Impact of land use change on soil respiration and methane sink in tropical uplands, Southwestern China

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Chapter 1 General introduction

1.1 Overview

Land use and land cover change (LULCC), mainly deforestation, is the second largest contributor of anthropogenic carbon emissions to the atmosphere after fossil fuel combustion (Le Quéré *et al.*, 2015). From 1990 to 2010 the carbon emission by LULCC accounted for 12.5% of anthropogenic emissions (van der Werf *et al.*, 2009; Houghton *et al.*, 2012). Tropical forests have been the primary source of agricultural expansion in the tropics (Geist and Lambin, 2002); more than 55% of expansion of agricultural land (including tree plantation) was from intact forests and 28% came from disturbed forests during 1980 and 2000 (Gibbs *et al.*, 2010). Although deforestation rate declined to 5.5 M ha yr^{-1} from 2010 to 2015 in the tropics (58% of the rate in the 1990s), loss of forests in the tropics is continuing (Keenan *et al.*, 2015). In Southeast Asia, rubber plantations and oil palm plantations have expanded extensively in past decades, replacing natural forest and shifting agricultural land (Gunarso *et al.*, 2013; Fox *et al.*, 2014). The natural rubber area reached 11.7 million ha in 2017, with expansion of 4.3 million ha worldwide from 2000 to 2017 (FAOSTAT, 2019).

On the other hand, it is known that estimating the net carbon fluxes from LULCC is associated with large uncertainties in the global carbon budget, such as uncertainties in the carbon density of land undergoing changes, the rate of deforestation and forest degradation (Houghton *et al.*, 2012; Li *et al.*, 2017), the fate of the carbon, such as rate of decomposition, and subsequent land management, etc. (Prentice *et al.*, 2001). In addition, the heterogeneity of carbon fluxes at spatiotemporal scale and an incomplete understanding of associated processes also cause uncertainties in estimating the net fluxes from LULCC (Houghton *et al.*, 2012). In order to predict the capacity of terrestrial ecosystems to mitigate climate change, and to evaluate the land based mitigation pathways and policies, more reliable estimations of carbon emissions at local or regional scale are required needing a better understanding of carbon cycling, especially the underlying biogeochemical processes and driving factors (Arneth *et al.*, 2017). CO_2 and CH_4 are the two most important greenhouse gases (GHG). CO_2 and CH_4 fluxes from soils are important components of carbon cycling, because the CO_2 flux respired from soils is the second largest carbon flux in terrestrial ecosystems (Reichstein *et al.*, 2003). Furthermore, the uptake of atmospheric CH_4 by oxic soils is the only known biological methane sink (Ciais *et al.*, 2013).

Therefore, identifying the controlling factors of carbon fluxes and assessing how land use change alters the underlying processes are of importance to improve the estimation of carbon emissions from LULCC, and contribute further to better modeling their impact on carbon emissions and identifying mitigation options. Space-for-time is a common approach used in assessing the impact of land use change, but the land use effects are often subject to confounded controlling factors that associated with natural variability and unclear site history (Fukami and Wardle, 2005). In this thesis, the controlling factors of soil surface CO_2 and CH_4 fluxes were identified and quantified, with special efforts made in addressing the inference of covariates and confounded factors in statistical analysis. Subsequently, CH_4 processes were further investigated and modeled based on CH_4 concentration and carbon-13 isotope profiles measured *in situ*. The seasonality of CH_4 fluxes and the differences between natural forest and rubber plantations at processes level were grasped by combining the surface fluxes, concentration profiles and isotopic signature profiles. This study was conducted in Xishuangbanna, Southwest China, representing the extensive rubber expansion into marginal growing area in the past decades. This study was part of SURUMER (Sustainable rubber cultivation in the Mekong region) as well as Green Rubber project that comprehensively assessed land use change impact aiming for sustainable rubber cultivation.

1.2 Expansion of rubber plantations and environmental impact

1.2.1 Scale and trajectory of rubber expansion

Driven by increasing demand of natural rubber latex in the past decades, rubber plantations (*Hevea brasiliensis*) have extensively expanded in the tropics and into non-traditional growing areas, replacing natural forests and shifting agricultural lands (Fox, 2014). The harvested area of natural rubber reached 11.7 million ha in 2017, with 89% distributed in Asia (FAOSTAT, 2019). Since the price boom in the beginning of the millennium, the area of rubber plantations rapidly increased by 4.3 million ha worldwide and 3.7 million ha expansion occurred in Asia during 2000 - 2017 (FAOSTAT, 2019; Figure 1.1). Rubber plantations have increasingly expanded into sub-optimal environments, such as higher elevation and steeper slopes, making them susceptible to insufficient water availability, frost, or wind damage and the production might not be sustainable in the long-term (Ahrends *et al.*, 2015; Chen *et al.*, 2016).

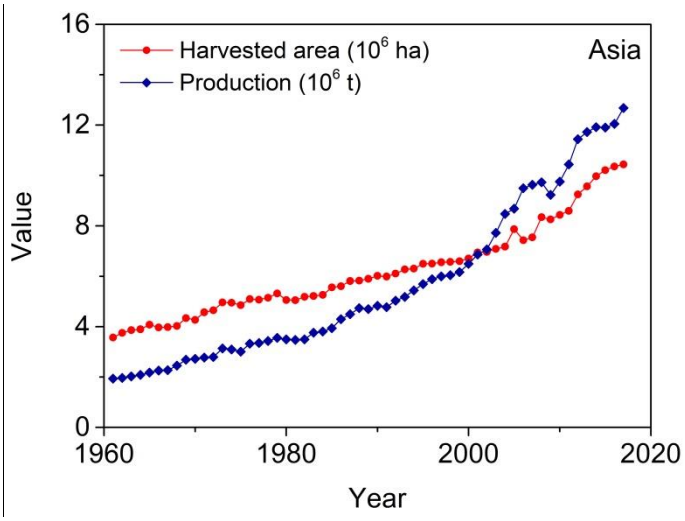

Figure 1.1 The trajectory of world harvested area of natural rubber plantations, the production and the consumption of natural rubber latex. The harvested area and production data are from FAOSTAT (2019), and consumption data are from International Rubber Study Group (IRSG, 2019).

Since the first establishment of rubber plantations on state farms in 1950s, the area of rubber plantations has tremendously increased in the past decades in China. In the study site, Xishuangbanna prefecture for example, rubber plantations accounted for only 0.31% of total land area in 1963, but steadily increased to 1.10%, 4.54%, 7.14%, 11.30% and 22.14% of total land area in 1976, 1992, 1998, 2003 and 2010, respectively (Wu *et al.*, 2001; Li *et al.*, 2007; Xu *et al.*, 2014).

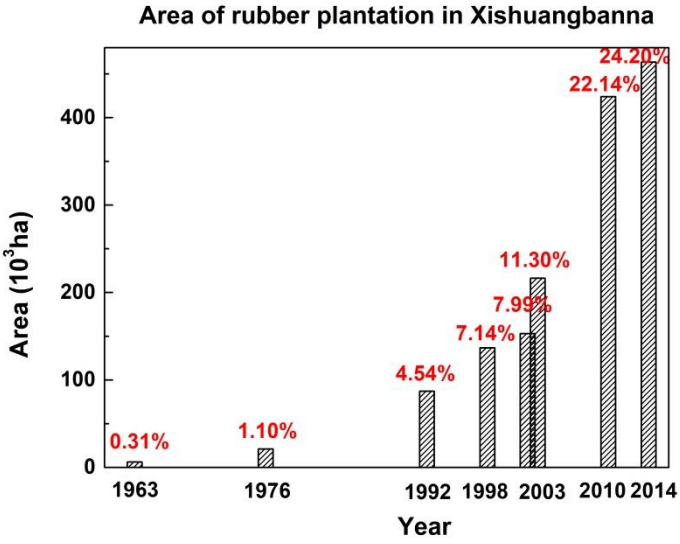

Figure 1.2 Expansion of rubber plantations in Xishuangbanna. The area of rubber plantations referred to Wu *et al.* (2001), Li *et al.* (2007) and Xu *et al.* (2014).

1.2.2 Impact on the environment

Despite the contribution to the local rural economy and providing over 40% of smallholder income (Min *et al.*, 2017), previous studies have shown that this massive land use change could have a profound impact on the environment and sustainability in the long term (Fox *et al.*, 2014). The northern Asia tropics, where rubber plantations have expanded into, is one of Indo-Burma biodiversity hotspots. Recently established rubber plantations in the region are mostly intensively managed monocultures, where common practices include establishing terraces to plant rubber trees, applying mineral fertilizers in the young plantation, clearing the understory vegetation by spraying herbicide, and applying sulfur to prevent powdery mildew and anthracnose diseases (Li *et al.*, 2016).

Assessments have been carried out to evaluate the impact of converting forests to rubber plantations on different aspects. Compared to natural forest, the species number was 30-50% lower in the rubber plantation (Cotter *et al.*, 2017) but not necessarily low for the diversity of soil biota (Kerfahi *et al.*, 2016). Clearing the understory vegetation in the plantation increases runoff and risk of soil erosion. Experiments have shown that allowing the understory to growth or reducing herbicide usage can lower runoff and soil loss from erosion processes (Liu *et al.*, 2016; Liu *et al.*, 2017; Liu *et al.*, 2020). Such land use conversions also have been suggested to decrease nutrient availability or nutrient loss in converted plantations due to leaching (Kurniawan *et al.*, 2018; Vrignon-Brenas *et al.*, 2019). The analysis of the impact of disturbances on the hydrological cycle by this land use transformation has been inconsistent so far. Tan *et al.* (2011) and Guardiola‐Claramonte *et al.* (2010) found rubber plantations lost more water than forest and hence contributed to water shortage in the dry season, while in fact the reported transpiration and evapotranspiration rates of rubber plantations were not very high for a tree crop growing in the tropics (<3 mm d^{-1}) (Carr, 2011; Niu *et al.*, 2017). Applying fertilizer, herbicide and sulfur could change major soil microbial and nutrient properties in rubber plantations (Li *et al.*, 2016).

Carbon stock is one of mostly assessed properties in the land use change assessments. In general, converting arable land into rubber plantations tends to increase carbon sequestration, while carbon loss usually prevails in converting forest into rubber plantations (Blagodatsky *et al.*, 2016; Shanmugam *et al.*, 2018). For instance, converting primary forest and secondary forest into rubber plantations resulted in average to 14%±37% and 16%±9% of soil carbon loss respectively (Shanmugam *et al.*, 2018), decreasing the biomass carbon pool up to 166 Mg C ha^{-1} (Kotowska *et al.*,

2015). The organic carbon loss prominently occurs in the topsoil when converting forest into rubber plantations, i.e. soil carbon stock decreased by 19-23% in the top 30 cm soil (de Blécourt *et al.*, 2013; Guillaume *et al.*, 2015), while the carbon stock in deep subsoil remained stable (Borchard *et al.*, 2019). Unlike biomass carbon, soil carbon changes occur more slowly after land use conversion, and the dynamics depend on the balance of organic inputs to the soil and net carbon loss from the soil (soil respiration, organic carbon loss through erosion) (Smith, 2008). To date, the dynamics of CO_2 emissions from soils under rubber plantations at different age (chronosequence) were investigated only in a few studies (Blagodatsky *et al.*, 2016), and studies on soil CH_4 fluxes were even less (Ishizuka *et al.*, 2005; Hassler *et al.*, 2015), making the understanding of driving factors and mechanisms for the impact of land use changes incomplete.

1.3 Impact of rubber expansion on gaseous carbon fluxes

Two of the most important well-mixed greenhouse gases, CO_2 and CH_4, have increased from 278 (276-280) ppm to 390.5 (390.3-390.7) ppm, and from 722±25 ppb to 1803±2 ppb for CO_2 and CH_4, respectively from preindustrial era in 1750 to 2011 (Myhre *et al.*, 2013). CH_4 is a potent greenhouse gas, with the Global warming potential (GWP) of 28-34 times of CO_2 in a 100-year time horizon (Myhre *et al.*, 2013; Neubauer and Megonigal, 2015).

Soil CO_2 flux, or soil respiration, represents the second largest carbon flux (smaller than photosynthesis) between terrestrial ecosystem and atmosphere, and emitted more than 10 times of CO_2 than the emission from fossil fuel combustion annually (Raich and Schlesinger, 1992; Reichstein *et al.*, 2003). Because of this large magnitude, small changes in soil respiration could significantly increase or mitigate the current atmospheric CO_2 increment and further feedback to climate change. In addition to the immediate biomass carbon loss and topsoil carbon loss by erosion (Guillaume *et al.*, 2015), a growing amount of literature suggested that soil carbon stock decreases over extended time periods after tree plantations established following deforestation (de Blécourt *et al.*, 2013; van Straaten *et al.*, 2015; Borchard *et al.*, 2019).

Aerated soil is the only known biological CH_4 sink, accounting for 4-6% of total CH_4 sink (Ciais *et al.*, 2013). Although uplands soils usually function as net CH_4 sink, land use changes and managements could meditate CH_4 processes and affect the soil function as CH_4 sink (Aronson and Helliker, 2010; Reay *et al.*, 2018). Converting natural forests into agricultural systems, including tree plantations, often decreased more than half CH_4 consumption by soils (Hassler *et al.*, 2015; Wanyama *et al.*,

2019).

Space-for-time, or space-substitute-time is the most commonly applied approach in assessing the impact of land use changes on greenhouse gas fluxes and various other ecosystem functions (Filippi *et al.*, 2016). Despite the efforts on selecting comparable references and converted land use pairs, the shortcomings of the space-for-time approach, such as inherent dissimilar factors and unclear site histories (Fukami and Wardle, 2005), making the land use change effect difficult to disentangle from inherent site factors.

1.3.1 Impact of rubber expansion on soil CO_2 fluxes

Soil respiration consists of autotrophic and heterotrophic components. Microbial respiration is a major component of heterotrophic respiration, which includes the respiration of rhizosphere microorganisms decomposing root exudates and respiration of soil non-rhizosphere microorganisms decomposing humus and plant residues; while root respiration is the only significant autotrophic respirations in soil (Kuzyakov and Larionova, 2006). Comparing the magnitude of the fluxes, respiration from soil fauna and the emission of CO_2 due to physical and chemical processes are much less important (Sapronov and Kuzyakov, 2007). The autotrophic component reflects the plant activity and allocation of carbon compounds from the canopy to the roots, while the heterotrophic component eventually determines the soil carbon storage (Binkley *et al.*, 2006). Definitions and terms for the components may differ from studies, depending on the partition method used in the field or in the laboratory. In this thesis, soil CO_2 fluxes were measured from the soil surface, which included all respiration components i.e. root respiration, microbial respiration from decomposing root exudates, soil organic matter in bulk soil and plant residuals on soil surface, and respiration from soil fauna. Those factors affecting the activities of plant roots and soil microbes directly or indirectly control the variation of soil respiration.

The dynamic of soil respiration is controlled by both abiotic and biotic factors (Arevalo *et al.*, 2010). Soil temperature is the most often studied abiotic factor, with great efforts on deriving the empirical functions to represent the non-linear positive relationship between soil temperature and soil respiration. Temperature sensitivity-Q_{10}, a parameter reflecting the respiration rate to a temperature increase of 10 ℃, have been extensively used to describe the temperature effect on soil respiration. For example, the earliest empirical exponential function proposed by van't Hoff was valid for a limited temperature range (van't Hoff, 1899). In contrast, the Arrhenius equation introduced activation energy and was able to predict an increasing Q_{10} towards lower

temperatures, while equations introduced optimal or minimum temperature to account for large variation of Q_{10} with temperature in the field or lab data (Lloyd and Taylor, 1994; Kirschbaum, 1995). Soil water content is another abiotic factor controlling soil respiration and affecting the temperature dependency of soil respiration. Similar as soil temperature, soil respiration also has an optimum range for soil moisture, too wet conditions will inhibit soil respiration via reducing the supply of O_2 for the activities of roots and aerobic microbes, while too dry conditions will impose water stress for both plants and microbes (Manzoni *et al.*, 2012). Therefore, recent studies started to use either manipulated experiments or empirical regressions to differentiate the effect of soil temperature and moisture (Zimmermann *et al.*, 2015; Demyan *et al.*, 2016). Soil acidity, or pH, have been found to affect soil respiration rate differently depending on the acidity of the soil, i.e., in acidic soils low pH can constrain microbial growth, while its effect in near-neutral soils is linked to the alleviation of acid retardation and resource acquisition (Malik *et al.*, 2018). Other abiotic factors, such as O_2 and nutrient availability, have been found to affect soil respiration and were linked with soil water contents to some extent (Skopp *et al.*, 1990).

As a biological process, biotic factors are important determinants of soil respiration (Reichstein and Beer, 2008). Since growth and activities of roots and microorganisms rely on the carbon supply from the photosynthetic assimilation by plants and incorporated plant residuals into the soil, biotic factors, such as plant photosynthetic activity (Tang *et al.*, 2005), fine root biomass (Wang *et al.*, 2017), substrate quantity and quality (Wan and Luo, 2003) have shown a controlling effect on soil respiration.

