubber is typically grown on terraces built during the establishment of the plantation. The spacing between tree rows and inter-row distance of 9-year-old young rubber plantation was 2.5 m and 6.0 m respectively. In 22-year-old rubber monoculture and intercropping, two rows of rubber trees were planted closely with row distance of 2.5 m, followed by 19 m inter-row spacing between another two rows of closely planted rubber trees, tree spacing within a row was 3.1 m. The RT site was located on the upper slope of the MR site, with tea planted only on the spacious inter-row space with no tillage, fertilization and harvest of tea in recent years. MR and RT sites follow the same management for rubber trees, such as applying of mineral fertilizers in April before the rainy season starts and in July during the mid of rainy season. No fertilization was applied at YR site. Location and topographic characteristic of each site are presented in Fig. 1 and Table 1.

## 2.2. Soil surface $\text{CO}_2$ and $\text{CH}_4$ flux measurements

Surface soil  $\text{CO}_2$  efflux was measured with a LCi-SD1000 portable soil respiration system (ADC BioScientific Ltd., UK). This open chamber system calculates the  $\text{CO}_2$  flux from the difference of  $\text{CO}_2$  concentration between soil chamber and ambient air, using an integrated  $\text{CO}_2$  Infrared Gas Analyzer (IRGA). The respiration rate of

each measured soil collar was calculated as an average of 4 continuous recordings when readings started to stabilize. Soil temperature at 5 cm depth was measured by a thermistor sensor coupled to the respiration system, and soil moisture was measured by FieldScout TDR 100 at a depth of 0–12 cm (Spectrum Technologies Inc., US).

We installed 12 soil collars at each site to cover the spatial variation within site. Soil collars were cut from PVC tube with 11 cm diameter and inserted into the soil to 5 cm depth. We considered the reported coefficient of variation of soil respiration and required number of soil collars in rainforest and rubber plantations (Adachi et al., 2005; Song et al., 2013), and calculated the coefficient of variation (45%) from field testing of 20 collars in rubber plantation (unpublished data) to determine the required sample size. The minimum sample size for reliably estimating soil respiration rate within  $\pm 25\%$  of the sample mean at the 95% probability level was 12. Soil collars were laid out in two rows with 5 m distance in between, and 6 collars of each row were installed along the slope with 3 m distance in rainforest, while we slightly adjusted this distance in rubber plantations to cover different locations in a row, including 2 positions on the terrace and 4 positions on the slope between rubber tree rows. Considering the clear seasonal change of temperature and rainfall of the monsoon climate, we measured soil respiration with approximately monthly intervals from November of 2012 to December of 2013.

Based on the first year's observation of contrasting respiration fluxes between rubber plantations and rainforest during the very wet period, we additionally conducted two times  $\text{CO}_2$  and  $\text{CH}_4$  flux measurements on the same sites in late August and September of 2014, using the static closed chamber and Gas Chromatography (GC) method. We installed 3 chambers on each site being 5 cm

**Table 1**  
Sites characteristics.

Site	Rainforest (RF)	22-year-old rubber monoculture (MR)	22-year-old rubber-tea intercropping (RT)	9-year-old rubber monoculture (YR)
Location	21°55'8.7"N 101°16'13.7"E	21°54'27.3"N 101°16'14.5"E	21°54'26.7"N 101°16'12.3"E	21°56'37.1"N 101°14'34.8"E
Elevation (m.a.s.l.)	561	596	611	585
Aspect (degree)	Southwest 220	Southeast 130	Southeast 130	Southwest 225
Slope (degree)	30	17.5	17	31



inserting into the soil, the volume and surface area of the chamber were 42.66 L and 0.20 m<sup>2</sup> respectively. At the MR, YR and RT sites, one chamber was installed on the terrace and two on the slope between tree rows, while the chamber on the long slope at RT site was under tea growth. We sampled 100 mL of headspace air every 15 min during a total 45 min closure time. Gas samples were stored in Multi-layer foil sampling bags (LB-101, Dalian Delin Gas Packing Co., Ltd., CN) and further analyzed for CO<sub>2</sub> and CH<sub>4</sub> concentrations with a gas chromatograph (GC) (HP 6890, Agilent Technologies, Inc., Santa Clara, CA). Soil temperature at 5 cm was recorded by a HOBO Pendant Temperature Data Logger (Onset Computer Corporation, US), soil moisture was measured using a FieldScout TDR 100. Fluxes were calculated from the concentration of four consecutive gas samples taken from each chamber using Eq. (1),

$$R = \frac{1}{V_0} \cdot \frac{P_1}{P_0} \cdot \frac{T_0}{T_1} \cdot \frac{V}{a} \cdot \frac{dc}{dt} \quad (1)$$

where  $R$  is gas flux ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $V_0$  is the gas volume constant with a value of 22.4 L mol<sup>-1</sup>,  $P_0$  is standard atmospheric pressure at sea level,  $P_1$  is atmospheric pressure at sampling site corrected for altitude and temperature effects,  $T_0$  is a constant with value of 273.15 K,  $T_1$  is air temperature in K recorded during the gas sampling,  $V$  is chamber volume in L,  $a$  is the soil surface area covered by the chamber in m<sup>2</sup>,  $dc/dt$  is the regression slope of gas concentration change during closure time. We further converted CH<sub>4</sub> fluxes into hourly mass based fluxes by multiplying the molar mass of carbon in methane and converting seconds into hours.

We calculated water filled pore space (WFPS, %) using Eq. (2),

$$\text{WFPS} = \frac{M}{1 - \frac{BD}{2.65}} \quad (2)$$

Where  $M$  is soil volumetric water content (%),  $BD$  is bulk density of soil at 5–10 cm depth ( $\text{g cm}^{-3}$ ), and  $2.65 \text{ g cm}^{-3}$  is the density of quartz.

### 2.3. Soil sampling and analysis

We sampled soil at 6 points at each site, with sampling depth intervals of 0–15 cm, 15–30 cm, 30–45 cm and 45–60 cm. The 6 samples of the same depth were composited as one sample for rainforest site, and 3 samples taken on the terrace and 3 samples on the inter-row were composited as two samples of rubber plantations for texture (International Society of Soil Science (ISSS) classification: sand >0.2 mm, clay <0.02 mm and silt between 0.02 and 0.2 mm), as well as for total C and total N, cation exchange capacity (CEC) and pH (CaCl<sub>2</sub>) analysis. Bulk density was determined from the weight of the core samples dried at 105 °C, core samples were taken at 6 points to keep consistency with sampling mentioned above. Additionally, we sampled the soil next to the chambers in the second rainy season at 0–5 and 5–10 cm, and composite samples of the same depth from two chambers on the slope as one sample. 2 mm sieved fresh soils were used for NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>-N analysis. Texture (Pipetting method), total C and total N (Vario MAX CN, Elementar Analysensysteme GmbH, DE), CEC (1 mol/L pH 7 ammonium acetate, distillation) and NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>-N (2 mol/L KCl extraction, Auto Analyzer, SEAL Analytical GmbH, UK) were all analyzed at the Central Laboratory in Xishuangbanna Tropical Botanical Garden, for details see (State Forestry Administration, 1999; Pansu and Gauthierou, 2007). Averaged soil properties of study sites are listed in Table 2.

### 2.4. Statistical analysis

Respiration rate, soil temperature and soil moisture of each collar were calculated from four continuous recordings from the

**Table 2**  
Soil properties of the study sites.

Site	Parameters	Depth (cm)	Rainforest (RF)				22-year-old rubber monoculture (MR)				22-year-old rubber-tea intercropping (RT)				9-year-old rubber monoculture (YR)			
			0–15	15–30	30–45	45–60	0–15	15–30	30–45	45–60	0–15	15–30	30–45	45–60	0–15	15–30	30–45	45–60
Texture	Bulk density ( $\text{g cm}^{-3}$ ) <sup>a</sup>	sand	1.02 ± 0.06 <sup>a</sup>	1.08 ± 0.06 <sup>a</sup>	1.16 ± 0.11 <sup>a</sup>	1.15 ± 0.13 <sup>a</sup>	1.07 ± 0.02 <sup>ab</sup>	1.13 ± 0.03 <sup>a</sup>	1.19 ± 0.01 <sup>a</sup>	1.32 ± 0.02 <sup>ab</sup>	1.09 ± 0.06 <sup>ab</sup>	1.16 ± 0.04 <sup>a</sup>	1.15 ± 0.03 <sup>a</sup>	1.18 ± 0.04 <sup>a</sup>	1.22 ± 0.01 <sup>b</sup>	1.28 ± 0.06 <sup>a</sup>	1.38 ± 0.02 <sup>a</sup>	1.43 ± 0.01 <sup>b</sup>
		silt	27	26	20	19	23	22	21	23	21	17	12	12	43	42	43	43
		clay	32	32	32	31	38	38	35	36	35	34	34	32	27	26	25	24
			41	42	48	50	39	40	44	41	44	49	54	56	30	32	32	33
Total C (%)	Total C (%)		2.26	1.2	0.96	0.8	1.7	1.7	1.51	1.19	1.66	1.11	0.86	0.72	1.17	0.83	0.62	0.45
			0.25	0.14	0.12	0.11	0.18	0.18	0.16	0.13	0.17	0.13	0.11	0.1	0.14	0.11	0.09	0.07
Total N (%)	Total N (%)		9.2	8.7	8.3	7.3	9.7	9.4	9.6	9.5	9.6	8.6	8	7.5	8.6	7.7	7.1	6.2
			13.5	12.2	11.9	11.8	14.3	14.7	15.2	14.2	12.9	12.5	12.2	11.6	9.4	9	8.5	9
CEC (cmol(+)kg <sup>-1</sup> )	pH (CaCl <sub>2</sub> )		3.8	3.6	3.5	3.4	4.5	4.5	4.7	4.9	4.1	3.7	3.8	3.8	3.7	3.8	3.8	3.8
			8.7	6.3	n.d.	n.d.	6.2	5–10 cm	n.d.	n.d.	10.5	5–10 cm	n.d.	n.d.	0–5 cm	5–10 cm	n.d.	n.d.
NH <sub>4</sub> <sup>+</sup> -N (mgN kg <sup>-1</sup> )	NO <sub>3</sub> <sup>-</sup> -N (mgN kg <sup>-1</sup> )		13.5	8.8	n.d.	n.d.	3.9	1.7	n.d.	n.d.	3.2	1.5	n.d.	n.d.	2.7	1.2	n.d.	n.d.

n.d.: not determined.