Understanding the controlling factors of soil respiration is needed in order to quantify the impact of land use change and predict the carbon dynamics under different land use scenarios to mitigate climate change (Arevalo *et al.*, 2010). Considering the slow release of soil carbon in conversion of natural forest to tree plantations, using a chronosequence approach is necessary to understand the temporal dynamics and driving factors of soil respiration (Sheng *et al.*, 2010). Converting natural forest into rubber plantations mostly resulted in loss of soil organic carbon (Li *et al.*, 2008; Guillaume *et al.*, 2015; Blagodatsky *et al.*, 2016), but the fluxes of this slow release of soil carbon have not been well understood because of lacking comparisons in both land uses using the same methodology and measuring devices. Furthermore, the large temporal and spatial heterogeneity in tropical systems require a large number of replicates in the field to reliably estimate CO_2 emissions from soils (Adachi *et al.*, 2005). However, most studies on tropical forests and rubber plantations often did not sufficiently consider such requirements, thus detecting the land use change effect and identifying the factors for the differences were hampered due to large variations and

insufficient replicates in measured soil CO_2 fluxes. Moreover, the temporal variability in rainfall (seasonal, annual and inter-annual) is large under tropical monsoon climate, which poses great challenges in quantifying the inference of soil moisture on the temperature dependency of soil respiration.

1.3.2 Impact of rubber expansion on soil CH_4 fluxes

Methane fluxes are the result of physical gas diffusion, biological oxidation and production processes in the soil. Methanotrophic bacteria in the soil oxidize CH_4 with O_2 into CO_2 under aerobic conditions, while methanogenic Archaea produce CH_4 via the acetoclasstic pathway using substrates of degraded organic carbon such as acetate and methanol, or via the hydrogenotrophic pathway using H_2 and CO_2 as substrates (Conrad, 1994; Le Mer and Roger, 2001). The net CH_4 flux between soil and atmosphere is the balance between these two biological processes (Chan and Parkin, 2001a; Bodelier and Laanbroek, 2004). Nevertheless, the physical diffusion process determines the rate of atmospheric CH_4 and O_2 diffusing into soils for methanotrophic oxidation, thus primarily controls CH_4 fluxes (Dörr *et al.*, 1993). Upland soils can support low rates of methanogenesis under wet conditions, therefore, methanotrophs in the oxic topsoil oxidize CH_4 not only from the atmosphere but also from the produced CH_4 in the wet subsoil (Conrad and Smith, 1995; Chan and Parkin, 2001a). Tropical upland soils are dominated by CH_4 oxidation and mostly act as a net CH_4 sink (Dalal and Allen, 2008), but alterations into a source of CH_4 has been also observed during periodical water saturation in the rainy season (Fang *et al.*, 2010).

The net CH_4 flux from soil is regulated by soil physical and chemical properties that determine the gas diffusivity and microbial activities of both methanotrophs and methanogens (Le Mer and Roger, 2001; Wolf *et al.*, 2012). Soil physical properties, such as texture, compaction and soil water content, are key factors determining the gas diffusivities in soil media. Texture and compaction determine the pore size distribution and pore network, gas permeability and water infiltration in the soil (Moldrup *et al.*, 1996; Antille *et al.*, 2015). Because gas diffusion resistance is larger in water media (10^4 times slower) than in soil-air (Neira *et al.*, 2015), increasing soil water content means creating water-blockages in the pore network and slowing the gas diffusion in the soil media. Therefore, changes of soil water content control the dynamics of gas diffusivity through soil-air porosity, water-induced disconnectivity and solid-induced tortuosity (Thorbjørn *et al.*, 2008). As a key parameter in modeling methane processes within soil profiles and indicator of soil aeration, many studies have developed and continue improving empirical functions of soil gas diffusivity from easily measurable parameters (Moldrup *et al.*, 2013). The rate of CH_4 diffusion

from the atmosphere into the soil exerts the primary control on CH_4 fluxes and is dependent on soil physical structure and soil moisture content (Dörr *et al.*, 1993).

The biological activity of methanotrophs and methanogens are affected by environmental factors including soil temperature and soil moisture, substrates availability, interactions with nitrogen, etc. (Bodelier, 2011; Tate, 2015). The temperature control on methanogens differs with methanotrophs. Methanogenesis is sensitive to temperature change, at low temperature not only the activity of methanogens decreases, but also that of other bacteria involved in methanogenic fermentation (Le Mer and Roger, 2001). Methanotrophs are less sensitive to soil temperature compared to methanogens, leading to a minor influence of temperature on CH_4 uptake especially in tropical systems where variations of soil temperature are very small (Dörr *et al.*, 1993; Wanyama *et al.*, 2019). Soil water content, often expressed as water-filled pore space (WFPS), regulates the activities of methanotrophs and methanogens differently depending on the range. Activities of methanotrophs can be limited due to water stress in arid systems (von Fischer *et al.*, 2009), but excessive water alters soil aeration from aerobic to anaerobic and the substrate O_2 becomes limited for methanotrophs, which inhibits CH_4 oxidation and favors methanogens for CH_4 production (Ridgwell *et al.*, 1999). The substrate CH_4 is much less likely to become limited compared to O_2 in methanotrophic oxidation, as high-affinity methantrophs in aerated soils could oxidize CH_4 at atmospheric and sub-atmospheric concentrations (nM range) (Bender and Conrad, 1992).

Nutrient availability, especially mineral nitrogen content, is known to interact with CH_4 oxidation and production via different pathways. Low nitrogen availability could limit the growth of methanotrophic bacteria and enzyme synthesis, in nitrogen limited soils. Adding mineral nitrogen at low rates could eliminate nitrogen limitations and stimulate the activity of methanotrophs and CH_4 oxidation (Bender and Conrad, 1995; Koehler *et al.*, 2012; Geng *et al.*, 2017). However, the meta-analysis by Aronson *et al.* (2013) displayed a general trend of decreasing CH_4 uptake by fertilization in upland soils. Ammonia could competitively inhibit CH_4 uptake, because monooxygenase (MMO) in methanotroph oxidizes not only CH_4, but also ammonia under aerated conditions. Furthermore, this methanotrophic oxidation of ammonia produces intermediate products (nitrite and hydroxylamine) that are toxic for methantrophs (Dunfield and Knowles, 1995). Nitrate could inhibit CH_4 production by methanogens under wet conditions, as nitrate reducers are stronger competitors for electrons than methanogens, and the intermediate products of nitrate reduction (NO_2^-, NO and N_2O) are toxic for methanogens (Chidthaisong and Conrad, 2000).

Tropical forest soils are normally net CH_4 sinks. Converting natural forests into rubber plantations and other cultivated systems, such as oil palm plantation, cacao agroforestry system, have led to a reduced consumption of atmospheric CH_4 by soils (Werner *et al.*, 2006; Veldkamp *et al.*, 2008; Hassler *et al.*, 2015). However, the main factors accounting for this change and the mechanisms how CH_4 processes changed have not been well understood yet. For instance, as main controlling factor of temporal variation of CH_4 fluxes, soil water content was higher in converted rubber plantations, confounded with a more clayey soil texture compared to natural forests (Ishizuka *et al.*, 2002; Werner *et al.*, 2006). In addition, most assessments on tropical forest and converted plantations were based on net CH_4 fluxes measured with chambers from the soil surface. Those few studies which measured CH_4 concentrations in soil profiles so far are lacking detailed characterization at process level (Ishizuka *et al.*, 2002). Moreover, the complex interactions between mineral nitrogen and CH_4 processes were often based on simple correlations or univariate regression analysis (Dobbie *et al.*, 1996; Veldkamp *et al.*, 2013), which is insufficient considering the dependency of mineral nitrogen on soil water dynamics.

Analyzing the ^{13}C isotopic composition of CH_4, related substrates and products can help differentiate CH_4 production and oxidation from the net fluxes *in situ* (Teh *et al.*, 2006). Due to the strong discrimination against the heavier methane-$^{13}CH_4$ in methanotrophic oxidation, this fractionation enriches the ^{13}C signature of in soil remaining CH_4 (Coleman *et al.*, 1981). As $^{13}CH_4$ diffuses slower than $^{12}CH_4$ from atmosphere into the soil and within soil, this fractionation results in depleted ^{13}C signatures in soil CH_4 (De Visscher *et al.*, 2004). Isotopic approaches have been widely used to differentiate and quantify CH_4 production and oxidation from the net fluxes in water saturated systems, such as rice paddies and wetlands (Krüger *et al.*, 2002; Dorodnikov *et al.*, 2013; Preuss *et al.*, 2013), and aerated landfill soils (De Visscher *et al.*, 2004; Mahieu *et al.*, 2008). In contrast, much less is known for these processes in tropical forest systems, where soils undergo periodical water saturation and their clayey texture can support both oxidation and production at microsite scale (Teh *et al.*, 2006). Measuring the isotopic signature of CH_4 in soil air may provide insights into mechanisms of how land use change affects soil CH_4 processes in tropical upland systems.

1.4 Research gaps, objectives and hypotheses

The understanding of the impact of converting natural forest into rubber plantations on soil respiration is still limited, due to (1) lack of comparisons using the same approach in both forest and rubber plantations at different age (chronosequence), and (2) large

spatial heterogeneity and strong seasonality of soil respiration under monsoon climate, as well as interference of soil moisture on soil temperature as main controlling factors.

The incomplete understanding of the mechanisms of this land use conversion on the soil function as CH_4 sink is mainly due to three limitations from the methodological perspective: (1) paired land uses in comparisons are often confounded with soil properties that are intrinsically linked with main controlling factors of CH_4 fluxes, (2) lacking investigations on the underlying physical and biological processes within the soil profile, (3) mineral nitrogen status is not independent from the soil water dynamics (Bodelier, 2011), and it is often insufficiently considered in interpreting and identifying the pathways of the interactions between mineral nitrogen and CH_4 processes.

Therefore, besides assessing the land use change impact on CO_2 and CH_4 fluxes from soils, the main goals of this thesis were to identify and quantify the controlling factors of each gas, and to explain how converting natural forest into rubber plantations altered these factors and underlying processes. The specific objectives were to:

(1) assess CO_2 and CH_4 fluxes from soils under natural forest and rubber plantations;
(2) identify the main controlling factors for the temporal dynamics of soil CO_2 and CH_4 fluxes, and quantify their control on each gas flux;
(3) statistically tackle the influence of confounding controlling factors in chronosequences and land use type on CH_4 fluxes;
(4) investigate the mechanisms of land use change on physical and biological related CH_4 processes in the soil profile.

Correspondingly, the hypotheses tested in this thesis include:

(1) Converting natural forest into intensively managed rubber plantations reduces the soil CO_2 emission and CH_4 uptake by tropical upland soils;
(2) Soil moisture interferes with the dynamic of soil respiration under the monsoon climate, and controls the temporal variation of soil CH_4 fluxes;
(3) Land use change has a significant effect on CH_4 consumption by soils, apart from other confounding factors;
(4) Both physical diffusion of CH_4 and methanotrophic oxidation regulate CH_4 consumption in the soil profile, but the relative control depends on the season and land use.

1.5 Outline of the thesis

This cumulative thesis consists of three journal articles and a general introduction and discussion. In chapter 2, the interference of soil moisture on the temperature control on soil respiration is addressed using a mixed model. In chapter 3, by using combined CH_4 surface fluxes measured from two projects, not only the control of soil moisture on CH_4 fluxes is quantified, but also the confounding land use effect and texture effect, as well as interactions between CH_4 processes and mineral nitrogen are statistically addressed. In chapter 4, the land use change effect on the soil CH_4 sink is investigated at processes level, using CH_4 concentration gradients, isotopic profiles of $\delta^{13}CH_4$ and determined gas diffusivities. Physical diffusion and methanotrophic oxidation processes are modeled using a diffusion-oxidation model, in order to quantify their relative control on CH_4 sinks in forest and rubber plantations. In chapter 5, the overall impact of converting natural forest into rubber plantations on soil CO_2 and CH_4 fluxes were discussed in general.

Chapter 2 Seasonal differences in soil respiration and methane uptake in rubber plantation and rainforest[1]

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Highlights

• Rainforest emitted larger amount of CO_2 from soil than rubber plantations.

• Soil CO_2 flux was suppressed in wet period of rainy season under rubber plantation.

• Conversion rainforest into rubber plantations weakened the CH_4 uptake by soil.

• Considering moisture effect improved temperature sensitivity assessment.

2.1 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_2 fluxes during one year as well as CH_4 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.

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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_2 with an annual cumulative flux of 8.48 ±0.71 Mg C ha^{-1} yr^{-1}, compared to 6.75 ±0.79, 5.98 ±0.42 and 5.09 ±0.47 Mg C ha^{-1} yr^{-1} for mature rubber, rubber-tea intercropping, and young rubber, respectively. Additionally, the soil CH_4 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_2 emissions and weakened CH_4 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.

Keywords

Greenhouse gases, Temperature sensitivity, Soil moisture, Land use change, Carbon emission

2.2 Introduction

Soil respiration, emitting greenhouse gas CO_2 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 ±12 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_2 emission rate of 9.8 ±0.5 Pg C yr^{-1} (Le Quéré *et al.*, 2015). Methane (CH_4), with 28–32 times the CO_2 global warming potential (GWP) in a 100-year time horizon (Myhre *et al.*, 2013; Neubauer and Megonigal, 2015) is responsible for about 18% of human-induced radiative forcing. The estimated global emissions of anthropogenic CH_4 was 335 (273–409) Tg CH_4 yr^{-1} during 2000–2009, while the soil consumed 32 (26–42) Tg CH_4 yr^{-1} during the same period (Ciais *et al.*, 2013). Small changes in the

soil carbon flux pathways 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^{-1} 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 (Wicke *et al.*, 2011; Li and Fox, 2012; Kou *et al.*, 2015). 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 (Wu *et al.*, 2001; Li *et al.*, 2007; Xu *et al.*, 2014; Chen *et al.*, 2016).

Impacts of converting forests into rubber plantations generally leads to carbon losses from decreased living biomass carbon and soil organic carbon (Li *et al.*, 2008; de Blécourt *et al.*, 2013; Guillaume *et al.*, 2015; Blagodatskaya *et al.*, 2016). 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_4 exchange has often been assessed by comparing soil carbon fluxes under different land uses (space substitutes time) (Sheng *et al.*, 2010; Hassler *et al.*, 2015). 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 (Ishizuka *et al.*, 2002; Fang and Sha, 2006; Werner *et al.*, 2006; Lu *et al.*, 2009; Hassler *et al.*, 2015). 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_2 flux has not been well understood particularly in tropical ecosystems (Adachi *et al.*, 2006; Veldkamp *et al.*,

2008; Sheng *et al.*, 2010). Soil CO_2 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; Werner *et al.*, 2006; Geng *et al.*, 2012; Suseela *et al.*, 2012), while only soil temperature was extensively used as controlling factor to explain the seasonal variation of soil respiration (Raich and Schlesinger, 1992; Lloyd and Taylor, 1994; Jia *et al.*, 2013; 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 ℃. 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 (Qi and Xu, 2001; Tan *et al.*, 2013; Ali *et al.*, 2015; Demyan *et al.*, 2016), 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_2 flux to land use and climate change.

Upland soils are normally a net sink for atmospheric CH_4, but current understanding of CH_4 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_4 flux are scarce, compared to soil respiration studies. It is known that the production or consumption of CH_4 depends on the soil water content, soil gas diffusivity and oxygen availability in the soil profile. Whether a soil acts as CH_4 source or sink depends on the balance between methane production and oxidation (Smith *et al.*, 2003; Megonigal and Guenther, 2008; Wood and Silver, 2012). Ammonium fertilizers in cultivated soils can serve as competitive inhibitors for CH_4 oxidation decreasing the methane uptake (Nesbit and Breitenbeck, 1992). Compared to tropical forests, converted plantations showed a reduced CH_4 uptake by soil to a different extent (Verchot *et al.*, 2000; Hassler *et al.*, 2015), being sometimes comparable with uptake in forest (Ishizuka *et al.*, 2005).

Therefore, this study focused on (1) the temporal dynamics of soil CO_2 fluxes under rainforest and rubber plantations, and CH_4 fluxes estimated during the wet period of the rainy season when the largest differences in CO_2 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_2 and CH_4 fluxes data obtained in rubber plantations and rainforests in Southeast Asia. By comparing both soil CO_2 and CH_4 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.

2.3 Methods

2.3.1 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 (Figure 2.1). 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 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 Figure 2.1 and Table 2.1.