<sup>a</sup> Superscript indicated the significance of difference in mean comparison of bulk density at same depth between sites, values are mean ± standard error calculated from 6 samples.

respiration system and four points moisture measurements respectively. We further calculated cumulative CO<sub>2</sub> flux of each collar using linear interpolation between every two sampling dates and timed number of days in between. We used a one way ANOVA to compare sites for bulk density, cumulative CO<sub>2</sub> flux, and chamber measured CO<sub>2</sub> and CH<sub>4</sub> fluxes and soil moisture in 2014. Site was the factor and significance of difference was tested with Tukey Honest Significant Differences in multi comparison. The average soil temperature and moisture at each site over the measurement period was calculated from all available measurements (some dates had missing values), to account for the missing values and repeated measurement, we chose a mixed effect model and least square means for post-hoc comparison. Statistical analysis were carried out using R version 3.2.5 (R Development Core Team, 2016) with “nlme” and “lsmeans” packages. Figs. 2–5 were created in OriginPro 9.0 (OriginLab, Northampton, MA).

A log transformation was applied to the soil respiration rate to meet the statistical requirements of normality and homogeneity of variance. Relative importance of environmental factors to soil respiration was assessed by a standardized coefficient calculated from a linear mixed effect (LME) model using Eq. (3) (“scale” in the equation means standardization). We studied the relationship between soil respiration rate and controlling factors using LME models (Eq. (4)), where soil temperature and soil moisture were set as fixed effects, and soil collar as a random effect, measuring date was treated as temporal autocorrelation factor to account for repeated measurements of the same subject over time. Treating soil collar as random effect allowed estimating individual intercepts  $a$  for the 12 collars, with common slope value for  $b$ ,  $c$ , and  $d$  at each site. After comparing the models with different combinations of factors, interaction and orders, we excluded the interactions and obtained the final model (Eq. (4)). During the measurement period from November 2012 to December 2013, all measurements of each collar which had both soil moisture and soil temperature values were used in the mixed model with “nlme”

package in R.

$$\text{scale}(\log R) = a' + b' \cdot \text{scale}(T) + c' \cdot \text{scale}(M) \quad (3)$$

$$\log R = a + b \cdot T + c \cdot M + d \cdot (M)^2 \quad (4)$$

where  $T$  is soil temperature in °C,  $M$  is soil volumetric water content in%,  $a'$ ,  $b'$ ,  $c'$ ,  $a$ ,  $b$ ,  $c$  and  $d$  are parameters to be fitted.

We further determined the “tipping point” of soil water content from Eq. (4), where soil respiration rate first increased with temperature but reached a maximum and then decreased with increasing soil moisture (parabolic function). Therefore, the corresponding moisture value for the parabola vertex was calculated as  $-c/2d$ , with  $c$  and  $d$  as fitted parameters in Eq. (4).

## 2.5. Estimation of temperature sensitivity

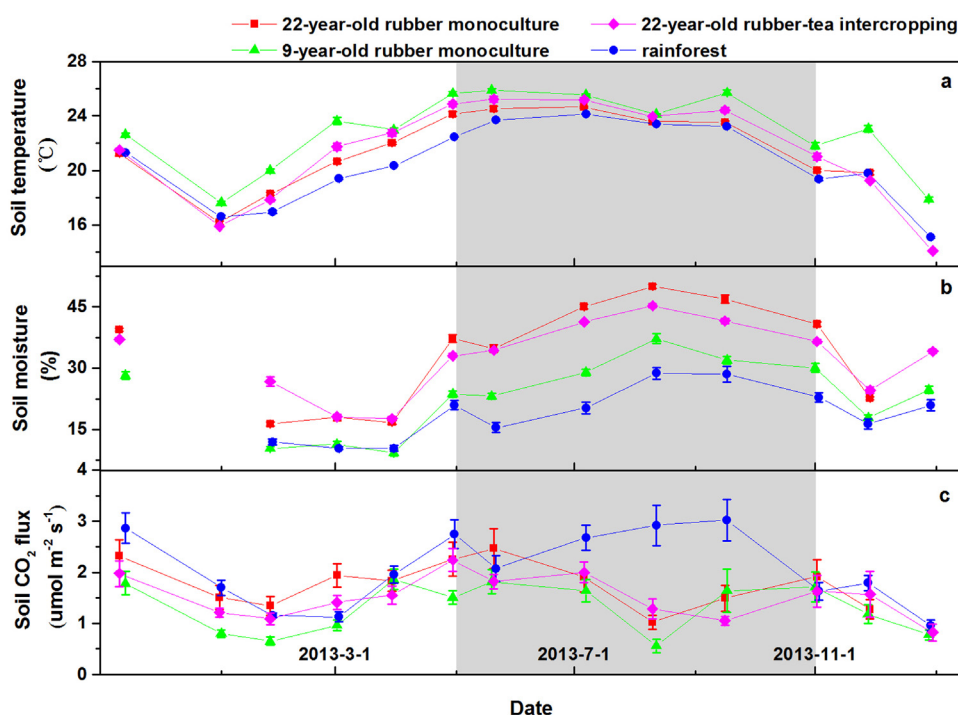
In order to obtain the most adequate function, we applied three different approaches for calculating temperature sensitivity of soil respiration rate, i.e. (1) the commonly used Lloyd-Taylor equation (Lloyd and Taylor, 1994) and (2) a two parameters exponential equation. We further determined temperature sensitivity expressed as  $Q_{10}$  considering the combined effects of soil temperature and soil moisture, using (3) the fitted LME model.

1) The Lloyd-Taylor equation describes the relationship between soil respiration rate ( $R$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and soil temperature ( $T$ , °C) as:

$$R = R_{\text{ref}} \cdot e^{E_0 \left( \frac{1}{T_{\text{ref}} + 273.15 - T_0} - \frac{1}{T + 273.15 - T_0} \right)} \quad (5)$$

where  $E_0$  is 308.56;  $T_0$  is 227.13 K,  $T_{\text{ref}}$  was set to 15 °C,  $R_{\text{ref}}$  is estimated respiration rate at reference temperature  $T_{\text{ref}}$ .  $R_{\text{ref}}$  was fitted separately for each site.

We used the fitted value of  $R_{\text{ref}}$  to calculate soil respiration rate at temperature  $(T + 10)$  (Eq. (6)),  $Q_{10}$  was further calculated with Eq. (7).  $Q_{10}$  of each site was reported as the average of  $Q_{10}$



**Fig. 2.** Dynamics of soil temperature at depth of 5 cm (a), soil volumetric water content at depth of 12 cm (b), and soil surface CO<sub>2</sub> flux rate (c). (Error bar is  $\pm 1$  standard error of 12 measurements, shaded area represents rainy season).

determined from all measured soil temperatures.

$$R_{T+10} = R_{ref} \cdot e^{\frac{E_0}{R} \left( \frac{1}{T_{ref}+273.15-T_0} - \frac{1}{T+10+273.15-T_0} \right)} \quad (6)$$

$$Q_{10} = \frac{R_{T+10}}{R} \quad (7)$$

2) We also estimated  $Q_{10}$  with the two parameter exponential equation using fitted parameter  $b$  according to Eqs. (8) and (9):

$$R = a \cdot e^{b \cdot T} \quad (8)$$

$$Q_{10} = e^{10 \cdot b} \quad (9)$$

In Eqs. (8) and (9),  $T$  is soil temperature in °C,  $a$  and  $b$  are fitted parameters.

3) Taking soil moisture into account, we calculated the soil respiration rate at measured temperatures (Eq. (11)), as well as after a temperature rise by 10 °C from the back transformation of the LME models (Eqs. (10), (12)).  $Q_{10}$  was then determined using Eq. (13).

$$\log R_{T+10} = a + b \cdot (T + 10) + c \cdot M + d \cdot M^2 \quad (10)$$

$$R = e^{a+b \cdot T+c \cdot M+d \cdot M^2} \quad (11)$$

$$R_{T+10} = e^{a+b \cdot (T+10)+c \cdot M+d \cdot M^2} \quad (12)$$

$$Q_{10} = \frac{R_{T+10}}{R} = e^{10 \cdot b} \quad (13)$$

Where  $T$  is soil temperature in °C,  $M$  is volumetric soil moisture in%,  $R$  is predicted respiration rate,  $R_{T+10}$  is predicted respiration rate by increasing temperature 10 °C, and  $a$ ,  $b$ ,  $c$ ,  $d$  are parameters fitted from LME model (Eq. (4)).  $b$  is fitted slope value for soil temperature, and the associated standard error of parameter  $b$  was used to determine the error of  $Q_{10}$  considering the error propagation in the back transformation.

### 3. Results

#### 3.1. Dynamics of soil respiration and $CH_4$ flux during wet period

All sites showed a very similar annual pattern of soil temperature (Fig. 2a) being lowest in January during the dry season, and gradually increasing until June in the early rainy season. Soil temperature at RF site was slightly lower than at other sites, but there was no significant statistical difference between sites (Table 3). Soil moisture patterns (Fig. 2b) exhibited similar trends but differed in the range between sites with average soil moisture at the RF site being significantly ( $p < 0.05$ ) lower than at MR and RT sites (Table 3). The range of soil moisture (maximum – minimum) at the RF site was lower than at the other sites, with a value of 28% compared with 41%, 33%, and 40% at MR, RT and PR sites respectively.

**Table 3**

Average and standard error of soil temperature at 5 cm depth, soil moisture at 12 cm depth, water filled pore space (WFPS), soil respiration rate (Ismeans comparison) and cumulative soil surface  $CO_2$  flux (Tukey HSD).

Site	Soil temperature (°C)	Soil moisture (%)	WFPS (%)	Soil respiration ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Cumulative $CO_2$ flux ( $\text{MgCha}^{-1} \text{year}^{-1}$ )
Rainforest (RF)	20.4 ± 0.2	18.8 ± 0.6 <sup>a</sup>	30.5 ± 1.0 <sup>a</sup>	2.0 ± 0.1 <sup>a</sup>	8.48 ± 0.71 <sup>a</sup>
22-year-old rubber monoculture (MR)	21.6 ± 0.2	33.4 ± 1.1 <sup>b</sup>	56.6 ± 1.9 <sup>b</sup>	1.8 ± 0.1 <sup>ab</sup>	6.75 ± 0.79 <sup>ab</sup>
22-year-old rubber-tea intercropping (RT)	21.4 ± 0.3	32.5 ± 0.7 <sup>b</sup>	54.6 ± 1.3 <sup>b</sup>	1.5 ± 0.1 <sup>ab</sup>	5.98 ± 0.42 <sup>b</sup>
9-year-old rubber monoculture (YR)	22.8 ± 0.2	23.0 ± 0.8 <sup>ab</sup>	42.7 ± 1.4 <sup>ab</sup>	1.3 ± 0.1 <sup>b</sup>	5.09 ± 0.47 <sup>b</sup>

<sup>a</sup>: different letters in superscript indicate significant difference at  $\alpha=0.05$  level.

Soil respiration rate at the RF site strongly differed from rubber sites during the wet period from July to September. During this wet period, soil respiration maintained a high rate at RF site while it was suppressed at rubber sites (Fig. 2c), thus showing dual peaks in annual dynamics. All sites showed low soil respiration rate in February and March during dry season, when rubber plantations completely shed leaves. Average soil respiration rate and cumulative  $CO_2$  flux at RF site were higher than those at all rubber sites (Table 3).

Soil respiration rate and moisture measured in 2014 consistently differed between sites during wet period (Fig. 3a and c). Negative  $CH_4$  fluxes at RF site at both sampling times indicated the important role of forest as a  $CH_4$  sink (Fig. 3b). In contrast, MR and YR exhibited positive  $CH_4$  fluxes at both sampling dates, while those under RT did not differ significantly from zero. However, there was no significant difference ( $p < 0.05$ ) between RF and rubber sites for  $CH_4$  fluxes due to the relatively large variation.

#### 3.2. Relative influence of environmental factors (proximal controllers) on soil respiration

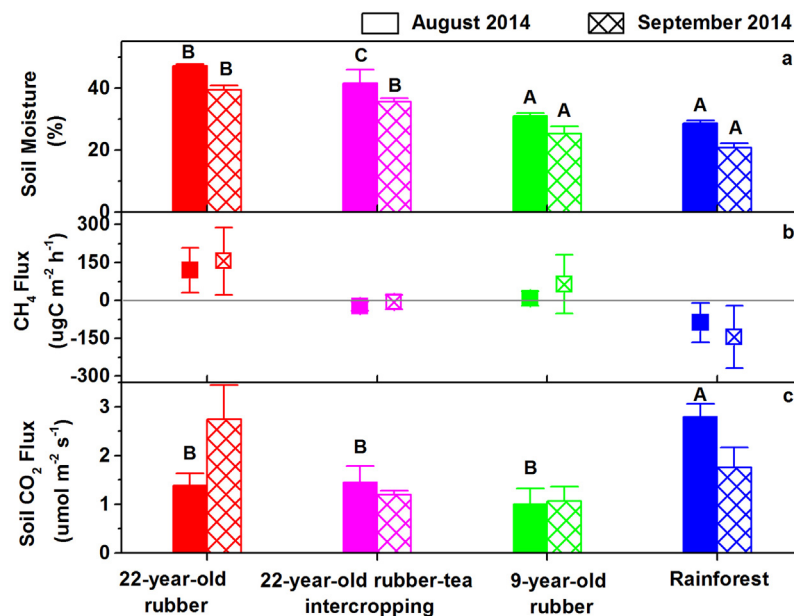
The relative importance of a single environmental factor effect on soil respiration rate was indicated by the standardized coefficient (beta coefficient) derived from Eq. (3). Soil temperature was relatively more important than moisture in explaining the temporal variation of soil respiration rate over a year (Table 4). Different from the positive coefficient at RF site, the coefficients of soil moisture were negative at rubber sites. All standardized coefficients of soil temperature were significant at  $\alpha=0.05$  level, while the corresponding coefficient of soil moisture was significant only at RF site.

According to the relative importance of environmental factors, the addition of the soil moisture variable in quadratic form improved model fit as compared to relationship considering temperature and moisture dependence described by first order relationship (i.e. Eq. (4) vs Eq. (3)). Estimated coefficients, standard errors and the fitting of the LME models with log transformed soil respiration are shown in Table 5. Reported intercept  $a$  in the table was the average of intercepts from 12 collars at each site. All estimated coefficients of the three predictors were significant at the 0.05 level. Soil respiration was positively related to both soil temperature and soil moisture in the first order, but negatively linked with the quadratic term of soil moisture.

The soil respiration tipping points caused by moisture change (see parameters in Table 5), occurred at volumetric water contents of 23.7%, 30.3%, 27.6% and 20.4% for RF, MR, RT and YR sites respectively, corresponding to 38.4%, 51.6%, 45.7% and 37.8% WFPS.

#### 3.3. Effects of soil properties on gaseous carbon fluxes

Soils in rubber plantations had higher bulk density than rainforest at all four sampling depths up to 60 cm (Table 2). However, only bulk density at YR site at depth of 0–15 and 45–60 cm were significantly higher ( $p < 0.05$ ) than those at RF site. All the soils had high clay contents and belong to either the light clay



**Fig. 3.** Soil CO<sub>2</sub> and CH<sub>4</sub> flux measured by static chamber method in rainy season 2014 (different letter indicates significant difference in mean comparison of sites in August and September respectively).

**Table 4**

Standardized coefficient of predictors of soil respiration rate (log transformed) in linear mixed effect model Eq. (3).

Fixed effect	Rainforest (RF)	22-year-old rubber monoculture (MR)	22-year-old rubber-tea intercropping (RT)	9-year-old rubber monoculture (YR)
Soil temperature (T) <i>b</i> *	0.62 ± 0.05*	0.21 ± 0.10*	0.45 ± 0.07*	0.34 ± 0.08*
Soil moisture (M) <i>c</i> *	0.13 ± 0.06*	−0.06 ± 0.10	−0.10 ± 0.07	−0.10 ± 0.08
N	131	131	142	143

\* Significant at  $\alpha = 0.05$  level.

or high clay class according to the International Society of Soil Science (ISSS) texture classification. Compared to the relatively more sandy texture (42–43% sand and 30–33% clay) at YR site, rainforest RF site had similar texture to MR and RT sites. All sites had acidic soils, with low pH (CaCl<sub>2</sub>) ranging from 3.4 to 4.9 (Table 2).

The total C and total N content of topsoil (0–15 cm) decreased in the order of RF, MR, RT, and YR. Both total C and N contents decreased with soil depth at all sites, with the most distinct decrease occurring in subsoil of rainforest. A slightly lower clay content, highest bulk density and lowest total C and N content in topsoil on YR site corresponded to the lowest soil CO<sub>2</sub> flux. Significant correlation between cumulative soil CO<sub>2</sub> fluxes and total C in topsoil (correlation coefficient  $r^2 = 0.98$ ) suggested that total C content mainly determined the annual soil CO<sub>2</sub> fluxes. Soil C:N ratios were below 10 for all sites, indicating no N limitation for mineralization at the current organic carbon level.

The dominant mineral N form in surface soil differed between rainforest and all rubber plantation sites in August 2014. NH<sub>4</sub><sup>+</sup>-N

was the dominant N form at all rubber sites, while rainforest site with a similar NH<sub>4</sub><sup>+</sup>-N content as rubber sites had larger amounts of NO<sub>3</sub><sup>−</sup>-N than NH<sub>4</sub><sup>+</sup>-N (Table 2). Though the highest CH<sub>4</sub> uptake rate took place at rainforest site where total N and NO<sub>3</sub><sup>−</sup>-N were highest in the topsoil, we did not observe significant correlations between CH<sub>4</sub> flux and total N or mineral N at the four sites.

### 3.4. Temperature sensitivity – $Q_{10}$

$Q_{10}$  values determined from Lloyd and Taylor equation were similar for all sites when  $T_{ref} = 15^\circ\text{C}$ , but varied largely between sites when the two parameter exponential function or the LME model were used (Table 6). However, the fit of Lloyd and Taylor equation and the two parameter function were very poor in terms of coefficient of determination ( $R^2$ ), i.e. the highest  $R^2$  was only 0.31. Adding a soil moisture variable into the log transformed LME model substantially improved the model fit ( $R^2$  ranging from 0.40 to 0.75).  $Q_{10}$  derived by the LME model was higher at rainforest site (3.1) than the other three rubber sites (1.7–2.3).

**Table 5**

Parameters of linear mixed effect (LME) model with log transformed soil respiration rate (Eq. (4):  $\log R = a + b \cdot T + c \cdot M + d \cdot (M)^2$ ).

Parameters	Rainforest (RF)	22-year-old rubber monoculture (MR)	22-year-old rubber-tea intercropping (RT)	9-year-old rubber monoculture (YR)
Intercept <i>a</i>	−2.361 ± 0.255	−1.697 ± 0.591	−2.330 ± 0.503	−2.481 ± 0.474
Soil temperature (T) <i>b</i>	0.113 ± 0.009*	0.055 ± 0.026*	0.080 ± 0.011*	0.085 ± 0.019*
Soil moisture (M) <i>c</i>	0.057 ± 0.018*	0.073 ± 0.024*	0.075 ± 0.027*	0.076 ± 0.023*
Quadratic Moisture (M <sup>2</sup> ) <i>d</i>	−0.001 ± 0.000*	−0.001 ± 0.000*	−0.001 ± 0.000*	−0.002 ± 0.000*
N	131	131	142	143
DF	116	116	127	128
R <sup>2</sup>	0.75	0.52	0.53	0.40

\* Significant at  $\alpha = 0.05$  level.