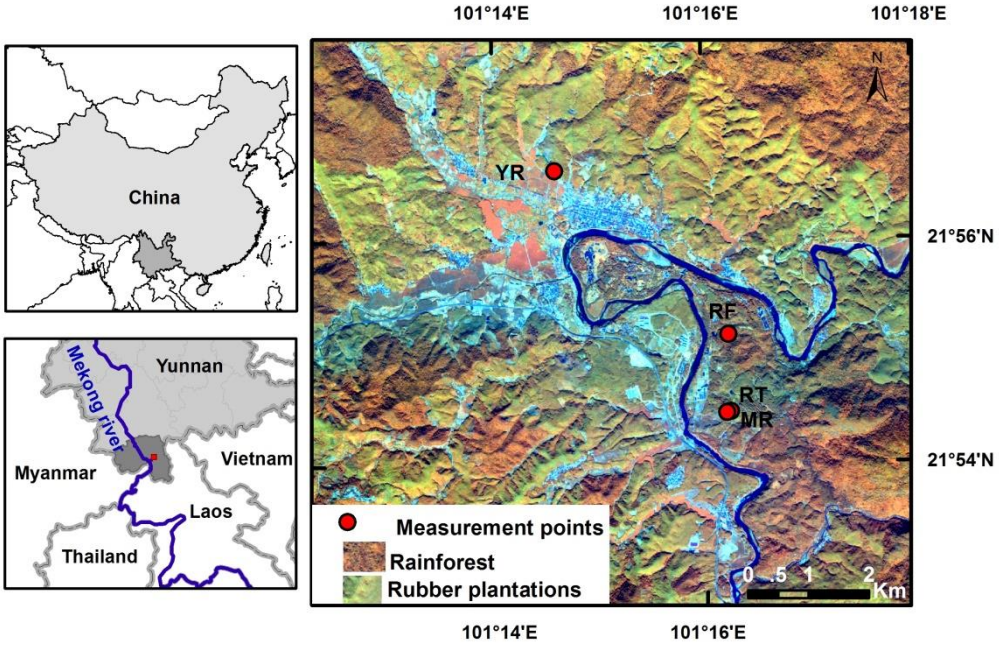

Figure 2.1 Location of the study sites. Measured sites are rainforest (RF), 22-year-old rubber monoculture (MR), 22-year-old rubber-tea intercropping (RT), and 9-year-old rubber monoculture (YR).

Table 2.1 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

2.3.2 Soil surface CO_2 and CH_4 flux measurements

Surface soil CO_2 efflux was measured with a LCi-SD1000 portable soil respiration system (ADC BioScientific Ltd., UK). This open chamber system calculates the CO_2 flux from the difference of CO_2 concentration between soil chamber and ambient air, using an integrated 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 ±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 CO_2 and 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 inserting into the soil, the volume and surface area of the chamber were 42.66 L and 0.20 m^2 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_2 and CH_4 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 Equation 2.1,

$$R = \frac{1}{V_0} \cdot \frac{P_1}{P_0} \cdot \frac{T_0}{T_1} \cdot \frac{V}{a} \cdot \frac{dc}{dt} \quad \text{(Equation 2.1)}$$

where R is gas flux (μmol m^{-2} s^{-1}), V_0 is the gas volume constant with a value of 22.4 L mol^{-1}, 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^2, dc/dt is the regression slope of gas concentration change during closure time. We further converted CH_4 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 Equation (2.2),

$$WFPS = \frac{M}{1-\frac{BD}{2.65}} \quad \text{(Equation 2.2)}$$

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

2.3.3 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 >0.02 mm, clay <0.002 mm and silt between 0.002 and 0.02 mm), as well as for total C and total N, cation exchange capacity (CEC) and pH ($CaCl_2$) analysis. Bulk density was determined from the weight of the core samples dried at 105 ℃, 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_4^+-N and NO_3^--N analysis. Texture (Pipetting method), total C and total N (Vario MAX CN, Elementar Analysensysteme GmbH, DE), CEC (1 mol L^{-1} pH 7 ammonium acetate, distillation) and NH_4^+-N and NO_3^--N (2 mol L^{-1} 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 Gautheyrou, 2007). Averaged soil properties of study sites are listed in Table 2.2.

2.3.4 Statistical analysis

Respiration rate, soil temperature and soil moisture of each collar were calculated from four continuous recordings from the respiration system and four points moisture measurements respectively. We further calculated cumulative CO_2 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_2 flux, and chamber measured CO_2 and CH_4 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. Figure 2.2-Figure 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 Equation 2.3 ("scale" in the equation means standardization). We studied the relationship between soil respiration rate and controlling factors using LME models (Equation 2.4), 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 (Equation 2.4). 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.

Table 2.2 Soil properties of the study sites

Site		**Rainforest (RF)**				**22-year-old rubber monoculture (MR)**				**22-year-old rubber-tea intercropping (RT)**				**9-year-old rubber monoculture (YR)**			
Parameters	**Depth (cm)**	**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**
Bulk density		1.02	1.08	1.16	1.15	1.07	1.13	1.19	1.32	1.09	1.16	1.15	1.18	1.22	1.28	1.38	1.43
($g\ cm^{-3}$)[a]		±0.06[a]	±0.06[a]	±0.11[a]	±0.13[a]	±0.02[ab]	±0.03[a]	±0.01[a]	±0.02[ab]	±0.06[ab]	±0.04[a]	±.05[a]	±04[a]	±0.01[b]	±0.06[a]	±0.02[a]	±0.01[b]
Texture	sand	27	26	20	19	23	22	21	23	21	17	12	12	43	42	43	43
(%)	silt	32	32	32	31	38	38	35	36	35	34	34	32	27	26	25	24
	clay	41	42	48	50	39	40	44	41	44	49	54	56	30	32	32	33
Total C (%)		2.26	1.20	0.96	0.80	1.70	1.70	1.51	1.19	1.66	1.11	0.86	0.72	1.17	0.83	0.62	0.45
Total N (%)		0.25	0.14	0.12	0.11	0.18	0.18	0.16	0.13	0.17	0.13	0.11	0.10	0.14	0.11	0.09	0.07
C:N		9.2	8.7	8.3	7.3	9.7	9.4	9.6	9.5	9.6	8.6	8.0	7.5	8.6	7.7	7.1	6.2
CEC ($cmol(+)kg^{-1}$)		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	9.0	8.5	9.0
pH ($CaCl_2$)		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
		0-5 cm	5-10 cm			0-5 cm	5-10 cm			0-5 cm	5-10 cm			0-5 cm	5-10 cm		
NH_4^+-N ($mgN\ kg^{-1}$)		8.7	6.3	n.d.	n.d.	6.2	8.8	n.d.	n.d.	10.5	8.7	n.d.	n.d.	8.9	7.3	n.d.	n.d.
NO_3^--N ($mgN\ kg^{-1}$)		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

[a]: 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.

$$scale(logR) = a' + b' \cdot scale(T) + c' \cdot scale(M) \quad \text{(Equation 2.3)}$$

$$logR = a + b \cdot T + c \cdot M + d \cdot (M)^2 \quad \text{(Equation 2.4)}$$

here T is soil temperature in ℃, 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 Equation 2.4, 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 Equation 2.4.

2.3.5 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-Tylor 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, μmol m^{-2} s^{-1}) and soil temperature (T, ℃) as:

$$R = R_{ref} \cdot e^{E_0\left(\frac{1}{T_{ref}+273.15-T_0}-\frac{1}{T+273.15-T_0}\right)} \quad \text{(Equation 2.5)}$$

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

We used the fitted value of R_{ref} to calculate soil respiration rate at temperature (T + 10) (Equation 2.6), Q_{10} was further calculated with Equation 2.7. Q_{10} of each site was reported as the average of Q_{10} determined from all measured soil temperatures.

$$R_{T+10} = R_{ref} \cdot e^{E_0\left(\frac{1}{T_{ref}+273.15-T_0}-\frac{1}{T+10+273.15-T_0}\right)} \quad \text{(Equation 2.6)}$$

$$Q_{10} = \frac{R_{T+10}}{R} \quad \text{(Equation 2.7)}$$

2) We also estimated Q_{10} with the two parameter exponential equation using fitted

parameter *b* according to Equations 2.8 and 2.9:

$$R = a \cdot e^{b \cdot T} \quad \text{(Equation 2.8)}$$

$$Q_{10} = e^{10 \cdot b} \quad \text{(Equation 2.9)}$$

In Equations 2.8 and 2.9, *T* is soil temperature in ℃, *a* and *b* are fitted parameters.

3) Taking soil moisture into account, we calculated the soil respiration rate at measured temperatures (Equation 2.11), as well as after a temperature rise by 10 ℃ from the back transformation of the LME models (Equations 2.10, 2.12). Q_{10} was then determined using Equation 2.13.

$$logR_{T+10} = a + b \cdot (T + 10) + c \cdot M + d \cdot M^2 \quad \text{(Equation 2.10)}$$

$$R = e^{a+b \cdot T+c \cdot M+d \cdot M^2} \quad \text{(Equation 2.11)}$$

$$R_{T+10} = e^{a+b \cdot (T+10)+c \cdot M+d \cdot M^2} \quad \text{(Equation 2.12)}$$

$$Q_{10} = \frac{R_{T+10}}{R} = e^{10 \cdot b} \quad \text{(Equation 2.13)}$$

Where *T* is soil temperature in ℃, *M* is volumetric soil moisture in%, *R* is predicted respiration rate, R_{T+10} is predicted respiration rate by increasing temperature 10 ℃, and *a*, *b*, *c*, *d* are parameters fitted from LME model (Equation 2.4). *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.

2.4 Results

2.4.1 Dynamics of soil respiration and CH_4 flux during wet period

All sites showed a very similar annual pattern of soil temperature (Figure 2.2a) 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 2.3). Soil moisture patterns (Figure 2.2b) 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 2.3). 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.

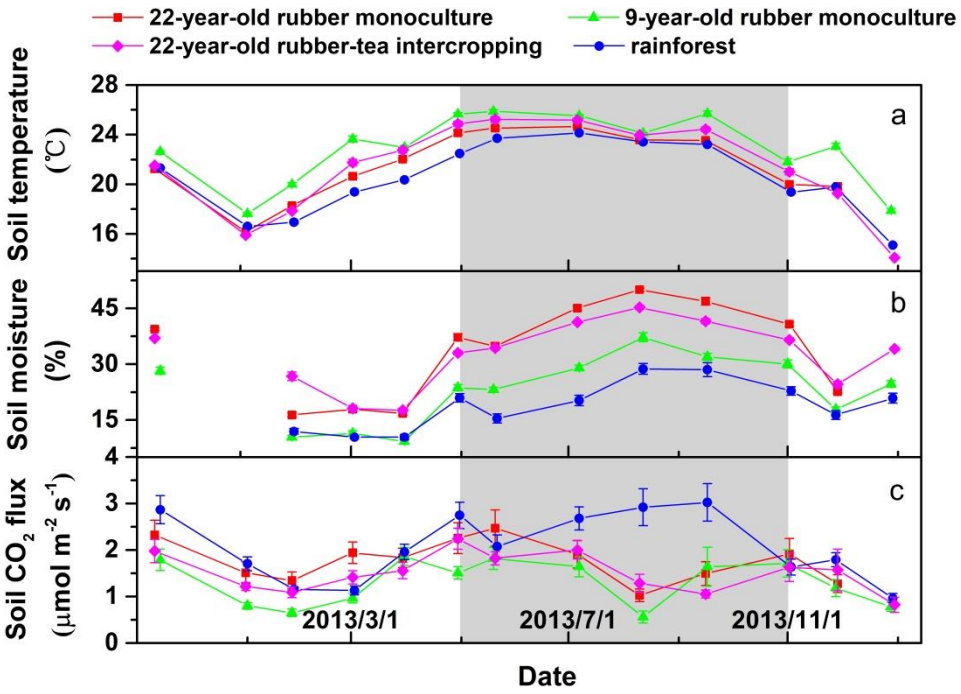

Figure 2.2 Dynamics of soil temperature at depth of 5 cm (a), soil volumetric water content at depth of 12 cm (b), and soil surface CO_2 flux rate (c). (Error bar is ±1 standard error of 12 measurements, shaded area represents rainy season).

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 (Figure 2.2c), 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 2.3).

Table 2.3 Average and standard error of soil temperature at 5 cm depth, soil moisture at 12 cm depth, water filled pore space (WPFS), soil respiration rate (ls-means comparison) and cumulative soil surface CO_2 flux (Tukey HSD)

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

*: different letters in superscript indicate significant difference at α=0.05 level

Soil respiration rate and moisture measured in 2014 consistently differed between sites during wet period (Figure 2.3a and c). Negative CH_4 fluxes at RF site at both sampling times indicated the important role of forest as a CH_4 sink (Figure 2.3b). 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.

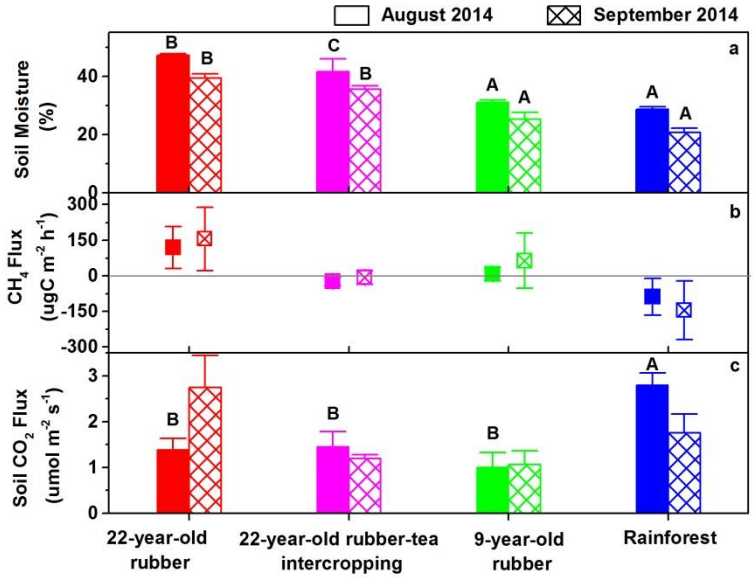

Figure 2.3 Soil CO_2 and CH_4 flux measured by static chamber method in rainy season 2014 (different letter indicates significant difference in mean comparison of sites in August and September respectively).

2.4.2 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 Equation 2.3. Soil temperature was relatively more important than moisture in explaining the temporal variation of soil respiration rate over a year (Table 2.4). 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 α=0.05 level, while the corresponding coefficient of soil moisture was significant only at RF site.

Table 2.4 Standardized coefficient of predictors of respiration rate (log transformed) in linear mixed effect model Equation 2.3

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) *b'*	0.62 ±0.05*	0.21 ±0.10*	0.45 ±0.07*	0.34 ±0.08*
Soil moisture (M) *c'*	0.13 ±0.06*	-0.06 ±0.10	-0.10 ±0.07	-0.10 ±0.08
n	131	131	142	143

*: significant at α=0.05 level

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. Equation 2.4 vs Equation 2.3). Estimated coefficients, standard errors and the fitting of the LME models with log transformed soil respiration are shown in Table 2.5. 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.

Table 2.5 Parameters of linear mixed effect (LME) model with log transformed soil respiration rate (Equation 2.4: $logR = a + b \cdot T + c \cdot M + d \cdot (M)^2$)

Parameters	Rainforest (RF)	22-year-old rubber monoculture (MR)	22-year-old rubber-tea intercropping (RT)	9-year-old rubber monoculture (YR)
Intercept *a*	-2.361 ±0.255	-1.697 ±0.591	-2.330 ±0.503	-2.481 ±0.474
Soil temperature (T) *b*	0.113 ±0.009*	0.055 ±0.026*	0.080 ±0.011*	0.085 ±0.019*
Soil moisture (M) *c*	0.057 ±0.018*	0.073 ±0.024*	0.075 ±0.027*	0.076 ±0.023*
Quadratic Moisture (M^2) *d*	-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^2	0.75	0.52	0.53	0.40

*: significant at α=0.05 level

The soil respiration tipping points caused by moisture change (see parameters in Table 2.5), 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.

2.4.3 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 2.2). 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 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 ($CaCl_2$) ranging from 3.4 to 4.9 (Table 2.2).

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_2 flux. Significant correlation between cumulative soil CO_2 fluxes and total C in topsoil (correlation coefficient r=0.98) suggested that total C content mainly determined the annual soil CO_2 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_4^+-N was the dominant N form at all rubber sites, while rainforest site with a similar NH_4^+-N content as rubber sites had larger amounts of NO_3^--N than NH_4^+-N (Table 2.2). Though the highest CH_4 uptake rate took place at rainforest site where total N and NO_3^--N were highest in the topsoil, we did not observe significant correlations between CH_4 flux and total N or mineral N at the four sites.

2.4.4 Temperature sensitivity – Q_{10}

Q_{10} values determined from Lloyd and Taylor equation were similar for all sites when T_{ref}=15 ℃, but varied largely between sites when the two parameter exponential function or the LME model were used (Table 2.6). 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 2.6 Temperature sensitivity Q_{10} derived from three functions (see Equations 2.5-2.13)

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 ±0.00	1.81 ±0.00	1.82 ±0.00	1.77 ±0.00
Two parameter exponential	2.87 ±0.41	1.42 ±0.26	1.60 ±0.21	2.27 ±0.48
Linear mixed effect model	3.11 ±0.28	1.73 ±0.45	2.23 ±0.24	2.32 ±0.44

We back transformed the LME model (Equation 2.11) and plotted results demonstrate how soil moisture modifies the response of soil respiration rate to temperature change (Figure 2.4). 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 Equation 2.4). 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 (Figure 2.4).

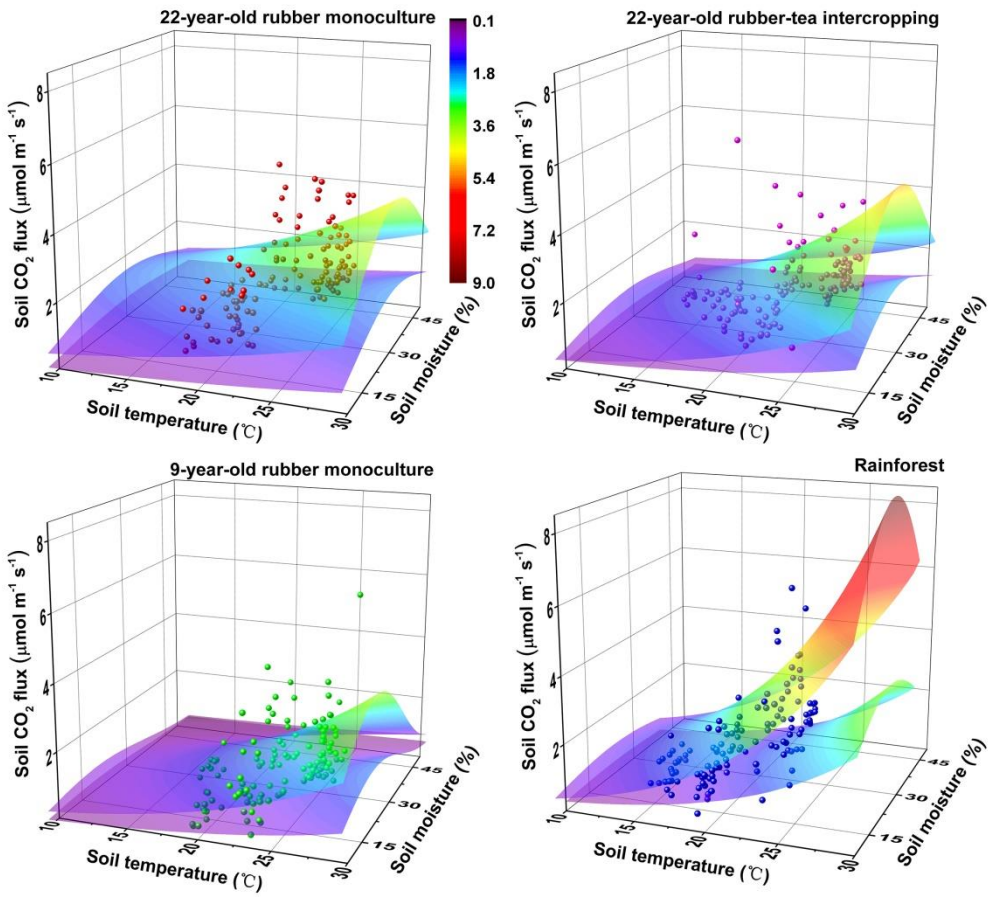

Figure 2.4 Soil temperature and moisture effect on surface soil CO_2 flux (Simulated 3-D surfaces are back transformations of linear mixed effect (LME) model (Equation 2.11), with maximum and minimum intercept a). Points are field measurements.

2.5 Discussion

2.5.1 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 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 (Figure 2.4). 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_2 flux by filling pores of topsoil with water, creating a barrier and inhibiting CO_2 diffusion out of soil (Sotta *et al.*, 2004). Furthermore, persistent

moist conditions in combination with high clay content can reduce O_2 availability in the soil, which would limit the aerobic respiration and decrease the CO_2 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 (Figure 2.4): 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_2 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^3 m^{-3} 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 (Ishizuka *et al.*, 2005; Hassler *et al.*, 2015). 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).

2.5.2 Soil CH_4 flux during the wet period

The observed contrast of rainforest soils acting as CH_4 sink while becoming a weaker sink or even CH_4 source under rubber plantations during the wet period indicates that intensive rubber cultivation might weaken the CH_4 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_4 flux was negatively correlated to WFPS and the relative decline of CH_4 uptake was larger under rubber plantations compared to rainforest. Fang *et al.* (2010) observed a steady increment of CH_4 fluxes from January to September under rainforest, and where months with soil moisture around 0.4 m^3 m^{-3} resulted in net CH_4 emission during the rainy season (1.18 ± 1.64 kg CH_4 ha^{-1} $season^{-1}$). In Sumatra, rubber plantations consumed less CH_4 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_4 sink or stronger CH_4 source compared to rubber plantations (Ishizuka *et al.*, 2002; Hassler *et al.*, 2015).

Interaction with soil mineral nitrogen also modulates the CH_4 processes in the soil. Increased NH_4^+-N, directly or indirectly through fertilization, has been demonstrated having a competitive inhibitory effect on CH_4 oxidation, and substantially reduced CH_4 oxidation potential in cultivated soils (Nesbit and Breitenbeck, 1992; Le Mer and Roger, 2001; Bodelier and Laanbroek, 2004). Comparing with well aerated forest soils with NO_3^--N as dominant mineral N form, the high NH_4^+-N in soils of rubber plantations, as in our study, is likely to inhibit CH_4 oxidation potential under aerobic conditions, and shift towards CH_4 production when O_2 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_4 production comparable to rubber plantations under wet condition.

The differences in temporal patterns of soil CO_2 and CH_4 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_4 studies for rubber worldwide, except those reported in Sumatra. Given the extent of land use conversion to rubber and the importance of CH_4 on climate change, further studies are needed. Our short measurements of CH_4 flux and the scarce studies on tropical upland soils are not enough to fully verify the changes of mechanism in soil CH_4 processes after forest conversion into rubber plantations.

2.5.3 Temperature sensitivity Q_{10}

In most studies Q_{10} 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_{10} values similar to those obtained in our study (Table 2.6), 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 CO_2 emitted from rainforest is likely to increase more than that emitted from rubber plantations in response to a warming climate.

2.5.4 Land use change impact on soil gaseous carbon fluxes

We summarized our measurements and previously published annual soil CO_2 fluxes and CH_4 fluxes of tropical rainforests and rubber plantations in the main rubber growing region of Southeast Asia in Figure 2.5 and Table A1. Data based on short period measurements were excluded to avoid determining the annual flux from single time point or seasonal measurements. Annual soil CO_2 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 (Figure 2.5), except for the data from Ishizuka *et al.* (2002) showing low soil CO_2 emissions in Sumatra.

The annual soil CO_2 flux in this study was in the lower range of reported values in Southeast Asia. Meanwhile, the observed difference between soil CO_2 emissions under rainforest and rubber plantations was of the same order, as found in Hainan (Zhou *et al.*, 2013; Wu *et al.*, 2014) and on clay Acrisols in Indonesia (Hassler *et al.*, 2015); the difference became smaller in mature rubber plantations (Figure 2.5, Table A1). Soil CH_4 fluxes were characterized by large spatial and temporal variation. If annual soil CH_4 fluxes in the region are considered, only the clay Acrisols site by Hassler *et al.* (2015) showed consistently lower CH_4 consumption rates by soils under rubber monoculture compared to soils under jungle rubber and rainforests (Figure 2.5).

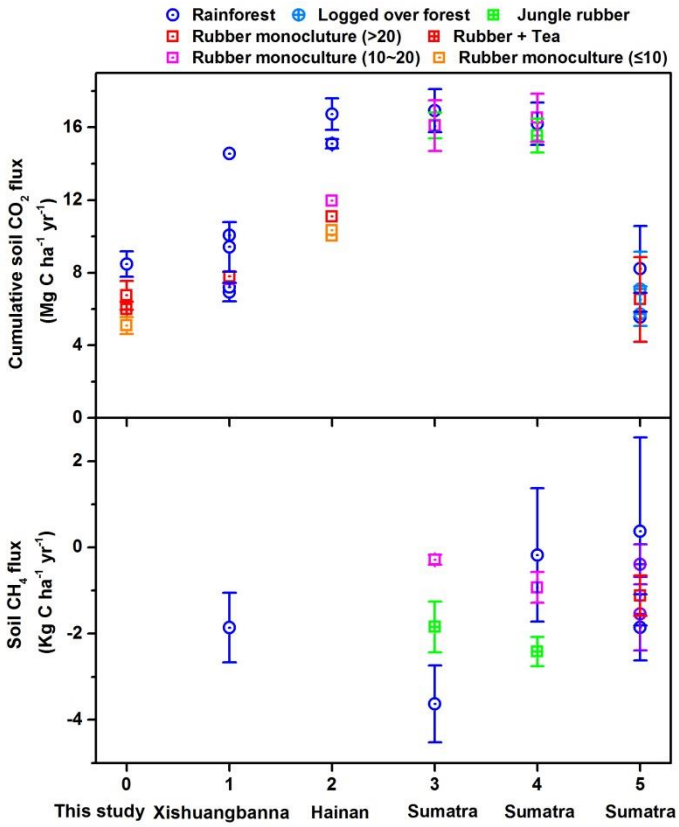

Figure 2.5 Soil CO_2 and CH_4 fluxes in rubber plantations and forests in the study region. Studies in group 1-Xishuangbanna include Sha *et al.* (2005), Fang *et al.* (2010), Zhang *et al.* (2015), Fang and Sha (2006) and Lu *et al.* (2009), group 2-Hainan referred to Zhou *et al.* (2013) and Wu *et 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.

Land conversion from forest to rubber plantation affects soil CO_2 and CH_4 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^{-1} to 12.96 Mg ha^{-1} (Ren *et al.*, 1999; Tang *et al.*, 2010; Kotowska *et al.*, 2016). 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^{-1}) 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_2 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 understory with sparse vegetation, which also reduce soil CO_2 emission under young plantations. Looking at the contribution of autotrophic and heterotrophic respiration components (Ferré *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_2 flux and carbon stock.

Another factor controlling seasonal dynamics of soil respiration and overall CH_4 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_4 production in rubber plantations.

The impact of converting forest into rubber plantation on soil CH_4 consumption is insufficiently studied and poorly understood. Existing literature on CH_4 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_4 processes, more frequent measurement and information on substrates, vertical gas concentration gradient and $\delta^{13}CH_4$ 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_4 by soil was two orders of magnitude lower than the soil CO_2 flux even when their GWP is considered (Fang *et al.*, 2010; Hassler *et al.*, 2015), CH_4 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.

2.6 Conclusion

Converting rainforest to rubber plantations tended to reduce soil CO_2 emissions and weakened CH_4 uptake especially during the very wet period. Different soil aeration conditions were likely the main reason for suppression of soil respiration and low CH_4 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.

Chapter 3 Converting forests into rubber plantations weakened the soil CH_4 sink in tropical uplands[2]

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3.1 Abstract

Large-scale conversion of natural forest to rubber plantations has taken place for decades in Southeast Asia, help to make it a deforestation hot spot. Besides negative changes in biodiversity, ecosystem water, and carbon budgets, converting forests to plantations often reduced CH_4 uptake by soils. The latter process, which might be partly responsible for resumed increase in the growth rate of CH_4 atmospheric concentrations since 2006, has not been adequately investigated. We measured soil surface CH_4 fluxes during 2014 and 2015 in natural forests and rubber plantations of different age and soil textures in Xishuangbanna, Southwest China—a representative area for this type of

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land-use change. Natural forest soils were stronger CH_4 sinks than rubber soils, with annual CH_4 fluxes of -2.41 ± 0.28 and -1.01 ± 0.23 kg C ha^{-1} yr^{-1}, respectively. Water-filled pore space was the main factor explaining the differences between natural forests and rubber plantations, even reverting rubber soils temporarily from CH_4 sink into a methane source during the rainy season in older plantations. Soil nitrate content was often lower under rubber plantations. Added as a model covariate, this factor improved explanation power of the CH_4 flux—water-filled pore space regression. Although soils under rubber plantation were more clayey than soils under natural forest, this was not the decisive factor driving higher soil moisture and lower CH_4 uptake in rubber soils. Thus, the conversion of forests into rubber plantations exerts a negative impact on the CH_4 balance in the tropics and likely contributes to global climate.

Keywords

deforestation, land-use change, methane, rubber plantation, soil moisture, soil texture, tropics

3.2 Introduction

An unprecedented agricultural expansion across the tropics driven by economic development is associated with extensive deforestation; that is, more than 55% of new agricultural land (including tree plantations) derived at the expense of intact forests, and 28% from disturbed forests from 1980 to 2000 (Gibbs *et al.*, 2010). Remarkably, the global forest loss occurred almost exclusively in the tropics during 2010–2015 (Keenan *et al.*, 2015). Deforestation and forest degradation contributed almost half to greenhouse gas (GHG) emissions in agricultural production, land use, land-use change, and forestry sector, comprising 11% of total global anthropogenic GHG emissions (49 ± 4.5 Gt CO_2 eq yr^{-1}) in 2010 (Ciais *et al.*, 2013). Considering the important role of tropical forests in regulating climate and weather patterns at regional and even global scales, deforestation and forest degradation exert a more profound influence than changes in other terrestrial biomes (Brandon, 2014).

Tree plantations account for a large portion of total agricultural land; they increased rapidly in Southeast Asia (Gibbs *et al.*, 2010). Rubber (*Hevea brasiliensis*) was one of the tree crops extensively expanding into nontraditional growing areas due to an increasing latex demand and a price boom in the first decade of the new millennium (Fox, 2014; Ahrends *et al.*, 2015; Warren-Thomas *et al.*, 2015; Sarathchandra *et al.*, 2018). The area of rubber plantation in Asia reached 10.4 million ha in 2017, accounting for 89% of world total area (FAOSTAT, 2019), and an expansion by 4.3–8.5

million ha in a decade was predicted to meet the continually growing demand for natural rubber (Warren-Thomas *et al.*, 2015).

Rubber plantations have been highly profitable and have contributed to the increase of household income and development of local rural economy (Fox *et al.*, 2014; Min *et al.*, 2017). However, the rubber expansion in the Indo-Burma biodiversity hot spot resulted in loss of biodiversity (Cotter *et al.*, 2017) and substantial decline in ecosystem services compared with forest, including increase of evapotranspiration and resulting in water shortages in dry season (Tan *et al.*, 2011), and decrease of carbon sequestration in aboveground biomass (Kotowska *et al.*, 2016; Yang *et al.*, 2016) and in soil (de Blécourt *et al.*, 2013), as well as lowering of ecosystem carbon stocks if compared with swidden agriculture (Blagodatsky *et al.*, 2016; Bruun *et al.*, 2018; Guillaume *et al.*, 2018).

The degradation of soils by converting natural forest into intensified agricultural land, including plantations, often has reduced soil functions such as CH_4 sink (Reay *et al.*, 2018). The oxidation of CH_4 in soils is the only known biotic CH_4 sink, which is approximately three times larger than the latest estimate of the mean net annual CH_4 emission during 2003–2012 (Saunois *et al.*, 2016). The majority of tropical upland forest soils are net CH_4 sinks (Ishizuka *et al.*, 2005; Werner *et al.*, 2006; Dalal and Allen, 2008; Veldkamp *et al.*, 2013), but converting forest into pastures, cacao agroforestry systems, rubber plantations, and oil palm plantations in humid tropics in Indonesia already showed a tendency of declining CH_4 uptake by soils (Veldkamp *et al.*, 2008; Pendall *et al.*, 2010; Hassler *et al.*, 2015).

The atmospheric CH_4 consumption by soils is primarily controlled by physical factors that regulate CH_4 entry into the soil (Bodelier, 2011). Aerobic conditions favor CH_4 oxidation by methanotrophs, whereas anaerobic conditions favor CH_4 production by methanogens. As an indicator of soil aeration and a regulator of gas diffusion in soil media, soil moisture or water-filled pore space (WFPS) was often found negatively correlated with CH_4 uptake in tropical forests and plantations (Butterbach-Bahl *et al.*, 2004; Werner *et al.*, 2006; Fang *et al.*, 2010; Gütlein *et al.*, 2018). Soil texture is a key factor, important not only for gas transport but also in controlling the microenvironment, affecting microbial CH_4 production and oxidation (Le Mer and Roger, 2001; Ishizuka *et al.*, 2002). Soil chemical properties, such as nitrogen input and status, are further known to have a range of possible interactions with CH_4 processes (Bodelier and Steenbergh, 2014).

To mitigate the impact of forest-to-rubber conversion on ecological (including control

on soil CH_4 fluxes) and socioeconomic sustainability, the complex interactions between affected driving factors need to be clarified. Land-use change also affects C and N cycling, but research done so far interpreted the correlation or univariate regression between CH_4 fluxes and soil nitrogen (Dobbie and Smith, 1996; Fang *et al.*, 2010; Veldkamp *et al.*, 2013) without considering the fact that mineral nitrogen content and status were not independent from soil water dynamics (Bodelier, 2011). Another unsolved problem is interaction of intrinsic soil properties and changed land cover types. Thus, assessed land-use pairs are often confounded with soil texture differences in field surveys; that is, assessed plantations have higher clay content than natural reference systems (Ishizuka *et al.*, 2002; Werner *et al.*, 2006). Very few studies have explicitly addressed the effect of texture on soil moisture, especially when the latter appeared to be the main factor controlling soil CH_4 uptake during forest-to-rubber conversion.