**Table 6**Temperature sensitivity  $Q_{10}$  derived from three functions (see Eqs. (5)–(13)).

Function/site	$Q_{10}$			
	Rainforest (RF)	22-year-old rubber monoculture (MR)	22-year-old rubber-tea intercropping (RT)	9-year-old rubber monoculture (YR)
Lloyd & Taylor function	$1.84 \pm 0.00$	$1.81 \pm 0.00$	$1.82 \pm 0.00$	$1.77 \pm 0.00$
Two parameter exponential	$2.87 \pm 0.41$	$1.42 \pm 0.26$	$1.60 \pm 0.21$	$2.27 \pm 0.48$
Linear mixed effect model	$3.11 \pm 0.28$	$1.73 \pm 0.45$	$2.23 \pm 0.24$	$2.32 \pm 0.44$

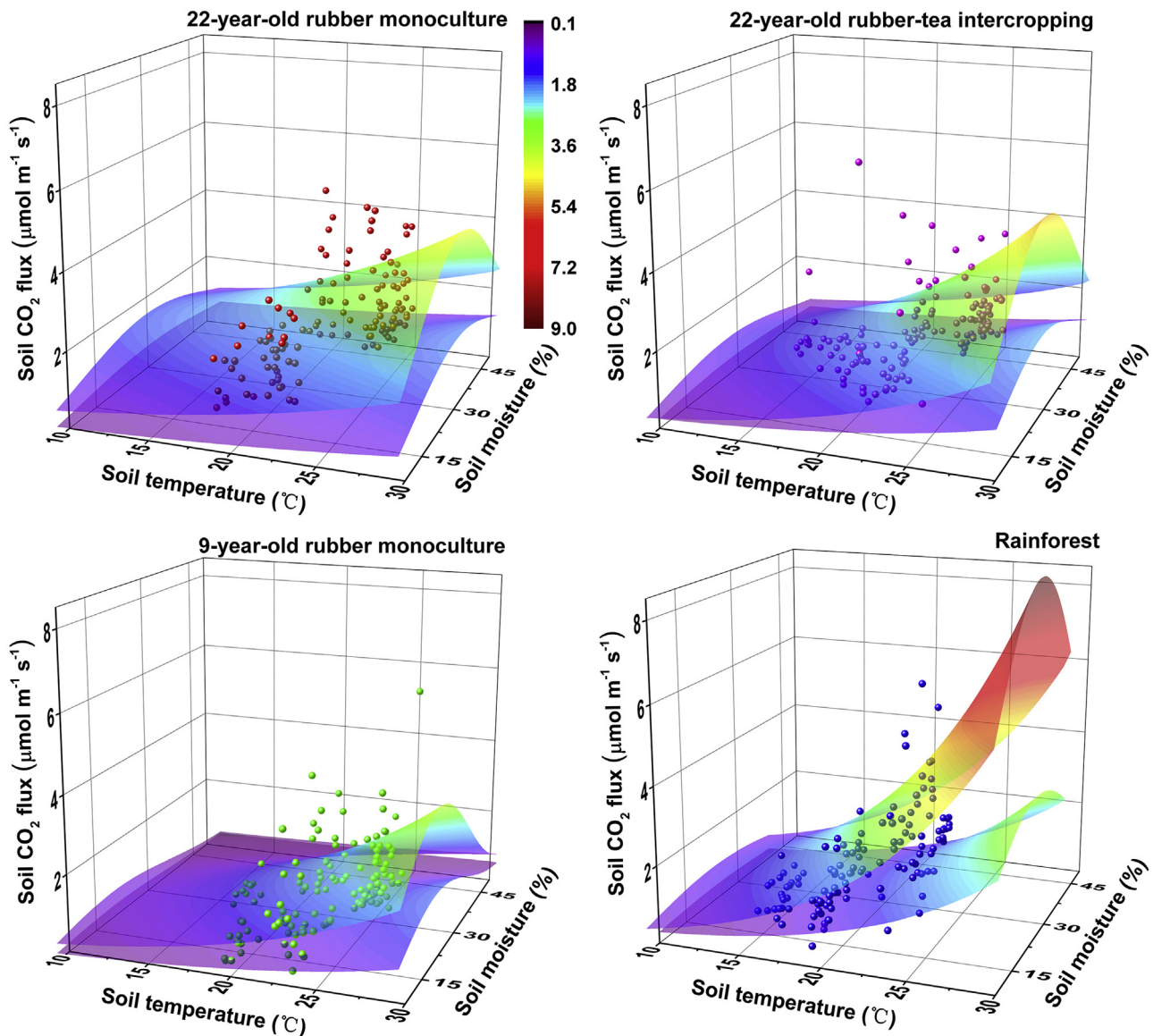
We back transformed the LME model (Eq. (11)) and plotted results demonstrate how soil moisture modifies the response of soil respiration rate to temperature change (Fig. 4). The two response surfaces represent the back transformed model predictions of maximum and minimum soil respiration within each site, according to estimated maximum and minimum intercepts (“ $a$ ” in Eq. (4)). Thus, the space between two plotted surfaces indicated the large spatial variation within each site. A more flat surface in soil moisture axis direction at RF site means that soil moisture had a less profound effect on respiration rate as compared to rubber plantation sites. The steeper slope in soil temperature axis direction

at RF site represented higher temperature sensitivity in rainforest compared to rubber plantation sites (Fig. 4).

#### 4. Discussion

##### 4.1. Decline of soil respiration in rubber plantations during rainy season

Our observations of the presence of dual soil respiration peaks under rubber plantations in contrast to the rainforest site suggested that the land use change from forest to rubber had a



**Fig. 4.** Soil temperature and moisture effect on surface soil  $\text{CO}_2$  flux (Simulated 3-D surfaces are back transformations of linear mixed effect (LME) model (Eq. (11)), with maximum and minimum intercept  $a$ ). Points are field measurements.



major impact on wet seasonal patterns of soil respiration. With the help of the linear mixed effect (LME) model we were able to separate temperature and soil moisture effects on soil respiration and thus could demonstrate that the different soil water regimes in the two land use types mainly explained the different soil respiration patterns during the wet period (Fig. 4). The rainy season of the tropical monsoon climate at our study sites is characterized by high temperature and intensive rainfall. Hence, excessive soil water facilitated by heavy soil texture could alter the biophysical and biochemical conditions of soils. For example, short periods of high moisture after rainfall reduced soil CO<sub>2</sub> flux by filling pores of topsoil with water, creating a barrier and inhibiting CO<sub>2</sub> diffusion out of soil (Sotta et al., 2004). Furthermore, persistent moist conditions in combination with high clay content can reduce O<sub>2</sub> availability in the soil, which would limit the aerobic respiration and decrease the CO<sub>2</sub> flux (Silver et al., 1999).

The suppression of soil respiration by high moisture in tropical rainforests has sometimes been reported as a univariate quadratic function of soil moisture (Schwendenmann et al., 2003; Sha et al., 2005). Using our novel linear mixed effect (LME) model we describe soil moisture as a modifier of temperature effect on respiration rate (Fig. 4): soil temperature drove the seasonal variation, while the initial positive effect of soil moisture on soil respiration declined when it was over the tipping point. Thus, comparing the estimated tipping point of soil water content and observed ranges of moisture during the wet period indicated that persistent high soil moisture was the major factor responsible for the observed decline of soil respiration in rubber plantations. Our estimated soil moisture tipping point for soil respiration at RF site was similar to the 38% WPFS defined as upper limit for positive soil moisture effects for lowland rainforest (Koehler et al., 2009), and slightly lower than estimates of Zhang et al. (2015) and Sha et al. (2005) for upland rainforests in Xishuangbanna. MR and RT sites exhibited high soil moisture contents (>40%) exceeding the estimated tipping points from July to September. These persistent moist conditions inhibited aerobic respiration and resulted in decreased CO<sub>2</sub> fluxes when temperature was high. Similar to Wood et al. (2013), the more sandy YR site showed a lower optimal moisture value compared with clay soil sites.

We showed that soil temperature is driving seasonal soil respiration variation, while intra-seasonal soil moisture variation determines the degree of suppression of soil respiration once a tipping point has been reached. Consideration of this dual temperature and moisture impact advances our understanding of the conflicting results on soil respiration in tropical forests and plantations observed in the literature. Hence, in other studies conducted in Xishuangbanna and Hainan, temporal patterns of soil respiration differed in the rainy season, depending on the duration of period with high soil moisture and amount of rainfall. For example, from July to September, soil respiration was suppressed when moisture was consistently above 30% in rainforest and rubber plantation (Fang and Sha, 2006) or higher than 0.4 m<sup>3</sup> m<sup>-3</sup> in rainforest (Fang et al., 2010). In contrast, heavy rainfall events only decreased soil respiration temporally with soil moisture fluctuating between 25 and 35% in well drained forests (Zhou et al., 2013). The single peak pattern of soil respiration observed by Zhang et al. (2015) in rainforest was likely due to consequent limitation of soil respiration by high soil moisture (higher than tipping point) and decreasing soil temperature in late rainy season. Similar to our estimation of a lower critical moisture level in the more sandy soil at YR site, Satakhun et al. (2013) observed a suppression of soil respiration at intermediate soil moisture levels (~20–30%) in a rubber plantation on a sandy soil in Thailand. Studies in the humid tropics of Sumatra showed no apparent seasonal dynamic due to small temperature change and the variation of soil respiration was mainly driven by periodic changes

in soil water content (Hassler et al., 2015; Ishizuka et al., 2005). Concluding, the appearance of plateau or double peak in temporal dynamics of soil respiration in tropics depends on combination of soil temperature and moisture effects: at moisture contents higher than the tipping point combined with high temperature, soil respiration is suppressed and critical moisture values depend, in turn, on soil properties controlling diffusivity, e.g. bulk density or clay content (Moyano et al., 2013).

#### 4.2. Soil CH<sub>4</sub> flux during the wet period

The observed contrast of rainforest soils acting as CH<sub>4</sub> sink while becoming a weaker sink or even CH<sub>4</sub> source under rubber plantations during the wet period indicates that intensive rubber cultivation might weaken the CH<sub>4</sub> uptake function by the soil. We speculated that the high soil moisture in rubber plantations changed aeration and limited methane oxidation during the wet period. This is coincident with watering experiments conducted by Werner et al. (2006), where the CH<sub>4</sub> flux was negatively correlated to WFPS and the relative decline of CH<sub>4</sub> uptake was larger under rubber plantations compared to rainforest. Fang et al. (2010) observed a steady increment of CH<sub>4</sub> fluxes from January to September under rainforest, and where months with soil moisture around 0.4 m<sup>3</sup> m<sup>-3</sup> resulted in net CH<sub>4</sub> emission during the rainy season (1.18 ± 1.64 kg CH<sub>4</sub> ha<sup>-1</sup> season<sup>-1</sup>). In Sumatra, rubber plantations consumed less CH<sub>4</sub> by soil than forest in the dry season (Ishizuka et al., 2005). However, this was not always the case and became site dependent during the wet season, when reference forest soils can be a stronger CH<sub>4</sub> sink or stronger CH<sub>4</sub> source compared to rubber plantations (Hassler et al., 2015; Ishizuka et al., 2002).