Therefore, we conducted this study in the northern Asian tropics, where monsoon climate dominates and rubber plantations expanded extensively, to assess the impact of converting forest into rubber plantation on soil functions such as CH_4 sink with consideration of the main gaps mentioned above. We hypothesized that (a) soils under intensively managed rubber monocultures have lower CH_4 uptake than natural forests; (b) soil water content is a key factor in determining temporal variation of CH_4 fluxes; and (c) disentangling the intrinsic connection between soil water content, soil texture, and mineral nitrogen helps in assessing the impact of land-use change per se. We aimed to assess the impact of land-use change on soil function as CH_4 sink and to differentiate the effects of land use and soil texture.

3.3 Materials and Methods

3.3.1 Study site

The Naban River Watershed National Nature Reserve (22°4′22.0″N–22°16′57.5″N, 100°32′12.5″E–100°44′4.6″E) is located in Xishuangbanna Prefecture, Southwest China (Figure 3.1). The altitude decreases from the northwest to the south, ranging from 539- to 2304-m a.s.l. Annual air temperature was 22.30 ± 0.58 ℃, and annual precipitation was 1157 ± 169 mm, with 85% falling between May and October (Jinghong meteorological station [582 m a.s.l] 1954–2015, located 19 km from the study site).

According to Yang *et al.* (2016) and land-use maps produced during previous projects (Living Landscapes China (LILAC), https://lilac.uni-hohenheim.de/index.php; and

Sustainable Rubber Cultivation in the Mekong Region (SURUMER), https://surumer.uni-hohenheim.de/), rubber plantations in this nature reserve increased from 1.3% to 8.4% and 9.3% of total area in 1989, 2007, and 2013, whereas forest accounted for 54.9%, 64.8%, and 60.4% of the total area, respectively.

This study includes two datasets gathered from (a) the SURUMER project, referred to as Project I and (b) the Green Rubber project, referred to as Project II in the following text (Figure 3.1). The combination of these two datasets facilitated the statistical identification of common factors controlling the temporal variation of CH_4 fluxes and factors explaining differences in CH_4 uptake between natural forest and rubber plantation.

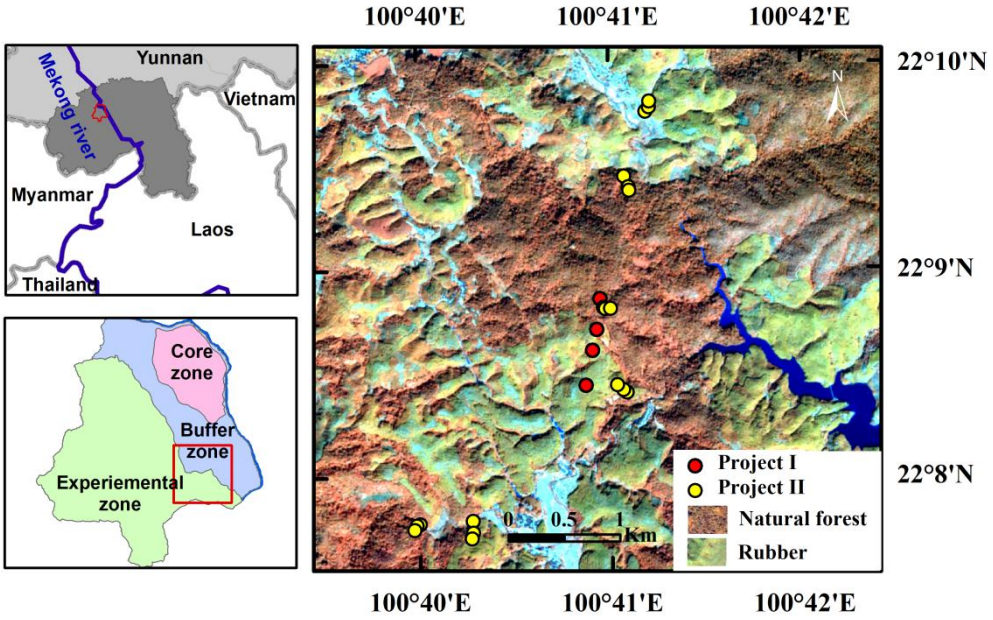

Figure 3.1 Location map of the transects in two projects in the Naban River Watershed

Project I consisted of one plot in natural forest and three plots in rubber monocultures of different ages (9, 17, and 30 years since planting), referred to as young, mid-age, and old rubber plots (Figure B1a). Each plot had three chambers installed. Project II employed a hierarchical sampling scheme. Three groups of sites (Mandian, Manfei, and Manlü) were selected as spatial replicates at the first sampling level. A neighboring pair (distance <1 km) of natural forest and mid-age rubber plantation land use was selected at each site as the second sampling level, and three plots were laid out under each land use at upper, middle, and lower slope positions as the third sampling level (Figure B1b). Each plot also had three chambers installed. Details of the site selection and sampling layout of the Project II are described in Goldberg *et al.* (2017).

Rubber plantations in the region were established on terraces, with inter-row distance and tree spacing of 8–10 and 2.5–3.0 m (7.3 and 2.6 m for old rubber plot in Project I) on former state farms, whereas averaged spacing in smallholder plantations (young and mid-age rubber) was 6 and 2.5 m. The width of terraces was much narrower than slopes between tree rows, with terrace width ranging from <1 m in smallholder plantations to about 1.5 m in plantations on former state farm (e.g., Figure 1 in de Blécourt *et al.*, 2014).

It is typical to fertilize young rubber trees with compound fertilizer to the soil pits between every two trees on the terrace (Min *et al.*, 2017). However, in Project I, no fertilizers were applied in recent years because of the low latex price and increasing labour cost. A 45% compound fertilizer (N–P–K = 15-15-15) was applied at rate of 1.5 kg per tree in Project II (Goldberg *et al.*, 2017). Understory vegetation was cleared by spraying glyphosate on both terrace and slope, whereas the remaining herbicide-resistant plants or shrubs were slashed.

3.3.2 Soil physical and chemical properties

In Project I, soil was sampled at six points in each plot at a depth of 0–15 cm, air-dried, and passed through a 2-mm sieve. Samples were mixed to obtain one composited sample for each forest plot and two composited samples (one for the terrace and one for the slope) in rubber plots, for subsequent texture, pH, total C, and total N analysis. We dug a profile in each plot and sampled three soil cores using 100-cm^3 core rings and calculated the bulk density based on 105 °C oven-dry soil weight. Fresh soil samples at 0- to 5- and 5- to 10-cm depth were taken on three of the gas sampling dates for mineral nitrogen analysis (NH_4^+–N and NO_3^-–N). In order to properly mix wet soils with clayey texture, fresh soil was sieved and stored at 0–4 ℃ in the fridge for a maximum of 3 days before extracting with 2-mol L^{-1} KCl and analyzed using an Auto Analyzer 3 (SEAL Analytical Ltd., USA). Soil texture was determined using the pipette method and the International Soil Science Society particle size classification system (sand: 0.02–2 mm, silt: 0.002–0.02 mm, and clay: 0–0.002 mm), whereas pH was measured by pH meter (Hanna HI 2211, Hanna Instruments, USA) in 0.01 mol L^{-1} $CaCl_2$ solution (Pansu and Gautheyrou, 2007). Total C and total N were analyzed by element analyzer (vario MAX CNS, Elementar, DE).

In Project II, soil was sampled at 0–10 cm, once in the rainy season (September 2014) and once in the dry season (March 2015). Then, samples at each slope position were mixed and analyzed as one composite sample for texture, pH, organic matter, total N, NH_4^+–N, and NO_3^-–N analysis. Soil bulk density was sampled with 100 cm^3 soil core

rings at depths of 0–5 and 5–10 cm from a soil pit at each slope position. Sieved fresh soil samples were stored at −20 ℃ before determining mineral nitrogen in the lab as detailed in Goldberg *et al.* (2017).

Site characteristics of the two projects are shown in Tables B1 and B2.

3.3.3 Soil surface CH_4 flux, soil moisture, and temperature

Soil surface CH_4 fluxes were measured using static chambers and gas chromatography. Three chambers were installed as subsamples, aiming to cover the spatial variation in each plot of Project I, with one placed on the terrace and two on the slope between rubber tree rows. Thus, three chambers were installed along the slope on the natural forest plot, and nine chambers were installed in the three rubber plots of different age. In Project II, three chambers were installed as subsamples in each plot at sampling level of slope position, which resulted in 27 chambers installed in natural forests and 27 chambers installed in mid-age rubber plantations. Chambers were inserted into soil at 5-cm depth, covering soil surface area of 0.20 m^2 with total volume of 42.66 L. CH_4 fluxes were determined from five consecutive samples taken from headspace during 45-min closure time, detailed in Lang *et al.* (2017). We measured soil surface CH_4 fluxes for Project I on five dates from August 2014 to August 2015 and for the Project II on 11 dates between November 2014 and December 2015 at approximately monthly intervals.

Soil moisture was measured using FieldScout TDR 100 (Spectrum Technologies Inc., USA) at 0- to 12-cm depth in Project I, where four points were measured around each chamber. Soil temperature of Project I was determined by a Pendant temperature logger (UA-002-08, Onset Computer Corporation, USA) at 5-cm soil depth. In Project II, HOBO stations (Onset Computer Corporation, USA) including data loggers (U30-NRC), frequency domain reflectometry soil moisture sensors (S-SMC-M005), and soil temperature sensors (S-TMB-M006) were installed to measure soil moisture and soil temperature at 5-, 10-, 30-, and 70-cm depth at each slope position. In order to keep the soil moisture and temperature inputs for statistical analysis comparable for the two projects, we chose soil temperature at 5-cm depth and soil moisture at 10-cm depth from HOBO station in Project II. WFPS was calculated from measured volumetric water content and bulk density, using the equation $WFPS = SM/(1 - BD/2.65)$ (Werner *et al.*, 2006), where *WFPS* is the water-filled pore space in units of %, *SM* is the soil volumetric water content in %, *BD* is the bulk density in g cm^{-3}, and 2.65 is the density of quartz.

Cumulative CH_4 flux of each chamber installed in Project II was calculated by linear interpolation between every two sampling dates. We did not calculate the cumulative flux for Project I due to the limited number of measurements and long intervals between samplings.

3.3.4 Statistical analysis

Statistical analysis was performed using SAS University Edition/SAS Studio (SAS Institute Inc., USA), and graphs were prepared using OriginPro 9.0 (OriginLab, Northampton, USA). Mixed effect models were used in comparing means of CH_4 fluxes between land uses and regression analysis to relate CH_4 fluxes to controlling factors and covariates. Hierarchical sampling levels were adjusted and defined as levels of nested random effects to account for different sampling layout in the two projects (Figure B2). The temporal autocorrelation in repeated measurements of CH_4 fluxes over the same chamber was addressed by comparing and selecting proper covariance structures (Figure B2). We assessed the distribution of residuals of each model according to Shapiro–Wilk test and skewness of histograms. Coefficients of determination (R^2) for regressions with mixed models were determined using the average semivariance method proposed by Piepho (2019).

Means of CH_4 fluxes from natural forest and rubber plantation were compared using joint datasets from the two projects. Land use, measurement date, and their interaction were set as fixed effects to test the land-use effect on CH_4 fluxes and whether the differences depend on sampling date. Additionally, each sampling level was crossed with the date and set as random effect to account for autocorrelations between dates, which resulted in three levels of random effects in the initial model. A random effect was removed from the model when the variance was estimated to be 0. Chambers were defined as subjects of repeated measurements, and covariance structures were selected according to the Akaike information criterion (AIC).

Because Project I did only have one slope position, the site effect from the three groups of sites and the slope position effect from three slope positions on CH_4 fluxes were tested using only the Project II dataset. When testing site/slope position effects, we set site/slope position, land use, measurement date, and all their interactions as fixed effects (three-factorial full model). Random effects, covariance structure, and repeated measurements were handled similarly as described above.

Annual cumulative CH_4 flux from Project II was also compared at land-use level, site, and slope position level. Due to the aggregation of flux to cumulative flux, there were

no date factor and repeated statement in the defined model.

We selected the environmental factors controlling CH_4 fluxes according to the Pearson correlation matrix between CH_4 flux, WFPS, and soil temperature measured on multiple dates. Thereafter, we employed a regression analysis using the MIXED procedure with the controlling factor in linear form and subsequently compared the output to the model with the controlling factor in quadratic form. Selected variables, the land-use factor, and their interactions were set as fixed effects. Date was treated as random effect in order to obtain a more general model. Repeated measurements and temporal correlation were addressed as described above. Insignificant interactions and main effects were removed from the regression model based on *F* tests, and regression was performed with the generalized linear model (GLM) procedure when all random effects showed a variance of 0. For Project II, because of only one soil temperature and WFPS recording for three chambers installed on the same slope position, we averaged CH_4 fluxes of the three chambers per slope position as input for regression analysis.

In order to explain the interactions of CH_4 flux with main controlling factor and soil properties, we added soil properties one after another (forward selection), including total C, total N, NH_4^+–N, NO_3^-–N, pH, and clay content, as covariate to the regression model selected at the last step. We considered the covariate as improving model's explanatory power for CH_4 flux variation if its addition resulted in (a) the smaller AIC (using maximum likelihood in place of restricted maximum likelihood for estimating variance components), (b) smaller sum of variance from all random effects and residual effects from covariance parameter estimates, and (c) a significant fixed effect in *F* tests. To compare the relative importance of input variables having different units and magnitude, we estimated standardized regression coefficients by standardizing all input variables using STANDARD procedure. After the covariates that improved the model in both projects are identified, we did regression using unstandardized variables as input. In Project I, soil NH_4^+–N and NO_3^-–N contents were sampled on three dates of flux measurement. Data on mineral N content for another two flux measurement dates needed for the covariate analysis were taken from the nearest sampling date in the same season. Other analyzed soil properties in Project I were constants over time. In Project II, soil was sampled once in rainy season and once in dry season, so that in statistical analysis, multiple sampling dates for gas fluxes during rainy or dry season corresponded to either rainy season or dry season properties, except for soil texture, which was the same for all dates.

We compared means of WFPS between natural forest and rubber plantation in each project, using similar mixed model structures as in CH_4 flux comparisons. In Project II,

in order to disentangle the land-use effect and texture contribution, we analyzed the relationship between annual cumulative CH_4 flux and texture using the GLM procedure and analyzed the texture effect based on WFPS difference between land-use types using a mixed model.

3.4 Results

3.4.1 Seasonal and annual soil CH_4 fluxes in different land-use types

Soil surface CH_4 fluxes during the dry season were negative at most sampling dates both for natural forests and for rubber plantations (Figure 3.2b,c, unshaded periods). CH_4 fluxes increased with increasing precipitation and temperature from dry to rainy season, with soils under rubber tending to act as CH_4 source from August to September when precipitation was abundant (Figure 3.2b,c, shaded periods). The mean CH_4 fluxes from natural forests were significantly lower than fluxes measured under rubber plantations, with a mean flux of -27.2 ± 3.4 and -10.4 ± 2.6 μg C m^{-2} h^{-1}, respectively (Table 3.1). Comparison of annual CH_4 uptake in Project II further indicated significantly higher CH_4 uptake by natural forest soils than by rubber soils, with a cumulative CH_4 flux of -2.41 ± 0.28 and -1.01 ± 0.23 kg C ha^{-1} yr^{-1}, respectively (Table 3.1 and Figure 3.2d).

The comparison of CH_4 flux means in Project II at the site level and at slope position level revealed that neither site nor slope position was significant. Means of CH_4 fluxes in natural forest were generally lower than the fluxes in rubber plantation at each level of site or slope position (Table B3).

Comparison of the covariance structures showed that the temporal correlation of CH_4 fluxes between measurement dates was very weak.