Interaction with soil mineral nitrogen also modulates the CH<sub>4</sub> processes in the soil. Increased NH<sub>4</sub><sup>+</sup>-N, directly or indirectly through fertilization, has been demonstrated having a competitive inhibitory effect on CH<sub>4</sub> oxidation, and substantially reduced CH<sub>4</sub> oxidation potential in cultivated soils (Bodelier and Laanbroek, 2004; Le Mer and Roger, 2001; Nesbit and Breitenbeck, 1992). Comparing with well aerated forest soils with NO<sub>3</sub><sup>-</sup>-N as dominant mineral N form, the high NH<sub>4</sub><sup>+</sup>-N in soils of rubber plantations, as in our study, is likely to inhibit CH<sub>4</sub> oxidation potential under aerobic conditions, and shift towards CH<sub>4</sub> production when O<sub>2</sub> availability becomes limited under anaerobic conditions. Furthermore, even when forest soils are shortly under anaerobic conditions, methanogens are not favored in competing for electrons with nitrate, ferric iron and sulphate reducers (Chidthaisong and Conrad, 2000), therefore, in presence of high nitrate concentrations the forest soils is less likely to have high CH<sub>4</sub> production comparable to rubber plantations under wet condition.

The differences in temporal patterns of soil CO<sub>2</sub> and CH<sub>4</sub> fluxes between rainforest and rubber plantation suggested that land conversion modified soil properties, which in turn led to differences in soil water regime especially during the wet period of the rainy season. There are currently no CH<sub>4</sub> studies for rubber worldwide, except those reported in Sumatra. Given the extent of land use conversion to rubber and the importance of CH<sub>4</sub> on climate change, further studies are needed. Our short measurements of CH<sub>4</sub> flux and the scarce studies on tropical upland soils are not enough to fully verify the changes of mechanism in soil CH<sub>4</sub> processes after forest conversion into rubber plantations.

#### 4.3. Temperature sensitivity Q<sub>10</sub>

In most studies Q<sub>10</sub> values for rainforest and rubber plantations derived from the two parameter exponential function did not differ much for these two land use types (Table A1). Only Lu et al. (2009) reported Q<sub>10</sub> values similar to those obtained in our study (Table 6),

i.e. rainforest had a  $Q_{10}$  around 3 and rubber plantation was around 1.5. Higher  $Q_{10}$  values derived from the function including moisture effects as compared to the temperature only function reflect the fact that responses of soil respiration rate to high soil temperature during the rainy season were masked by high moisture as discussed above. Thus, excluding the moisture effect during temperature sensitivity estimation may result in the underestimation of  $Q_{10}$  values.

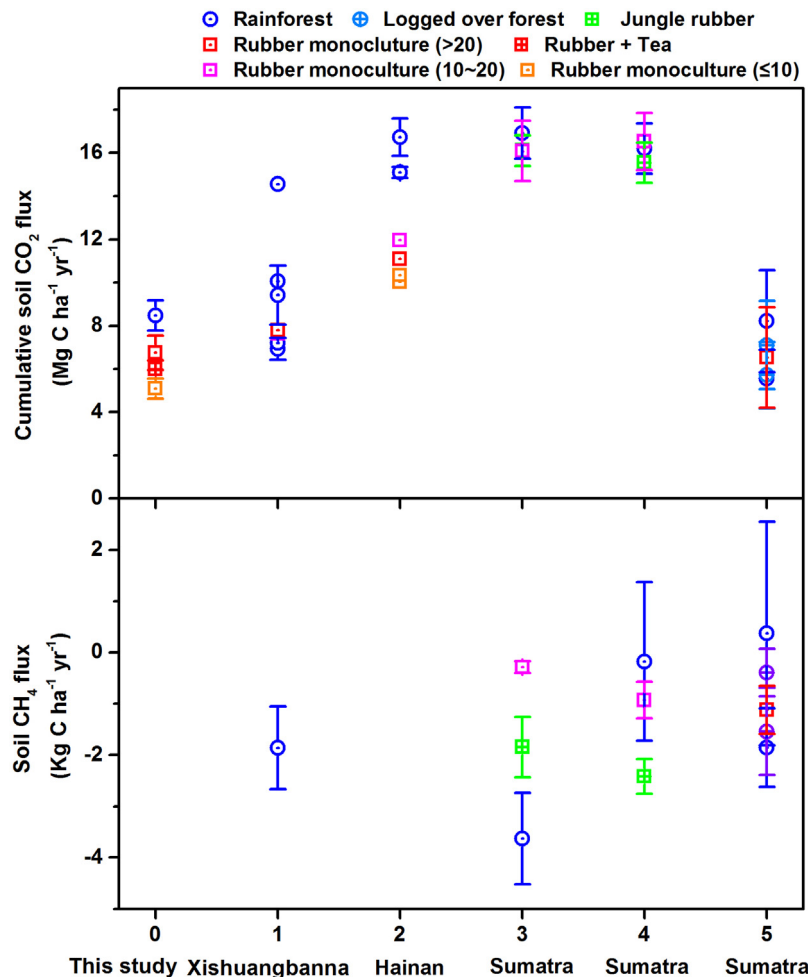
The intrinsic temperature sensitivity is controlled by ambient temperature and substrate. The physical and chemical protection of soil organic matter could constraint the substrate availability, often showing that temperature sensitivity under field conditions is less than theoretically predicted (Davidson and Janssens, 2006). Vegetation type modifies the microclimate and structure of the soil, quantity and quality of detritus supply to the soil (Raich and Tufekciogul, 2000). The environmental constraints such as soil water content (controlling the oxygen supply) also change the decomposition of organic matter in mineral soil (Davidson and Janssens, 2006) and as shown in our study. The soil temperature at our rainforest site was slightly lower but not significantly different compared to rubber sites. The decomposition of rubber leaves was faster than leaves from rainforest due to their different litter qualities (Ren et al., 1999). Therefore, the litter quality change cannot be taken as explanatory factor for the observed  $Q_{10}$  variation in our case.  $Q_{10}$  tended to increase with soil water content until reaching a threshold (optimum moisture content) and decline

after the threshold (Wang et al., 2006). Therefore, the difference in  $Q_{10}$  between rainforest and rubber plantations is likely caused by environmental constraints: high soil water content limiting the oxygen availability for aerobic decomposition.

The LME modeling approach used in this study allowed us to determine the temperature sensitivity *per se* separated from moisture effects. Jia et al. (2013) postulated that a fixed  $Q_{10}$ , derived from annual data, was adequate and more suitable in modeling annual carbon budgets across large spatial scales than seasonally varying, environmentally controlled  $Q_{10}$ . We, therefore, determined annual temperature sensitivity instead of seasonally varying  $Q_{10}$ . Thus, our approach is an advance to those studying temperature and moisture response separately and gives the possibility to calculate the  $Q_{10}$  based on the entire annual data record without separation of dry and rainy seasons as was done e.g. by Wu et al. (2014) (Table A1). The observed higher soil temperature sensitivity under rainforest indicated that soil  $\text{CO}_2$  emitted from rainforest is likely to increase more than that emitted from rubber plantations in response to a warming climate.

#### 4.4. Land use change impact on soil gaseous carbon fluxes

We summarized our measurements and previously published annual soil  $\text{CO}_2$  fluxes and  $\text{CH}_4$  fluxes of tropical rainforests and rubber plantations in the main rubber growing region of Southeast Asia in Fig. 5 and Table A1. Data based on short period



**Fig. 5.** Soil  $\text{CO}_2$  and  $\text{CH}_4$  fluxes in rubber plantations and forests in the study region. Studies in group 1-Xishuangbanna include Sha et al. (2005), Fang et al. (2010), Zhang et al. (2015), Fang and Sha (2006) and Lu et al. (2009), group 2-Hainan referred to Zhou et al. (2013) and Wu et al. (2014), group 3 and 4 were for clay Acrisol and loam Acrisol site in Sumatra by Hassler et al. (2015), and group 5 was from Ishizuka et al. (2002). More details can be found in Table A1.

measurements were excluded to avoid determining the annual flux from single time point or seasonal measurements. Annual soil CO<sub>2</sub> fluxes increased with the mean annual temperature and annual precipitation from Xishuangbanna, the northern edge of tropical Southeast Asia, to the humid tropics in Sumatra (Fig. 5), except for the data from Ishizuka et al. (2002) showing low soil CO<sub>2</sub> emissions in Sumatra.

The annual soil CO<sub>2</sub> flux in this study was in the lower range of reported values in Southeast Asia. Meanwhile, the observed difference between soil CO<sub>2</sub> emissions under rainforest and rubber plantations was of the same order, as found in Hainan (Wu et al., 2014; Zhou et al., 2013) and on clay Acrisols in Indonesia (Hassler et al., 2015); the difference became smaller in mature rubber plantations (Fig. 5, Table A1). Soil CH<sub>4</sub> fluxes were characterized by large spatial and temporal variation. If annual soil CH<sub>4</sub> fluxes in the region are considered, only the clay Acrisols site by Hassler et al. (2015) showed consistently lower CH<sub>4</sub> consumption rates by soils under rubber monoculture compared to soils under jungle rubber and rainforests (Fig. 5).

Land conversion from forest to rubber plantation affects soil CO<sub>2</sub> and CH<sub>4</sub> gaseous exchange in different ways. The change of carbon inputs from aboveground litterfall is one of the reasons responsible for differences in respiration rate in rubber plantations and forests. Annual aboveground litterfall production in rainforests in Xishuangbanna and Sumatra ranged from 8.42 Mg ha<sup>-1</sup> to 12.96 Mg ha<sup>-1</sup> (Kotowska et al., 2016; Ren et al., 1999; Tang et al., 2010). In contrast, the amount of litterfall was quite small during the early growth phase of rubber. Chronosequence studies showed that it took about 9–10 years to reach the maximum of litter production (6–10 Mg ha<sup>-1</sup>) in rubber plantations (Mandal and Islam, 2008; Satakhun et al., 2013). de Blécourt et al. (2013) found that organic carbon in the topsoil exponentially declined till reaching a steady state around 20 years after converting secondary forest into rubber plantations. This dynamic of litterfall production and soil carbon explains the low soil respiration in young rubber monocultures (incl. our observations), and comparable emission of CO<sub>2</sub> in older plantations when the amount of soil organic carbon stabilized or recovered to similar levels as under forest. Management practices, such as weeding and applying herbicide, leave the understorey with sparse vegetation, which also reduce soil CO<sub>2</sub> emission under young plantations. Looking at the contribution of autotrophic and heterotrophic respiration components (Ferréa et al., 2012) and the stability of soil organic matter in chronosequence of land use change will further help understanding the dynamics of soil CO<sub>2</sub> flux and carbon stock.

Another factor controlling seasonal dynamics of soil respiration and overall CH<sub>4</sub> uptake is soil water regime differing between natural forest and intensively managed rubber plantations. Removal of topsoil during terrace establishment and intensive management practices, including tapping and collecting latex tended to compact the soil under rubber plantations, which affects the gas diffusion and water infiltration process in the soil. As a measure to preserve water and nutrients, the terraces were built tilted to the slope. The observed appearance of standing water on the terraces during the very wet period indicated periodical anaerobic conditions, which are likely to suppress soil respiration and favor CH<sub>4</sub> production in rubber plantations.

The impact of converting forest into rubber plantation on soil CH<sub>4</sub> consumption is insufficiently studied and poorly understood. Existing literature on CH<sub>4</sub> consumption by soils under forest or rubber plantations is scarce comparing with large amounts of publications on rice fields and wetlands. In addition to the observed differences in soil aeration in the two land uses and possible mineral nitrogen interaction with CH<sub>4</sub> processes, more frequent measurement and information on substrates, vertical gas concentration gradient and δ<sup>13</sup>CH<sub>4</sub> signature in the soil profile would help understanding the dominant processes and their strength at certain depths of soil (Ishizuka et al., 2002; Preuss et al., 2013). Our study showed a typical case of land use change impact on soil gaseous carbon fluxes. Verifying our observations at larger scale requires real spatial replicates at landscape level and a sufficient number of replicates within site (as done here) to account for the large heterogeneity (Adachi et al., 2005; Song et al., 2013). Furthermore, comparability of chosen references and converted land uses in a chronosequence is also critical in such an assessment (Veldkamp et al., 2008).

Though the uptake of CH<sub>4</sub> by soil was two orders of magnitude lower than the soil CO<sub>2</sub> flux even when their GWP is considered (Fang et al., 2010; Hassler et al., 2015), CH<sub>4</sub> sink function is an important ecosystem service to mitigate GHG emission. From this point of view, it is necessary to link soil carbon turnover with comprehensive assessment of change in ecosystem functions induced by land use change, rather than a simple comparison of the carbon balance in different ecosystems.

## 5. Conclusion

Converting rainforest to rubber plantations tended to reduce soil CO<sub>2</sub> emissions and weakened CH<sub>4</sub> uptake especially during the very wet period. Different soil aeration conditions were likely the main reason for suppression of soil respiration and low CH<sub>4</sub> consumption in rubber plantations during the wet period. High soil water content decreased the temperature sensitivity and partly masked the response of respiration to increasing temperature in all three rubber plantation sites compared to the well aerated rainforest soil. The altered condition of soil aeration under converted land may have a pronounced impact on processes of carbon fluxes from the soil and thus mitigates the positive feedback of climate change given the large area of cultivated rubber.

## Acknowledgements

This study was supported by the German–Chinese joint project SURUMER (Sustainable Rubber Cultivation in the Mekong Region) funded by the German Federal Ministry of Education and Research (BMBF) under Grant number FKZ 01LL0919, and Green Rubber project funded by BMZ/GIZ (Project number 13.1432.7-001.00). We thank Prof. Dengpan Bu for providing the facility for GC analysis, and Dr. Stefanie Goldberg for advice on gas sampling. We acknowledge Dr. Juan Carlos Laso Bayas and Prof. Hans-Peter Piepho for their advice on statistical analysis and Dr. Scott Demyan for comments on our manuscript.

## Appendix A.

**Table A1**  
Reported annual soil CO<sub>2</sub> and CH<sub>4</sub> fluxes in the Southeast Asia.

NO	Source	Land use, age (years, if rubber)	Annual soil CO <sub>2</sub> flux (MgCha <sup>-1</sup> yr <sup>-1</sup> )	Annual soil CH <sub>4</sub> flux (kgCha <sup>-1</sup> yr <sup>-1</sup> )	Q <sub>10</sub>	Method	Average air temperature (°C)	Average precipitation (mm)	Elevation (m.a.s.l.)	Location	TC (%)	TN (%)	Depth (cm)
Xishuangbanna China													
0	This study	Rainforest	8.48 ± 0.71	n.d.	3.11 ± 0.28	LCi-SD <sup>a</sup>	21.5 ± 0.5	1522 ± 234	561		2.26	0.25	0–15
0		Rubber, 22	6.75 ± 0.79	n.d.	1.73 ± 0.45	LCi-SD			596		1.7	0.18	0–15
0		Rubber+Tea, 22	5.98 ± 0.42	n.d.	2.23 ± 0.24	LCi-SD			611		1.66	0.17	0–15
0		Rubber, 9	5.09 ± 0.47	n.d.	2.35 ± 0.44	LCi-SD			585		1.17	0.14	0–15
1	Sha et al. (2005)	Rainforest	14.56	n.d.	2.08	Static chamber, GC	21.4	1557	720	21.93°N, 101.27°E	1.14		0–20
1	Fang et al. (2010)	Rainforest	9.42	–1.86	2.16	Static chamber, GC	21.4	1557	720	21.93°N, 101.23°E	1.64	0.15	0–20
1	Zhang et al. (2015)	Rainforest	6.93 ± 0.51	n.d.	n.d.	LI-6400	21.7	1487	568	21.92°N, 101.27°E	1.16	ND	0–20
1	Fang and Sha (2006)	Rainforest	7.20 <sup>a</sup>	n.d.	2.16	Alkaline absorption	21.5	1557	756	21.95°N, 101.20°E	1.84	0.02	0–10
1		Rubber	7.64 <sup>a</sup>	n.d.	2.18	Alkaline absorption			580	21.93°N, 101.25°E	1.60	0.02	0–10
1	Lu et al. (2009)	Rainforest	10.07 <sup>a</sup>	n.d.	2.95–3.09	Li-820	21.5	1557	756	21.85°N, 101.20°E	2.05	0.2	0–20
1		Rubber	7.80 <sup>a</sup>	n.d.	1.49–1.55	Li-820			580	21.93°N, 101.25°E	1.51	0.2	0–20
Hainan, China													
2	Zhou et al. (2013)	Primary rainforest	16.73 ± 0.87	n.d.	2.17	LI-8100	19.7 ± 0.9	2198	870	18.73N 108.88°E	3.12 ± 0.16	0.16 ± 0.02	0–10
2		Secondary rainforest	15.10 ± 0.26	n.d.	1.86	LI-8100	20.0 ± 0.7	2198	880	18.73°N, 108.87°E	3.66 ± 0.22	0.17 ± 0.01	0–10
2	Wu et al. (2014)	Rubber, 5	10.03	n.d.	1.92 <sup>c</sup> , 1.22 <sup>d</sup>	LI-6400	20.5 ~ 28.5	1607 ~ 2000	144	19.53°N, 109.48°E	0.78		0–60
2		Rubber, 10	10.34	n.d.	1.33 <sup>c</sup> , 1.77 <sup>d</sup>	LI-6400					0.78		0–60
2		Rubber, 19	11.96	n.d.	2.37 <sup>c</sup> , 1.44 <sup>d</sup>	LI-6400					0.83		0–60
2		Rubber, 33	11.09	n.d.	2.26 <sup>c</sup> , 1.10 <sup>d</sup>	LI-6400					1.04		0–60
Sumatra, Indonesia. Clay Acrisol													
3	Hassler et al. (2015)	Rainforest	16.93 ± 1.19	–3.63 ± 0.89	n.d.	Static chamber, GC	26.7 ± 0.1	2235 ± 385	35–95	1.94°S– 2.14°S,	3.3 ± 0.5 <sup>e</sup>	263.4 ± 67.1 <sup>f</sup>	
3		Jungle rubber	16.11 ± 0.72	–1.85 ± 0.59	n.d.	Static chamber, GC				102.58°E– 102.85°E	4.3 ± 0.4 <sup>e</sup>	331.4 ± 34.1 <sup>f</sup>	
3		Rubber, 7–16	16.09 ± 1.40	–0.29 ± 0.12	n.d.	Static chamber, GC					2.8 ± 0.4 <sup>e</sup>	198.4 ± 32.5 <sup>f</sup>	
Sumatra, Indonesia. Loam Acrisol													
4	Hassler et al. (2015)	Rainforest	16.21 ± 1.17	–0.18 ± 1.55	n.d.	Static chamber, GC				1.79°S– 2.19°S,	2.6 ± 0.2 <sup>e</sup>	182.9 ± 10.8 <sup>f</sup>	
4		Jungle rubber	15.55 ± 0.94	–2.42 ± 0.34	n.d.	Static chamber, GC				103.24°E– 103.36°E	2.7 ± 0.3 <sup>e</sup>	186.19 ± 11.0 <sup>f</sup>	
4		Rubber, 14–17	16.52 ± 1.32	–0.93 ± 0.35	n.d.						2.0 ± 0.3 <sup>e</sup>	172.6 ± 23.8 <sup>f</sup>	



**Table A1** (Continued)

NO	Source	Land use, age (years, if rubber)	Annual soil CO <sub>2</sub> flux (MgCha <sup>-1</sup> yr <sup>-1</sup> )	Annual soil CH <sub>4</sub> flux (kgCha <sup>-1</sup> yr <sup>-1</sup> )	Q <sub>10</sub>	Method	Average air temperature (°C)	Average precipitation (mm)	Elevation (m.a.s.l)	Location	TC (%)	TN (%)	Depth (cm)
						Static chamber, GC							
5	Sumatra, Indonesia. Ishizuka et al. (2002)	Rainforest P1	5.55 ± 1.35 <sup>b</sup>	−1.86 ± 0.76 <sup>b</sup>	n.d.	Static chamber, GC		2060		1.09°S, 102.10°E	3	0.19	
5		Rainforest P2	8.21 ± 2.36 <sup>b</sup>	0.37 ± 2.18 <sup>b</sup>	n.d.	Static chamber, GC				1.09°S, 102.10°E	–	–	
5		Logged over forest L1	5.72 ± 1.54 <sup>b</sup>	−0.39 ± 0.46 <sup>b</sup>	n.d.	Static chamber, GC				1.06°S, 102.16°E	3.5	0.24	
5		Logged over forest L2	7.10 ± 2.05 <sup>b</sup>	−1.54 ± 0.85 <sup>b</sup>	n.d.	Static chamber, GC				1.09°S, 102.11°E	4.5	0.65	
5		Rubber	6.53 ± 2.32 <sup>b</sup>	−1.12 ± 0.46 <sup>b</sup>	n.d.	Static chamber, GC				1.09°S, 102.12°E	1.6	0.12	
	Satakhun et al. (2013)	Rubber, 15 Thailand	18.80	n.d.	n.d.	LI-8100	28.1	1328	69	13.68°N, 101.07°E	1	0.06	0–10

GC: gas chromatography; n.d.: not determined.