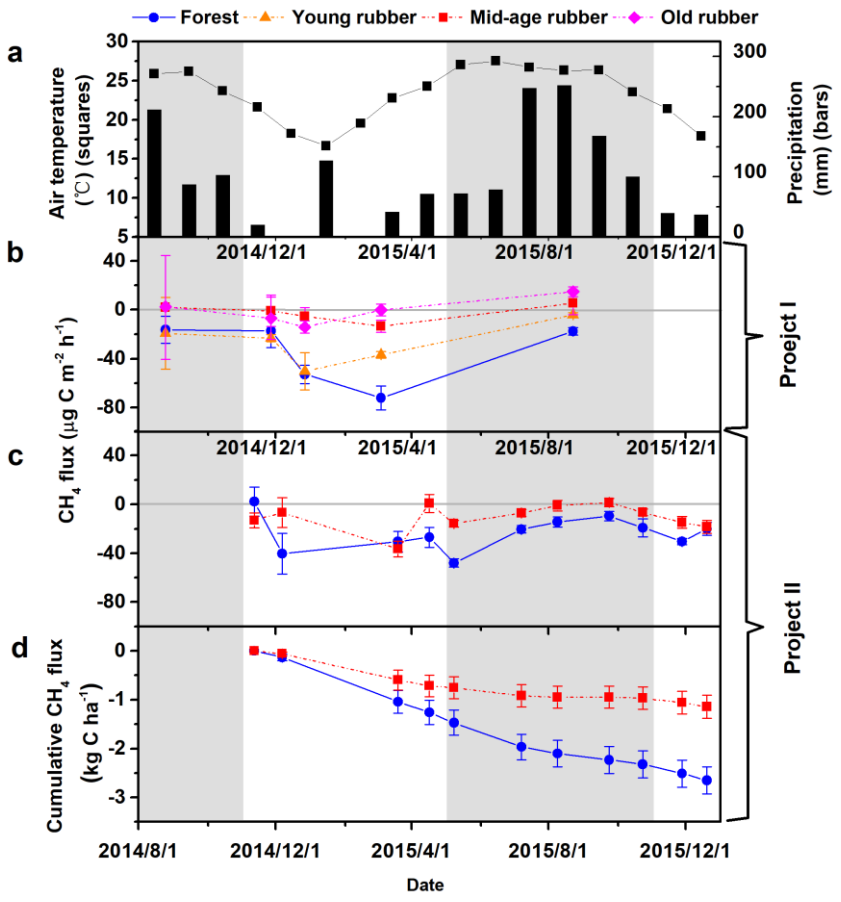

Figure 3.2 Climate conditions and dynamics of CH_4 fluxes during 2014 and 2015. Climate conditions (a), soil surface CH_4 fluxes measured in Project I (b) and in Project II (c), and cumulative CH_4 fluxes in Project II (d). Shaded parts of graphs represent rainy season. Negative CH_4 flux means CH_4 uptake; more negative flux represents higher uptake. Error bars are standard errors, $n = 3$ for each point in Project I and $n = 27$ for each point in Project II

Table 3.1 Soil CH_4 flux means from joint analysis and annual cumulative CH_4 fluxes from Project II only (mean ± standard error) for natural forests and rubber plantations

	Land use	**CH_4 flux (μg C m^{-2} h^{-1})**	***n***
Projects I and II	Natural forest	−27.2 ± 3.4[a]*	310
	Rubber	−10.4 ± 2.6[b]	341
	Land use	**Cumulative CH_4 flux (kg C ha^{-1} yr^{-1})**	***n***
Project II	Natural forest	−2.43 ± 0.26[a]	25
	Mid-age rubber	−1.01 ± 0.25[b]	27

* Means sharing no common letter in superscript suggest significant difference between natural forest and rubber plantation ($p < 0.05$).

3.4.2 Effect of WFPS on CH_4 fluxes

CH_4 flux was significantly correlated with both soil temperature and WFPS measured on multiple dates, with higher Pearson correlation coefficients for WFPS (r = 0.59 in Project I and r = 0.33 in Project II) than for soil temperature (Table 3.2).

According to the correlation matrix, WFPS was chosen as first controlling variable in the regression analysis for the description of temporal variation in CH_4 fluxes. Despite different ranges of WFPS and significantly lower WFPS in forest soils as compared with soils rubber is grown on (Table 3.3), land use was not a significant fixed effect in the CH_4 flux model, which led to a single regression equation. We found that the quadratic regression model explained the relationship between WFPS and CH_4 flux (Table B4) better for Project I, whereas a linear model was better for Project II. These two regression models were used as the base models in subsequent analyses of covariance.

Table 3.2 Pearson correlation coefficients between CH_4 flux and soil temperature and moisture measured on multiple dates. First controlling variables are shown in bold

		Soil temperature (5 cm)	Water-filled pore space (0–12 cm)	*n*
Project I	CH_4 flux	0.43*	**0.59***	59
	Soil temperature (5 cm)	1	0.68*	
		Soil temperature (5 cm)	Water-filled pore space (10 cm)	*n*
Project II	CH_4 flux	0.18*	**0.33***	198
	Soil temperature (5 cm)	1	0.19*	

* Significant correlation at α = 0.05 level.

Table 3.3 Means and range of water-filled pore space in Project I and Project II

Projects	Land use	Mean ± standard error	Range (min–max)	*n*
		Water-filled pore space (0–12 cm, %)		
Project I	Natural forest	28.8 ± 1.0[a]*	12.4–49.9	15
	Young rubber	41.1 ± 1.0[b]	26.7–61.5	15
	Mid-age rubber	43.2 ± 1.0[b]	31.4–59.6	15
	Old rubber	64.0 ± 1.0[c]	39.5–84.9	15
		Water-filled pore space (10 cm, %)		
Project II	Natural forest	37.7 ± 1.0[a]	15.3–62.0	99
	Mid-age rubber	50.7 ± 1.0[b]	35.3–74.2	99

* Means sharing no common letter in superscript suggest significant difference between natural land uses(p < 0.05).

According to the correlation matrix, WFPS was chosen as first controlling variable in the regression analysis for the description of temporal variation in CH_4 fluxes. Despite different ranges of WFPS and significantly lower WFPS in forest soils as compared with soils rubber is grown on (Table 3.3), land use was not a significant fixed effect in the CH_4 flux model, which led to a single regression equation. We found that the quadratic regression model explained the relationship between WFPS and CH_4 flux (Table B4) better for Project I, whereas a linear model was better for Project II. These two regression models were used as the base models in subsequent analyses of covariance.

Water-filled pore space alone explained 39% of CH_4 flux variation in Project I according to regression model from GLM procedure and 34% variation in Project II according to regression from mixed model (Figure 3.3 and Table 3.4). According to the applied regression models (Figure 3.3), WFPS varied from 12.4% to 84.9% in Project I and from 15.3% to 74.2% in Project II, leading to the 104–105% decrease in CH_4 uptake by soils. The largest relative decrease in CH_4 uptake (up to 109%) was recorded for the rubber plantations in Project I.

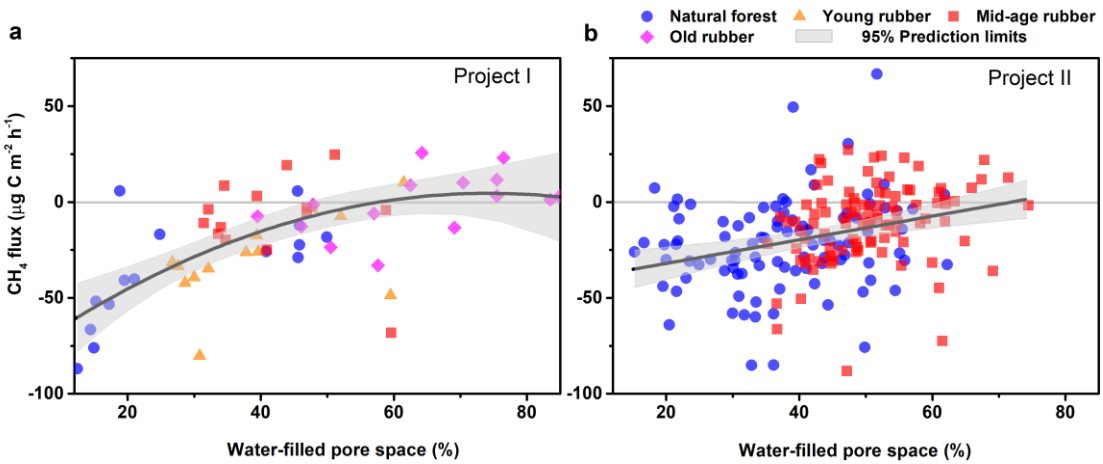

Figure 3.3 CH_4 flux regression model with water-filled pore space for Project I (a) and Project II (b). Regression lines and prediction limits were estimates from the model with only fixed effects, with model $y = -88.7744 + 2.5147\,x - 0.0169\,x^2$, $R^2 = 0.39$, and $n = 60$ for Project I and $y = -44.3421 + 0.6166\,x$, $R^2 = 0.34$, and $n = 198$ for Project II, respectively

Table 3.4 Regression parameters of CH_4 flux model with water-filled pore space (WFPS)

Project \ Regression	Parameter	Estimate	Standard error	*t* value	$P > \|t\|$	*n*	R^2
Project I	Intercept	−88.7744	16.4037	−5.41	<.0001	60	0.39
	WFPS	2.5147	0.7435	3.38	.0013		
	WFPS*WFPS	−0.0169	0.0078	−2.18	.0336		
Project II	Intercept	−44.3421	7.0864	−6.26	<.0001	198	0.34
	WPFS	0.6166	0.1566	4.01	.0001		

3.4.3 Complementary effects of soil chemical properties on CH_4 fluxes

By adding covariates, including total C, total N, NH_4^+–N, NO_3^-–N, pH, and clay content, to the selected CH_4 flux regression model with WFPS and comparing these models to the model without the covariate, we identified factors that improved model explanatory power. Nitrate content in the soil surface layer was the only covariate that improved model fit in both projects, and the regression model with nitrate covariate explained 55% and 36% the variation of CH_4 fluxes in Project I and Project II, respectively (Figure 3.4). At a given WFPS, an increase in nitrate content led to a decrease of the CH_4 flux (Figure 3.4).

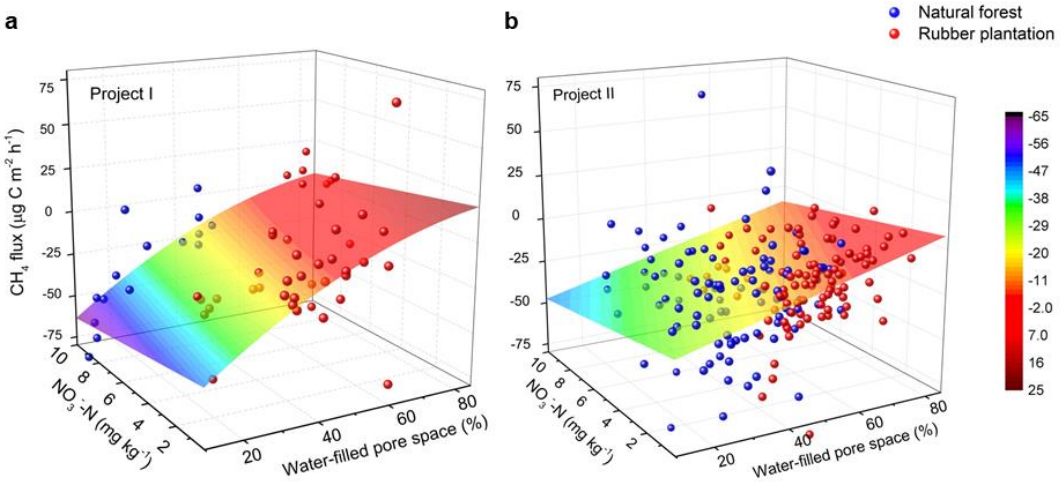

Figure 3.4 Simulated CH_4 flux surface (z) using water-filled pore space (x) and soil nitrate content (NO_3^-–N, y) as explanatory variables for Project I (a) and for Project II (b). Fitted equation of CH_4 flux was $z = -63.6152 + 1.6474\,x - 0.00791\,x^2 - 1.5548\,y$, $R^2 = 0.55$, and $n = 60$ for Project I and $z = -35.5297 + 0.5124\,x - 1.7177\,y$, $R^2 = 0.36$, and $n = 198$ for Project II

Ammonium was the dominant mineral N form in rubber soils. NH_4^+–N content was

comparable between natural forest and rubber plantations, but forest soils had higher nitrate content than rubber soils in both projects (Figure 3.5). Inclusion of total N in regression analysis did not improve the model for Project I, but it improved the model in Project II in terms of AIC and sum of variances although the effect was not significant (Table B5). Adding NH_4^+–N as a covariate showed no improvements in both projects. Total C, pH, and clay content had a positive effect on CH_4 flux, and adding these covariates improved the model in Project I, with clay content and pH having a significant effect.

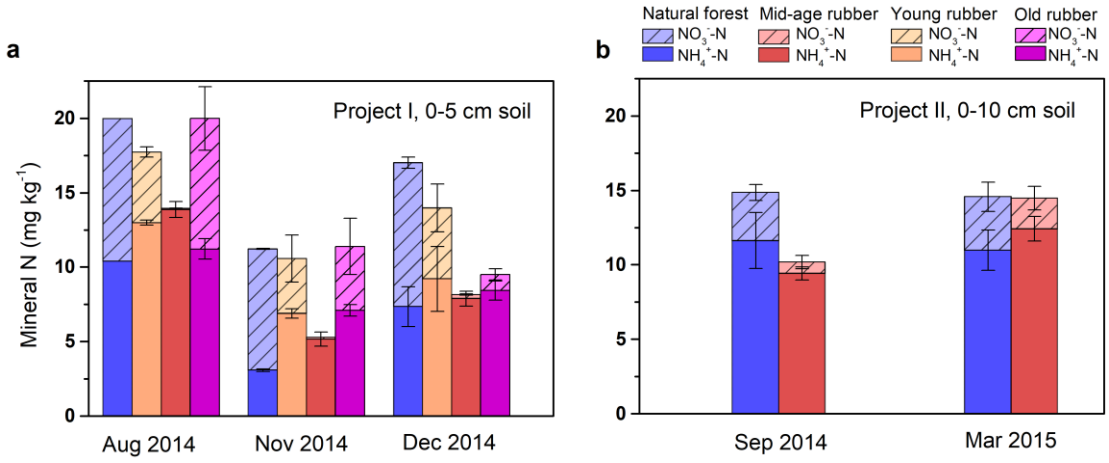

Figure 3.5 Mineral N content in topsoil under natural forests and rubber plantations of different age at different sampling dates in Project I (a) and in Project II (b). Error bars are standard error; in (a), n = 3 except natural forest on first two dates where composite sample was analyzed, and in (b), n = 9

3.4.4 Effect of soil texture on cumulative CH_4 flux and WFPS dynamics

Using the dataset from Project II, we found that soil clay content was positively but not significantly correlated with annual cumulative CH_4 flux (r = 0.43). As an independent variable, soil clay content explained only 18.6% variation of cumulative CH_4 flux (Figure 3.6a). We also tested the regression models separately for each land use. However, in these models, clay content was also nonsignificant (results not shown).

Considering the intrinsic linkage between texture and soil water holding capacity and higher average clay content and WFPS in soils under rubber than in forest soils (Table 3.4 and B2), we used mixed models to investigate the effect of soil texture on WFPS dynamics in Project II. The interaction between land use and clay content was not significant. Excluding this interaction from the regression resulted in two parallel regression lines for natural forest and rubber plantation with a slope of −0.2504 for both land uses (Figure 3.6b). Thus, although forest sites exhibited a wider range of clay

contents compared with rubber sites, the similar slope but different intercept of the regression confirmed that WFPS was different between natural forest and rubber plantation. Clay content had a limited effect on WFPS within land-use type.

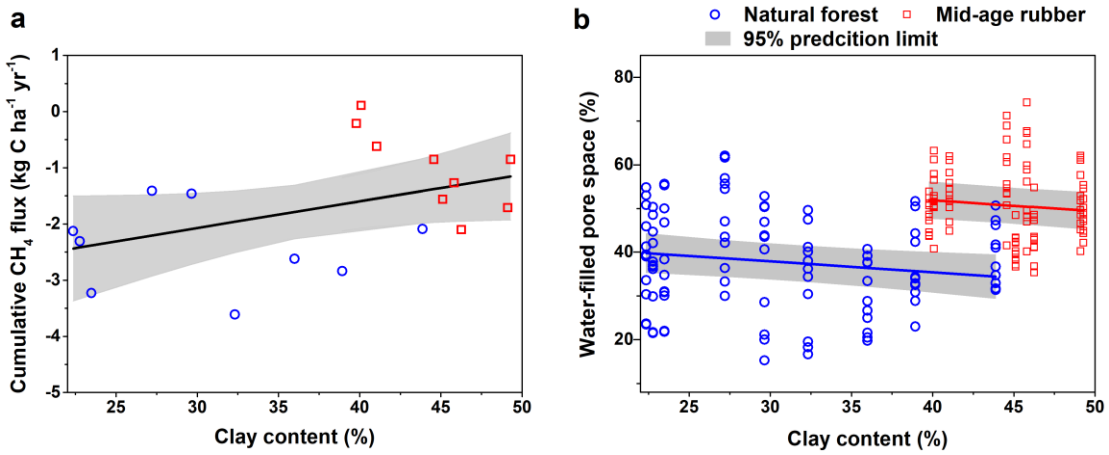

Figure 3.6 Texture effect on CH_4 flux and water-filled pore space in Project II. Regression between clay content and cumulative CH_4 flux (a) and between clay content and water-filled pore space (b). Gray shading represents 95% prediction limit. In (a), each point of annual cumulative CH_4 fluxes was averaged from three replicates at each slope position, $y = -3.5004 + 0.0476\ x$, $n = 18$, and $R^2 = 0.186$. In (b), regression from mixed model for natural forest and rubber plantation was $y = 45.4053 - 0.2504\ x$ and $y = 61.8806 - 0.2504\ x$, $n = 198$

The cumulative CH_4 fluxes negatively correlated to soil organic carbon content (0–10 cm) for Project II, but the correlation ($r = -0.35$, $p = 0.15$, $n = 18$) was not significant.