<sup>a</sup>Annual flux value were calculated from reported annual average flux by multiplying time.

<sup>b</sup> Annual flux value were calculated from reported annual average flux by multiplying time, mean ± std.

<sup>c</sup> Dry season.

<sup>d</sup> Rainy season.

<sup>e</sup> kg cm<sup>-2</sup>.

<sup>f</sup> g Nm<sup>-2</sup>.

<sup>g</sup> LCI-SD is open chamber respiration system, LI-series are closed chamber system.

## References

- Adachi, M., Bekku, Y.S., Konuma, A., Kadir, W.R., Okuda, T., Koizumi, H., 2005. Required sample size for estimating soil respiration rates in large areas of two tropical forests and of two types of plantation in Malaysia. *For. Ecol. Manage.* 210, 455–459.
- Adachi, M., Bekku, Y.S., Rashidah, W., Okuda, T., Koizumi, H., 2006. Differences in soil respiration between different tropical ecosystems. *Appl. Soil. Ecol.* 34, 258–265.
- Ahrends, A., Hollingsworth, P.M., Ziegler, A.D., Fox, J.M., Chen, H., Su, Y., Xu, J., 2015. Current trends of rubber plantation expansion may threaten biodiversity and livelihoods. *Global Environ. Change* 34, 48–58.
- Ali, R.S., Ingwersen, J., Demyan, M.S., Funkuin, Y.N., Wizemann, H.-D., Kandeler, E., Poll, C., 2015. Modelling in situ activities of enzymes as a tool to explain seasonal variation of soil respiration from agro-ecosystems. *Soil Biol. Biochem.* 81, 291–303.
- Baccini, A., Goetz, S.J., Walker, W.S., Laporte, N.T., Sun, M., Sulla-Menashe, D., Hackler, J., Beck, P.S.A., Dubayah, R., Friedl, M.A., Samanta, S., Houghton, R.A., 2012. Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. *Nat. Clim. Change* 2, 182–185.
- Blagodatsky, S., Xu, J., Cadisch, G., 2016. Carbon balance of rubber (*Hevea brasiliensis*) plantations A review of uncertainties at plot, landscape and production level. *Agric. Ecosyst. Environ.* 221, 8–19.
- Bodelier, P.L.E., Laanbroek, H.J., 2004. Nitrogen as a regulatory factor of methane oxidation in soils and sediments. *FEMS Microbiol. Ecol.* 47, 265–277.
- Bolstad, P.V., Vose, J.M., 2005. Forest and pasture carbon pools and soil respiration in the Southern Appalachian mountains. *For. Sci.* 51, 372–383.
- Bond-Lamberty, B., Thomson, A., 2010. Temperature-associated increases in the global soil respiration record. *Nature* 464, 579–582.
- Cao, M., Zou, X., Warren, M., Zhu, H., 2006. Tropical forests of Xishuangbanna, China. *Biotropica* 38, 306–309.
- Chen, H., Yi, Z., Schmidt-Vogt, D., Ahrends, A., Beckschäfer, P., Kleinn, C., Ranjekar, S., Xu, J., 2016. Pushing the limits: the pattern and dynamics of rubber monoculture expansion in Xishuangbanna, SW China. *PLoS One* 11, e0150062.
- Chidthaisong, A., Conrad, R., 2000. Turnover of glucose and acetate coupled to reduction of nitrate: ferric iron and sulfate and to methanogenesis in anoxic rice field soil. *FEMS Microbiol. Ecol.* 31, 73–86.
- Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J., Chhabra, A., DeFries, R., Galloway, J., Heimann, M., Jones, C., Quéré, C.L., Myneni, R.B., Piao, S., Thornton, P., 2013. Carbon and other biogeochemical cycles. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, USA.
- Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440, 165–173.
- Demyan, M.S., Ingwersen, J., Funkuin, Y.N., Ali, R.S., Mirzaeitalarposhti, R., Rasche, F., Poll, C., Müller, T., Streck, T., Kandeler, E., Cadisch, G., 2016. Partitioning of ecosystem respiration in winter wheat and silage maize – modeling seasonal temperature effects. *Agric. Ecosyst. Environ.* 224, 131–144.
- de Blécourt, M., Brumme, R., Xu, J., Corre, M.D., Veldkamp, E., 2013. Soil carbon stocks decrease following conversion of secondary forests to rubber (*Hevea brasiliensis*) plantations. *PLoS One* 8, e69357.
- Don, A., Schumacher, J., Freibauer, A., 2011. Impact of tropical land-use change on soil organic carbon stocks—a meta-analysis. *Global Change Biol.* 17, 1658–1670.
- Fang, Q., Sha, L., 2006. Soil respiration in a tropical seasonal rain forest and rubber plantation in Xishuangbanna, Yunnan, SW China. *J. Plant Ecol.* 30, 97–103 (in Chinese).
- Fang, H.J., Yu, G.R., Cheng, S.L., Zhu, T.H., Wang, Y.S., Yan, J.H., Wang, M., Cao, M., Zhou, M., 2010. Effects of multiple environmental factors on CO<sub>2</sub> emission and CH<sub>4</sub> uptake from old-growth forest soils. *Biogeosciences* 7, 395–407.
- Ferréa, C., Zenone, T., Comolli, R., Seufert, G., 2012. Estimating heterotrophic and autotrophic soil respiration in a semi-natural forest of Lombardy, Italy. *Pedobiologia* 55, 285–294.
- Geng, Y., Wang, Y., Yang, K., Wang, S., Zeng, H., Baumann, F., Kuehn, P., Scholten, T., He, J.-S., 2012. Soil respiration in Tibetan alpine grasslands: belowground biomass and soil moisture, but not soil temperature, best explain the large-scale patterns. *PLoS One* 7, e34968.
- Guillaume, T., Damriss, M., Kuzyakov, Y., 2015. Losses of soil carbon by converting tropical forest to plantations: erosion and decomposition estimated by delta 13C. *Global Change Biol.* 21, 1365–1486.
- Harris, N.L., Brown, S., Hagen, S.C., Saatchi, S.S., Petrova, S., Salas, W., Hansen, M.C., Potapov, P.V., Lutsch, A., 2012. Baseline map of carbon emissions from deforestation in tropical regions. *Science* 336, 1573–1576.
- Hassler, E., Corre, M.D., Tjoa, A., Damriss, M., Utami, S.R., Veldkamp, E., 2015. Soil fertility controls soil-atmosphere carbon dioxide and methane fluxes in a tropical landscape converted from lowland forest to rubber and oil palm plantations. *Biogeosciences* 12, 5831–5852.
- Ishizuka, S., Tsuruta, H., Murdiyarso, D., 2002. An intensive field study on CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O emissions from soils at four land-use types in Sumatra, Indonesia. *Global Biogeochem. Cycles* 16, 221–221.
- Ishizuka, S., Iswandi, A., Nakajima, Y., Yonemura, S., Sudo, S., Tsuruta, H., Murdiyarso, D., 2005. The variation of greenhouse gas emissions from soils of various land-use/cover types in Jambi province, Indonesia. *Nutr. Cycling Agroecosyst.* 71, 17–32.
- Jia, X., Zha, T., Wu, B., Zhang, Y., Chen, W., Wang, X., Yu, H., He, G., 2013. Temperature response of soil respiration in a Chinese pine plantation: hysteresis and seasonal vs diel Q<sub>10</sub>. *PLoS One* 8, e57858.
- Jiang, H., Deng, Q., Zhou, G., Hui, D., Zhang, D., Liu, S., Chu, G., Li, J., 2013. Responses of soil respiration and its temperature/moisture sensitivity to precipitation in three subtropical forests in southern China. *Biogeosciences* 10, 3963–3982.
- Koehler, B., Corre, M.D., Veldkamp, E., Sueta, J.P., 2009. Chronic nitrogen addition causes a reduction in soil carbon dioxide efflux during the high stem-growth period in a tropical montane forest but no response from a tropical lowland forest on a decadal time scale. *Biogeosciences* 6, 2973–2983.
- Kotowska, M.M., Leuschner, C., Triadiati, T., Hertel, D., 2016. Conversion of tropical lowland forest reduces nutrient return through litterfall, and alters nutrient use efficiency and seasonality of net primary production. *Oecologia* 180, 601–618.
- Kou, W., Xiao, X., Dong, J., Gan, S., Zhai, D., Zhang, G., Qin, Y., Li, L., 2015. Mapping deciduous rubber plantation areas and stand ages with PALSAR and Landsat images. *Remote Sens.* 7, 1048–1073.
- Le Mer, J., Roger, P., 2001. Production, oxidation, emission and consumption of methane by soils: a review. *Eur. J. Soil Biol.* 37, 25–50.
- Le Quéré, C., Moriarty, R., Andrew, R.M., Canadell, J.G., Sitch, S., Korsbakken, J.L., Friedlingstein, P., Peters, G.P., Andres, R.J., Boden, T.A., Houghton, R.A., House, J.I., Keeling, R.F., Tans, P., Arneeth, A., et al., 2015. Global carbon budget 2015. *Earth Syst. Sci. Data* 7, 349–396.
- Li, Z., Fox, J.M., 2012. Mapping rubber tree growth in mainland Southeast Asia using time-series MODIS 250 m NDVI and statistical data. *Appl. Geogr.* 32, 420–432.
- Li, H., Aide, T.M., Ma, Y., Liu, W., Cao, M., 2007. Demand for rubber is causing the loss of high diversity rain forest in SW China. *Biodivers. Conserv.* 16, 1731–1745.
- Li, H., Ma, Y., Aide, T.M., Liu, W., 2008. Past, present and future land-use in Xishuangbanna, China and the implications for carbon dynamics. *For. Ecol. Manage.* 255, 16–24.
- Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. *Funct. Ecol.* 8, 315–323.
- Lu, H., Sha, L., Wang, J., Hu, W., Wu, B., 2009. Seasonal variation of soil respiration and its components in tropical rain forest and rubber plantation in Xishuangbanna, Yunnan. *Chin. J. Appl. Ecol.* 20, 2315–2322 (in Chinese).
- Mandal, D., Islam, K., 2008. Carbon sequestration in sub-tropical soils under rubber plantations in north-east India. *International Symposium on Climate Change and Food Security in South Asia, Dhaka, Bangladesh Available at: <http://www.wamis.org/agm/meetings/rsama08/Bari401-Islam-Carbon-Sequestration-Rubber.pdf>. (Accessed in Aug 2016)*.
- Megonigal, J.P., Guenther, A.B., 2008. Methane emissions from upland forest soils and vegetation. *Tree Physiol.* 28, 491–498.
- Moyano, F.E., Manzoni, S., Chenu, C., 2013. Responses of soil heterotrophic respiration to moisture availability: an exploration of processes and models. *Soil Biol. Biochem.* 59, 72–85.
- Myhre, G., Shindell, D., Bréon, F.-M., Collins, W., Fuglestedt, J., Huang, J., Koch, D., Lamarque, J.-F., Lee, D., Mendoza, B., Nakajima, T., Robock, A., Stephens, G., Takemura, T., Zhang, H., 2013. Anthropogenic and natural radiative forcing. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press/Cambridge, United Kingdom and New York, USA.
- Nesbit, S.P., Breitenbeck, G.A., 1992. A laboratory study of factors influencing methane uptake by soils. *Agric. Ecosyst. Environ.* 41, 39–54.
- Neubauer, S.C., Megonigal, J.P., 2015. Moving beyond global warming potentials to quantify the climatic role of ecosystems. *Ecosystems* 18, 1000–1013.
- Pansu, M., Gautheyrou, J., 2007. *Handbook of Soil Analysis: Mineralogical, Organic and Inorganic Methods*. Springer, Berlin Heidelberg.
- Preuss, I., Knoblauch, C., Gebert, J., Pfeiffer, E.-M., 2013. Improved quantification of microbial CH<sub>4</sub> oxidation efficiency in Arctic wetland soils using carbon isotope fractionation. *Biogeosci.* 10, 2539.
- Qi, Y., Xu, M., 2001. Separating the effects of moisture and temperature on soil CO<sub>2</sub> efflux in a coniferous forest in the Sierra Nevada mountains. *Plant Soil* 237, 15–23.
- R Development Core Team, 2016. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Raich, J.W., Schlesinger, W.H., 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus B* 44, 81–99.
- Raich, J.W., Tufekciogul, A., 2000. Vegetation and soil respiration: correlations and controls. *Biogeochemistry* 48, 71–90.
- Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J., Valentini, R., Banza, J., Casals, P., Cheng, Y., Grünzweig, J.M., Irvine, J., Joffre, R., Law, B.E., Loustau, D., Miglietta, F., Oechel, W., et al., 2003. Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. *Global Biogeochem. Cycles* 17, 1104.
- Ren, Y., Cao, M., Tang, J., Tang, Y., Zhang, J., 1999. A comparative study on litterfall dynamics in a seasonal rain forest and a rubber plantation in Xishuangbanna, SW China. *Chin. J. Plant Ecol.* 23, 418–425 (in Chinese).
- Satakhun, D., Gay, F., Chairungsee, N., Kasemsap, P., Chantuma, P., Thanisawanyangkura, S., Thaler, P., Epron, D., 2013. Soil CO<sub>2</sub> efflux and soil carbon balance of a tropical rubber plantation. *Ecol. Res.* 28, 969–979.
- Sayer, J., Sun, C., 2003. Impacts of policy reforms on forest environments and biodiversity. In: Hyde, W.F., Belcher, B., Xu, J. (Eds.), *China's Forests: Global Lessons from Market Reforms*. Resources for the Future and CIFOR, Washington, DC, pp. 177–194.