3.5 Discussion

3.5.1 Soils under rubber plantation are weaker CH_4 sinks than natural forest soils

Our results confirmed the hypothesis that soils under intensively managed rubber plantations grown under monsoon climate have lower CH_4 uptake than soils under natural forests. The annual CH_4 uptake by soils under rubber plantation was reduced by 58.4%, as compared with natural forest soils (Table 3.1 and Figure 3.2 and Figure 3.7). This large decrease in CH_4 uptake by soils after natural forests transformation into intensively managed plantation systems makes the latter even temporal net methane emitters. A similar decrease in CH_4 uptake was observed after converting natural forest into agricultural land in temperate regions (Dobbie and Smith, 1996; Chan and Parkin, 2001a) and into traditional plantation systems in the lowland tropics, including cacao agroforestry (Veldkamp *et al.*, 2008), oil palm and rubber monocultures in Indonesia

(Hassler *et al.*, 2015), and home gardens and coffee plantations in tropical montane systems in Tanzania (Gütlein *et al.*, 2018).

The spatial and temporal variability of CH_4 flux is large, as has been shown in a lowland forest on a loamy Acrisol in Indonesia (-0.18 ± 1.55 kg C ha^{-1} yr^{-1}; Hassler *et al.*, 2015) and an upland forest in Xishuangbanna (0.89 ± 1.23 kg C ha^{-1} $season^{-1}$; Fang *et al.*, 2010). Although the temporal variation in CH_4 flux was also large in our study, natural forest soils still acted as a net CH_4 sink (-0.92 ± 0.58 kg C ha^{-1}) in the rainy season, and the higher CH_4 uptake by forest soils was consistent between sites. Converting forest into rubber plantations mediated CH_4 flux by soils and environmental factors; hence, the land-use change impact needs to be carefully studied and analyzed, in order to explain the observed variability in the results and clarify the real reasons for the differences between land uses, as we did in this study.

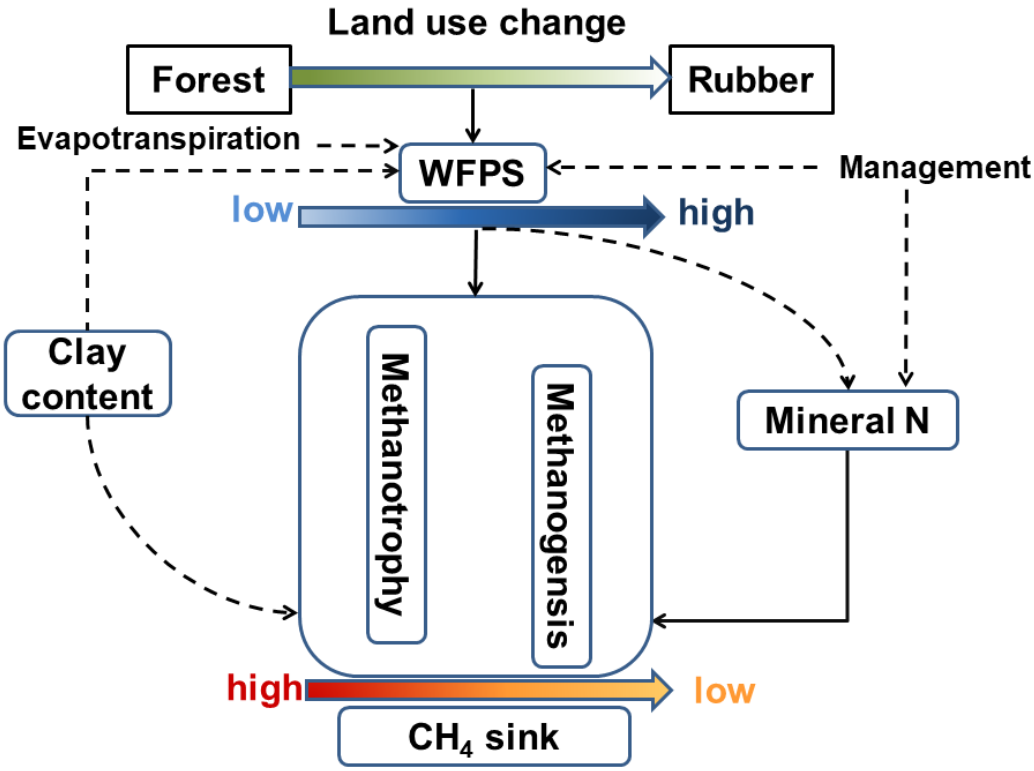

Figure 3.7 The impact of land-use change, soil texture, and management on soil function as atmospheric CH_4 sink.

Solid lines show statistically confirmed effects, and dashed lines are other effects tested and discussed in our study. Converting natural forest into rubber plantation weakened the soil function as CH_4 sink, mainly driven by increased water-filled pore space

(WFPS). As a controlling factor of methanotrophy and methanogensis, clay content partly contributed to differences in WFPS, but neither evapotranspiration and management nor clay content solely explained the large difference in WFPS between land uses. Land-use change and modified land management affected soil water regime and thus soil mineral N content, which further interacted with CH_4 processes.

3.5.2 Soil moisture content as a decisive driver for the CH_4 flux difference between forests and rubber plantations

Among measured environmental factors and soil properties, WFPS was the dominant factor that explained CH_4 spatial and temporal variation; thus, the second hypothesis was confirmed. Furthermore, in a multiple regression model of CH_4 flux, the significant WFPS effect rendered the land-use effect nonsignificant, suggesting that the effect of land-use change on CH_4 uptake was driven by altered WFPS (Table 3.3, Figure 3.7). Similar lower CH_4 uptake was measured in rubber plantations in Xishuangbanna, corresponding to higher WFPS compared with primary and secondary forest (Werner *et al.*, 2006). Increased CH_4 uptake was observed in an afforestation chronosequence as soil moisture decreased in older stands (Hiltbrunner *et al.*, 2012). Potential reasons for different soil WFPS values in natural forest and rubber plantation include contrasting soil texture, compaction due to terracing and tapping activities, and changes in water balance.

Rubber plantations expanded preferentially on more clayey soils because they better retain nutrients and water (Samarappuli *et al.*, 2014). More clayey soils are expected to support higher soil moisture when other considerations being equal. Similar to our study, clay content was found higher in soils under rubber trees than in reference forest soils in other studies (Ishizuka *et al.*, 2002; Werner *et al.*, 2006; Hassler *et al.*, 2015). However, very few studies have explicitly and adequately addressed the confounding effects of soil texture and land use. If soils under natural forest and rubber plantation are taken together in our study, the trend linking higher clay content and higher WFPS was very weak. Further analysis, based on the sufficient spatial replication and a relatively wide range of soil clay content values, showed that higher clay content did not result in higher WFPS within a single land use (Figure 3.6). This means that the observed difference in WPFS between soils under rubber or forest was not driven by contrasting soil texture but by the land use. Thus, following the third hypothesis, we disentangled the effect of soil texture and the effect of land use per se on soil water content and, respectively, on CH_4 uptake by soil.

Use of heavy machinery during terracing and other management activities could

potentially compact soil, reduce soil aeration, and increase WFPS, which decreases gaseous exchange between soil and atmosphere (Antille *et al.*, 2015; Epron *et al.*, 2016). As an easily measureable proxy for soil compaction, bulk density was compared to evaluate whether rubber cultivation compacted soil and resulted in high WFPS. The bulk density was slightly but not significantly higher in soils under rubber than in forest soils (Table B2). In our case, tapping might compact soil on walking routes along the terrace, but the results derived from measurements on nonwalking routes did not support the assumption that high WFPS in soils under rubber was due to soil compaction.

The differences in soil water content under forest and rubber plantations can stem from the differences in plant physiology and water usage by trees. In contrast to evergreen natural forests, rubber plantations growing under monsoon climate shed leaves completely for 2–4 weeks in the middle of the dry season, which reduces transpiration (Priyadarshan and Clément-Demange, 2004), whereas the flush of new leaves significantly induces uptake of deep soil water (Guardiola-Claramonte *et al.*, 2008). According to water balance studies (Tan *et al.*, 2011; Giambelluca *et al.*, 2016), rubber trees lose more water than native vegetation through higher evapotranspiration and act as water pump. Our study, however, does not support this observation: the top layer of rubber plantation soils was wetter compared with natural forest soils. The transpiration rates of rubber trees growing under tropical humid or monsoon climates are actually not very high (<3 mm day^{-1}; Carr, 2011); Kobayashi *et al.*, 2014); Niu *et al.*, 2017). To explain the difference in soil water usage between natural forest and rubber plantation, further studies need to cover both land uses and all components of the water cycle.

The observed difference in WFPS between natural forest and soils under rubber plantations cannot be explained solely by differences in soil texture, compaction, or hydraulic characteristics of rubber trees. It might be the combination of these factors and other factors, such as topography. The majority of remaining forest in the region is located on steeper slopes than rubber plantations, which may partially contribute to better drainage and difference in WFPS.

3.5.3 Impact of soil mineral N availability on soil CH_4 exchange

Adding nitrate content as covariate to CH_4 flux model with the main controlling factor improved the model explanatory power and showed a positive effect on CH_4 uptake (Figure 3.4 and Table B5). Under tropical monsoon climate, abundant rainfall during the rainy season often creates periodical anaerobic conditions even in upland soils, which not only limits the supply of CH_4 and O_2 for methanotrophs oxidizing CH_4 but

also provides favorable conditions for methanogens producing CH_4. Under anaerobic conditions, competing nitrate-reducing bacteria not only lower organic carbon availability for methanogens but also produce toxic compounds (NO_2^-, NO, and N_2O) inhibiting the activity of methanogens (Bodelier, 2011). The positive effect of NO_3^-–N on CH_4 uptake in soils with high moisture in our study is likely due to the competitive inhibition of methanogens by nitrate reducers, leading to the decrease of CH_4 production.

Although growth of methanotrophic bacteria can be limited by mineral N, such as in rice paddy soils (Bodelier and Laanbroek, 2004), N-limited CH_4 oxidation was often not supported by N amendment experiments in other soils. Stimulation of CH_4 oxidation occurred occasionally at low rates of N addition in forest and tree plantation systems (Koehler *et al.*, 2012; Geng *et al.*, 2017), but in general, adding nitrogenous fertilizer reduced CH_4 consumption by more than 20% in tree-based ecosystems (Zhang *et al.*, 2012; Zheng *et al.*, 2016). In our study, NH_4^+–N was the dominant mineral N form in soils under rubber, and its concentration was comparable with that in forest soils. Neither covariate of NH_4^+–N nor total N improved the CH_4 model with WFPS (Table B5). Therefore, unlike the findings of N-limited CH_4 oxidation by Hassler *et al.* (2015), it was not a significant mechanism in soil CH_4 turnover in our study.

The effect of mineral nitrogen is not independent from the physical factors that regulate the entry of CH_4 and O_2 into the soil (Bodelier, 2011). The covariate analysis in our study confirmed the third hypothesis and demonstrated the necessity of considering all major controlling factors when interpreting the interaction between CH_4 processes and mineral N. The practice of placing fertilizer in a soil pit between two trees on the terrace in Project II sites likely did not greatly change the mineral N content in soil samples taken from the slope between tree rows. Controlled N-adding experiments and more frequent mineral N sampling would improve the understanding of the interactions between CH_4 processes and mineral N in rubber plantations.

Other management factors, such as applying herbicide glyphosate to clear the understory vegetation and sulfur powder to control powdery mildew and anthracnose diseases in rubber plantations, may affect the soil faunal diversity but showed no significant changes in soil microbial community composition and function up to 23-year-old rubber plantations (Li *et al.*, 2016; Singh *et al.*, 2019). Because of lacking of controlled experiments, herbicide and sulfur effects on CH_4 uptake and production by soil microorganisms are even more uncertain and could not be separated from main controlling factors in our case.

3.6 Conclusion

Converting natural forests to rubber plantations weakened the soil function as a CH_4 sink, resulting in a reduction of annual CH_4 uptake by 58%. In Figure 3.7, we summarized the observed interactions between land-use change, soil water and mineral N status, and underlying physical and biological processes. The change in WFPS was the most important factor to explain differences in CH_4 uptake in our study. Higher clay content in soils under rubber than in natural forest soils had a limited effect on the difference in WFPS, which may partly contribute to soil pores structure and gas diffusion processes. On the other hand, difference in WFPS and management of rubber plantations determined mineral N status, which could interact with CH_4 processes via different pathways, that is, competitive inhibition of methanogens by nitrate reducers. More in-depth studies on gas transport, community composition, and activity of methanotrophs/methanogens in the soil profile are needed for better understanding the physical and biological mechanisms of the land-use change effect on soil function as CH_4 sink.

The degraded soil function as CH_4 sink in rubber plantations has a negative impact on the soil GHG budget. Given the extensive rubber expansion at large scales, that is, the natural rubber area having expanded 4.3 million ha worldwide from 2000 to 2017, with 3.7 million ha of expansion taking place in Asia (FAOSTAT, 2019) and the important role of tropical forests in regulating climate, converting natural forests to rubber plantations has a profound impact on the climate change at regional and even global scale.

Chapter 4 Mechanism of methane uptake in profiles of tropical soils converted from forest to rubber plantations[3]

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Highlights

- Land-use change mediates CH_4 sink by altering soil moisture and CH_4 diffusivity
- CH_4 oxidation was highest in the top 0-10 cm of mineral soil
- Methanotrophic activity controls profile CH_4 distribution more than diffusivity
- Simulated $\delta^{13}CH_4$ profiles reveal CH_4 production in subsoil during wet conditions

4.1 Abstract

Land-use change modulates the balance between methane (CH_4) oxidation by soil methanotrophs and production by methanogens through changes in soil physical, chemical and biological properties. The large-scale expansion of rubber plantations in Southeast Asia has decreased CH_4 uptake by soil, but a mechanistic understanding of the associated processes within the soil profile is missing. To assess such land-use change impacts, we quantified the relative controls of CH_4 diffusion and oxidation

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processes on soil profile methane fluxes using two datasets from Xishuangbanna, Southwest China. CH_4 concentration, bulk density, soil temperature and moisture were measured at 5, 10, 30 and 70 cm depths during the dry and rainy season to determine the effective CH_4 diffusion coefficient, diffusive flux, turnover rate and methanotrophic activity. Isotopic fractionation of carbon during CH_4 oxidation was estimated using $\delta^{13}CH_4$ profiles from *in situ* soil probes sampled in the dry season. This fractionation factor was used to model the seasonality of CH_4 fluxes under the two land uses. CH_4 consumption at 0-5 cm soil depth was significantly greater in natural forest than in rubber plantations, with a mean CH_4 flux of -23.8±1.0 and -14.4±1.0 ug C m^{-2} h^{-1}, respectively. Atmospheric CH_4 oxidized in the top 10 cm accounted for 93% and 99% of total consumption in forest and rubber profiles, respectively. CH_4 diffusivity at the four sampled depths was significantly lower in rubber plantations than in forest. Higher soil water content predominately explained the weakened CH_4 sink in converted rubber plantations. During the transition from dry season to rainy season, methanotrophic activity at 5-10 cm depth decreased by 99.6% and 83.3% in forest and rubber plantations, respectively. The estimated isotope fractionation factor for carbon due to CH_4 oxidation was 1.0292±0.0015 (n=12). A diffusion-oxidation model of the $^{13}CH_4$ profile explained the oxidative behavior in the dry season, but suggested CH_4 production in the subsoil during the rainy season. This production needs to be considered in future studies to explain changes in CH_4 processes caused by land use transformations. The weakened CH_4 sink function in soils under rubber monoculture exerts a negative effect on the global CH_4 budget and climate change, given the large extend of rubber plantations worldwide. More sustainable cultivation approaches, such as rubber agroforestry that also improve soil structure and aeration are needed to mitigate this negative impact.

Keywords

Land-use change, upland soil, concentration gradient, isotopic fractionation, methane oxidation

4.2 Introduction

Methane (CH_4) is a potent greenhouse gas and its atmospheric concentration increased by 157% between the start of industrial era and 2017 (WMO, 2018). Atmospheric CH_4 concentration stabilized from 2000 to 2006, and then steadily increased after 2006, before increasing dramatically between 2014 and 2017. Moreover, researchers have observed a shift in the $^{13}C/^{12}C$ isotopic ratio ($\delta^{13}CH_4$) of atmospheric methane. To date, there is no commonly accepted explanation for these

patterns (Kirschke *et al.*, 2013; Nisbet *et al.*, 2019; Turner *et al.*, 2019). The latest information on the latitudinal distribution of CH_4 emissions suggests the tropics (<30 °N) are responsible for ~65% of the global budget (Saunois *et al.*, 2019), possibly caused by underestimated biological sources linked with tropical wetlands and agricultural sources such as rice paddies and ruminants (Nisbet *et al.*, 2016). Microbial oxidation of CH_4 in aerated soils is the only known biological CH_4 sink, accounting for 4-6% of the total CH_4 sink (Ciais *et al.*, 2013). Depending on soil aeration, CH_4 oxidation by methanotrophs dominates in oxic soils, while CH_4 production by methanogens occurs under anaerobic conditions (Le Mer and Roger, 2001).