- Schwendenmann, L., Veldkamp, E., Brenes, T., O'Brien, J., Mackensen, J., 2003. Spatial and temporal variation in soil CO<sub>2</sub> efflux in an old-growth neotropical rain forest La Selva, Costa Rica. *Biogeochemistry* 64, 111–128.
- Sha, L., Zheng, Z., Tang, J., Wang, Y., Zhang, Y., Cao, M., Wang, R., Liu, G., Wang, Y., Sun, Y., 2005. Soil respiration in tropical seasonal rain forest in Xishuangbanna, SW China. *Sci. China Ser. D* 48, 189–197.
- Sheng, H., Yang, Y., Yang, Z., Chen, G., Xie, J., Guo, J., Zou, S., 2010. The dynamic response of soil respiration to land-use changes in subtropical China. *Global Change Biol.* 16, 1107–1121.
- Silver, W.L., Lugo, A.E., Keller, M., 1999. Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils. *Biogeochemistry* 44, 301–328.
- Smith, K.A., Ball, T., Conen, F., Dobbie, K.E., Massheder, J., Rey, A., 2003. Exchange of greenhouse gases between soil and atmosphere: interactions of soil physical factors and biological processes. *Eur. J. Soil Sci.* 54, 779–791.
- Song, Q., Tan, Z., Zhang, Y., Cao, M., Sha, L., Tang, Y., Liang, N., Schaefer, D., Zhao, J., Zhao, J., Zhang, X., Yu, L., Deng, X., 2013. Spatial heterogeneity of soil respiration in a seasonal rainforest with complex terrain. *iFOREST* 6, 65–72.
- Sotta, D.E., Meir, P., Malhi, Y., Nobre, A.D., Hodnett, M., Grace, J., 2004. Soil CO<sub>2</sub> efflux in a tropical forest in the central Amazon. *Global Change Biol.* 10, 601–617.
- State Forestry Administration, 1999. Forest soil analysis methods (Forestry standard of People Republic of China LY/T 1210 1275–1999). Standard press, China Beijing (in Chinese).
- Suseela, V., Conant, R.T., Wallenstein, M.D., Dukes, J.S., 2012. Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. *Global Change Biol.* 18, 336–348.
- Tan, Z., Zhang, Y., Liang, N., Song, Q., Liu, Y., You, G., Li, L., Yu, L., Wu, C., Lu, Z., Wen, H., Zhao, J., Gao, F., Yang, L.-Y., Song, L., Zhang, Y., Munemasa, T., Sha, L., 2013. Soil respiration in an old-growth subtropical forest Patterns, components, and controls. *J. Geophys. Res. Atmos.* 118, 2981–2990.
- Tang, J., Baldocchi, D.D., Xu, L., 2005. Tree photosynthesis modulates soil respiration on a diurnal time scale. *Global Change Biol.* 11, 1298–1304.
- Tang, J., Cao, M., Zhang, J., Li, M., 2010. Litterfall production, decomposition and nutrient use efficiency varies with tropical forest types in Xishuangbanna, SW China: a 10-year study. *Plant Soil* 335, 271–288.
- Veldkamp, E., Purbopuspito, J., Corre, M.D., Brumme, R., Murdiyarso, D., 2008. Land use change effects on trace gas fluxes in the forest margins of Central Sulawesi, Indonesia. *J. Geophys. Res. Biogeol.* 113, G02003.
- Verchot, L.V., Davidson, E.A., Cattaneo, J.H., Ackerman, I.L., 2000. Land-use change and biogeochemical controls of methane fluxes in soils of Eastern Amazonia. *Ecosystems* 3, 41–56.
- Wan, S., Luo, Y., 2003. Substrate regulation of soil respiration in a tallgrass prairie: results of a clipping and shading experiment. *Global Biogeochem. Cycles* 17, 1054.
- Wang, C., Yang, J., Zhang, Q., 2006. Soil respiration in six temperate forests in China. *Global Change Biol.* 12, 2103–2114.
- Warren-Thomas, E., Dolman, P.M., Edwards, D.P., 2015. Increasing demand for natural rubber necessitates a robust sustainability initiative to mitigate impacts on tropical biodiversity. *Conserv. Lett.* 8, 230–241.
- Werner, C., Zheng, X., Tang, J., Xie, B., Liu, C., Kiese, R., Butterbach-Bahl, K., 2006. N<sub>2</sub>O, CH<sub>4</sub> and CO<sub>2</sub> emissions from seasonal tropical rainforests and a rubber plantation in Southwest China. *Plant Soil* 289, 335–353.
- Wicke, B., Sikkema, R., Dornburg, V., Faaij, A., 2011. Exploring land use changes and the role of palm oil production in Indonesia and Malaysia. *Land Use Policy* 28, 193–206.
- Wood, T.E., Silver, W.L., 2012. Strong spatial variability in trace gas dynamics following experimental drought in a humid tropical forest. *Global Biogeochem. Cycles* 26, GB3005.
- Wood, T.E., Detto, M., Silver, W.L., 2013. Sensitivity of soil respiration to variability in soil moisture and temperature in a humid tropical forest. *PLoS One* 8, e80965.
- Wu, Z., Liu, H., Liu, L., 2001. Rubber cultivation and sustainable development in Xishuangbanna, China. *Int. J. Sust. Dev. World* 8, 337–345.
- Wu, Z., Guan, L., Chen, B., Yang, C., Lan, G., Xie, G., Zhou, Z., 2014. Components of soil respiration and its monthly dynamics in rubber plantation ecosystems. *Res. J. Appl. Sci. Eng. Technol.* 7, 1040–1048.
- Xu, J., Lebel, L., Sturgeon, J., 2009. Functional links between biodiversity, livelihoods, and culture in a Hani swidden landscape in southwest China. *Ecol. Soc.* 14, 20.
- Xu, J., Grumbine, R.E., Beckschäfer, P., 2014. Landscape transformation through the use of ecological and socioeconomic indicators in Xishuangbanna, Southwest China, Mekong Region. *Ecol. Indic.* 36, 749–756.
- Zhang, J., Cao, M., 1995. Tropical forest vegetation of Xishuangbanna, SW China and its secondary changes: with special reference to some problems in local nature conservation. *Biol. Conserv.* 73, 229–238.
- Zhang, X., Zhang, Y., Sha, L., Wu, C., Tan, Z., Song, Q., Liu, Y., Dong, L., 2015. Effects of continuous drought stress on soil respiration in a tropical rainforest in southwest China. *Plant Soil* 394, 343–353.
- Zhou, Z., Jiang, L., Du, E., Hu, H., Li, Y., Chen, D., Fang, J., 2013. Temperature and substrate availability regulate soil respiration in the tropical mountain rainforests, Hainan Island, China. *J. Plant Ecol.* 6, 325–334.
- Zhu, H., 2006. Forest vegetation of Xishuangbanna, south China. *For. Stud.* 8, 1–58.
- Zimmermann, M., Davies, K., Peña de Zimmermann, V.T.V., Bird, M.I., 2015. Impact of temperature and moisture on heterotrophic soil respiration along a moist tropical forest gradient in Australia. *Soil Res.* 53, 286–297.