Previous studies have shown that land cover transitions affect soil CH_4 fluxes (Dobbie *et al.*, 1996; McDaniel *et al.*, 2019). However, how these transformations mediate complex biotic and abiotic soil processes is poorly understood (McDaniel *et al.*, 2019). Tropical areas have been hotspots of deforestation for decades and forest loss is still continuing, while there have been forest gains at higher latitudes (Sloan and Sayer, 2015). Driven by growing demands of major commercial crops in regional and global markets, tree-based crops such as rubber (*Hevea brasiliensis*) have expanded into non-traditional growing areas in montane Southeast Asia, replacing natural forests, swidden cultivation areas and agricultural land (Fox, 2014). From 2000 to 2010, the area occupied by rubber plantations expanded by 2 million ha worldwide with 1.5 million ha of this expansion occurring in Southeast Asia (FAOSTAT, 2019). Assessing the impact of this large-scale land-use change on soil CH_4 fluxes and processes will improve estimation of global greenhouse gas emissions.

Although spatial and temporal variation in CH_4 fluxes is large, tropical forest soils mostly act as net CH_4 sinks (Dalal and Allen, 2008; Hassler *et al.*, 2015; Gütlein *et al.*, 2018). Compared to tropical natural forests, cultivated and managed systems, such as cacao agroforestry (Veldkamp *et al.*, 2008), rubber and oil palm plantations have reduced rates of CH_4 uptake by soils (Veldkamp *et al.*, 2008; Hassler *et al.*, 2015; Lang *et al.*, 2019). Although there is a clear trend of decreasing methane uptake by soils converted from natural forest into plantation systems, the mechanisms behind the weakened methane sink function have not been well established (Shukla *et al.*, 2013).

Given the diversity of controlling factors, various mechanisms have been proposed to explain the differences in CH_4 fluxes between natural and managed land use systems. Soil water content or water-filled pore space (WFPS), soil compaction and clay content have all been found to control CH_4 fluxes to different extent (Teepe *et al.*, 2004; Guckland *et al.*, 2009; Lang *et al.*, 2019). Hence, it has been suggested that these factors might be affecting gas transport and the soil micro-environment (Verchot

et al., 2000; Ishizuka *et al.*, 2005; Werner *et al.*, 2006; Veldkamp *et al.*, 2008). However, these studies are mostly based on surface net CH_4 exchange rates, as measured by the chamber method. The direct effects of soil moisture or WFPS on CH_4 transport across the soil profile and microbial oxidation within different soil layers have rarely been assessed (Teh *et al.*, 2006). In particular, studies on CH_4 diffusivity and microbial oxidation in tropical forest soils are lacking.

The rate of CH_4 diffusion within the topsoil exerts the primary control on CH_4 fluxes and is dependent on soil physical structure and soil moisture content (Dörr *et al.*, 1993). To quantify diffusive fluxes and turnover rates of a soil gas within the soil profile the concentration gradient method can be used, where gas molar fractions are measured at different soil depths (Goldberg *et al.*, 2017; Sánchez-Cañete *et al.*, 2017). While in fine-textured or water-logged soils, CH_4 uptake tends to be restricted by low CH_4 diffusivity, in dry tropical ecosystems, methanotrophic activity rather than gas diffusivity limits CH_4 uptake (Ridgwell *et al.*, 1999).

Our ability to separate the effects of physical diffusion and biological controls on CH_4 uptake has been partly constrained by the difficulties in directly measuring methanotrophic activity (von Fischer *et al.*, 2009). Both CH_4 production under anaerobic conditions and CH_4 oxidation under aerobic conditions occurred in profile of forest soils, though the magnitude of the former process was relatively low (Butterbach-Bahl and Papen, 2002). Assuming CH_4 production is negligible in oxic soils (Maier *et al.*, 2017), CH_4 flux is the result of diffusion and prevailing methanotrophic oxidation, thus methanotrophic activity can be derived by solving the diffusion-oxidation model with a known gas diffusivity and flux rate (von Fischer *et al.*, 2009; Maier *et al.*, 2017). This diffusion-oxidation model assumes no local CH_4 production and hence that all oxidized CH_4 is supplied from the atmosphere. Therefore, separation of diffusional and biological control using this approach would be unsatisfactory when soils vary, temporally and spatially, from oxic to anoxic conditions. Alternatively, isotopic approaches can be used to quantify each process, especially when methane production also occurs.

Analyzing the isotopic composition of methane and its signature in related substrates and products can help assess the relative contribution from diffusion, methane oxidation and production to the net CH_4 fluxes in situ (Teh *et al.*, 2006). As a consequence of the strong discrimination against the heavier isotope ^{13}C in microbial processes, referred to as isotopic fractionation, methane oxidation by methanotrophs results in the enrichment of residual methane with ^{13}C (Coleman *et al.*, 1981). As the heavier $^{13}CH_4$ also diffuses more slowly than the lighter $^{12}CH_4$ from atmosphere into

the soil and within soil, this fractionation results in a depleted ^{13}C signature in soil methane, with a theoretical fractionation factor of 1.0195 (De Visscher *et al*., 2004). Meanwhile, methane production by methanogens from different precursors also contributes to a shift in the isotopic signature of methane in the soil (Conrad, 2005).

Despite the wide usage of isotopic approaches in water-saturated soils, such as wetlands and rice paddies, or well-aerated soils in temperate regions, little is known about the relative control and the dynamics of methane processes in tropical soils, where the variability in CH_4 fluxes is large and clay-rich soils can support both methanotrophy and methanogenesis in different microsites, especially when soils are periodically saturated (Silver *et al*., 1999; Teh *et al*., 2005). Therefore, in addition to investigating surface CH_4 fluxes, it is necessary to combine measurements of gas diffusivity and isotopic composition of methane within soil profiles to understand the physical and biological controls on CH_4 fluxes.

We conducted this study in Xishuangbanna, Southwest China, representative of the recent expansion of rubber plantations into non-traditional growing areas. Based on findings from chamber measurements, where differences in WFPS was the primary factor explaining differences in CH4 fluxes between natural forest and rubber plantations (Lang *et al.*, 2019), we aimed to quantify the impact of land-use change on methane diffusion and oxidation processes. Hence, we measured CH_4 concentrations and determined CH_4 diffusivity in soil profiles of forest and rubber plantations, and modeled seasonal dynamics of CH_4 processes based on isotopic signatures of $^{13}CH_4$. We hypothesized that: (1) the difference in WFPS between forest and rubber plantation will result in differences in CH_4 diffusivity in the soil, which in turn controls the CH_4 uptake by soils, and (2) gas diffusivity controls the temporal dynamics of CH_4 fluxes, and the relative importance of physical diffusion and biological oxidation depends on the season and land use.

To our knowledge, this is one of very few studies that determined the carbon fractionation factor in CH_4 oxidation in tropical forest using delta $^{13}CH_4$ profiles from soil probes *in situ*. Modeling of the seasonality and vertical distribution of delta $^{13}CH_4$ in tropical upland soils under a monsoon climate has not been previously reported.

4.3 Material and methods

4.3.1 Study site

This study was carried out in the Naban river watershed national natural reserve, Xishuangbanna prefecture, Southwest China (Figure 4.1). Since establishing rubber

plantations on state farms, the rubber area increased from 1.3% to 9.3% of the total reserve area between 1989 and 2013 (Yang *et al.*, 2016; Sarathchandra *et al.*, 2018) . The prevailing monsoon climate results in a distinct dry season (November-April) and rainy season (May-October). Average annual precipitation is 1157±169 mm, with 85% falling in the rainy season, while the annual temperature is 22.30±0.58 ℃ (1954-2015 average for Jinghong meteorological station, located 19 km from our transect at an altitude of 582 m).

Soil types at our sampling sites were Latosols and Lateritic Red soils group in the Ferralsols order (Genetic Soil Classification of China), or Ferralsols and Acrisols (World Reference Base for Soil Resource).

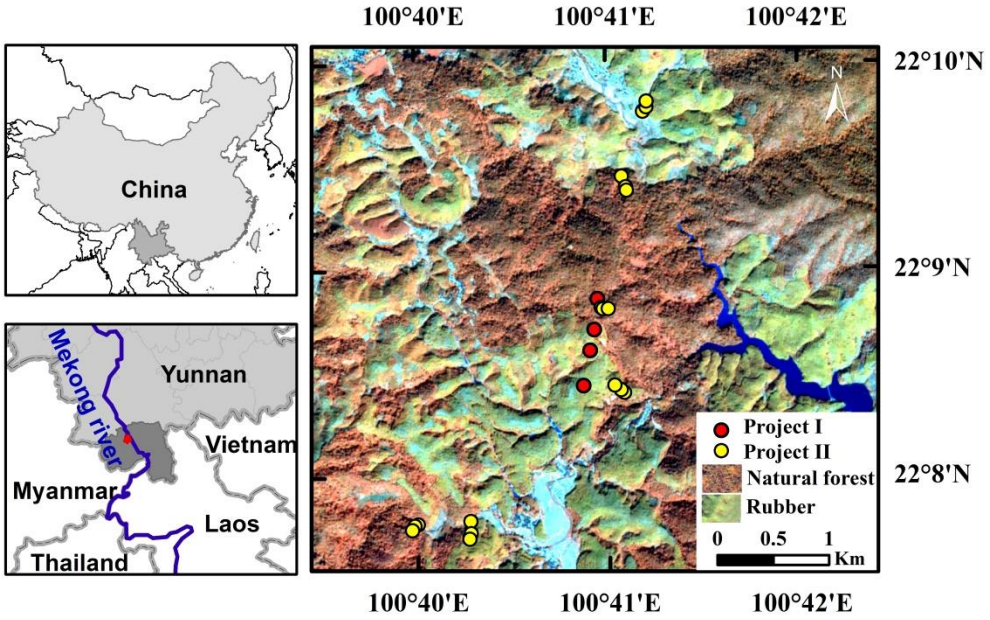

Figure 4.1 Location map of the study sites

This study includes two datasets gathered from a) the project of Sustainable Rubber Cultivation in the Mekong region (SURUMER, https://surumer.uni-hohenheim.de/), referred to as Project I, and b) the Green Rubber project (Goldberg *et al.*, 2017; Monkai *et al.*, 2018), referred to as Project II in the following text (Figure 4.1). The two projects performed complementary measurements. The isotopic signature of $^{13}CH_4$ soil profiles was sampled at representative times during the dry and rainy seasons in forest and rubber sites of different age in Project I, while Project II included replicates of land use at the landscape level and CH_4 concentration profiles measured more frequently for longer periods than Project I. Integrating the two datasets allowed a more robust statistical testing of the land-use effects and provided insights of changes in CH_4 processes in soil profiles from dry to wet conditions in

natural forests and rubber plantations.

Project I included one plot in natural forest and three plots in rubber plantations at the age of 9, 17 and 30 years, referred to as young, mid-age and old rubber plots in the text (Figure C1). The three soil profiles in each plot were equipped with soil gas samplers. In the rubber plantations, soil profiles covered three positions, including terrace, upper part and middle part of the slope between tree rows. Gas profiles in Project I were sampled four times from November 2014 to August 2015 (Figure C1).

Project II adopted a hierarchical sampling scheme, where three groups of sites were selected as spatial replicates at the first sampling level (Figure C1). At each group of sites, a pair of mid-age rubber plantation (17-23 year-old) and an adjacent natural forest area were selected at the second sampling level, and three plots were set at upper, middle and lower slope position under each land use at the third sampling level. Each plot had one soil profile equipped with gas samplers in the middle of slope between tree rows (Figure C1). Location and site characteristics are detailed in Lang *et al.* (2019).

4.3.2 Soil gas sampling, CH_4 concentration and $^{13}CH_4$ analysis

Self-assembled gas samplers, as described in Goldberg *et al.* (2017), were installed at depths of 5, 10, 30 and 70 cm in each soil profile. Gas samplers were 55 cm long and consisted of an inner tube and an outer tube with diameters of 20 mm and 25 mm respectively. Soil gas samplers were perforated for a length of 15 cm from one end and covered with stainless steel mesh (44 μm) to prevent soil fauna moving into the sampler. They were installed horizontally and parallel to the slope surface, with the perforated end down the slope to avoid accumulation of soil water in the sampler (Figure C2).

A volume of 100 mL soil gas was sampled from each sampler in the profile, stored in multi-layer foil sampling bag (LB-101, Dalian Delin Gas Packing Co., Ltd., CN) and further analyzed for CH_4 concentration by gas chromatography (HP 6890, Agilent Technologies, Inc., Santa Clara, CA). Ambient air samples were taken at 1 m above the soil surface on each sampling date. The gas concentration profiles were determined on four dates in Project I and seven dates in Project II. In Project I, additional gas samples were collected in the same way on 18 March 2015 during the dry season and 16 August 2015 during the rainy season for analyzing $^{13}CH_4$. The stable isotopic composition ($\delta^{13}C$) of CH_4 was analyzed using the pre-concentrator TraceGas (Isoprime Ltd., UK) connected to the isotope ratio mass spectrometer

ISOPRIME-100 (Isoprime Ltd., UK) at the Environmental Stable Isotope Lab, Chinese Academy of Agriculture Science. The $\delta^{13}C$ measurement precision was 0.5 ‰.

Soil temperature and volumetric water content were recorded by HOBO stations (Onset Computer Corporation, US), consisting of a data logger (U30-NRC), Frequency Domain Reflectometry based moisture sensors (S-SMC-M005) and temperature sensors (S-TMB-M006) at the four depths of the soil profile. Each plot in Project II had one HOBO station installed, while in Project I only the forest and old rubber plots contained one station.

4.3.3 Soil physical and chemical properties

Bulk density at each sample depth was determined and later used to calculate soil porosities and water-filled pore space (WFPS). In Project I, at each natural forest, young and mid-age rubber plot, three soil cores were sampled in the profile at depths of 5, 10, 30 and 70 cm using 100 cm^3 core rings to determine bulk density based on 105 ℃ oven-dry soil weight. Bulk density of old rubber plantation at the same depths was interpolated using Spline Tool (ASRIS, 2018) from a former sampling based on horizons in the soil profile. In Project II, at each slope position sampling level, nine soil cores were sampled at each depth from three sides of walls in a profile using 100 cm^3 core rings. Bulk density values of same depth of each profile were averaged in calculating total soil porosity, air-filled porosity and water-filled pore space (WFPS). Soil profiles for bulk density sampling in rubber plantations were located on the slope between two tree rows. Other soil properties from the two projects were published in Lang *et al.* (2019).

4.3.4 CH_4 diffusive flux and turnover rate

CH_4 diffusivity (effective diffusion coefficient), diffusive flux and turnover rate at each depth on each sampling date were calculated based on measured soil temperature, soil moisture and CH_4 concentration gradient in the soil profile. The effective diffusion coefficient in soil media was determined using the Structure-dependent Water-induced Linear Reduction model (SWLR) (Moldrup *et al.*, 2013) (Equation 4.1),

$$D_a = D(T,p) \cdot {P_g}^{1+C_m \cdot P_t} \cdot \left(\frac{P_g}{P_t}\right) \qquad \text{(Equation 4.1)}$$

where D_a is the effective diffusion coefficient in soil in $cm^2\ s^{-1}$, $D(T, p)$ is the temperature and pressure corrected diffusion coefficient in free air calculated using

Equation 4.2 (Massman, 1998), P_g is the air-filled porosity in m^3 soil air m^{-3} soil, P_t is the total soil porosity in m^3 void m^{-3} soil, and C_m is the media complexity factor with a suggested value of 2.1 for intact soil. $D(T, p)$ is calculated as

$$D(T,p) = D(0,1) \cdot \frac{p_0}{p} \cdot \left(\frac{T}{T_0}\right)^{\alpha} \quad \text{(Equation 4.2)}$$

where $D(0, 1)$ is the gas diffusion coefficient in free air under standard temperature T_0 and pressure p_0, T_0 is 273.15 K and p_0 is 101325 pa, α is a constant with a suggested value of 1.81. The diffusion coefficient of CH_4 in free air is 0.1952 cm^2 s^{-1} (Massman, 1998). Detailed step-by-step calculations of D_a are provided in the supplement C (Equations C1-C5).

CH_4 diffusive flux was calculated from concentration gradients according to Fick's first law (Equation 4.3) (Fick, 1855). CH_4 concentrations from ambient air and four depths in the soil profile were used in its calculation, with temperature and elevation (pressure) effects on gas molar concentration also accounted for.

$$F_d = \frac{([CH_4]_{lower} - [CH_4]_{upper}) \cdot D_a \cdot 3600 \cdot 24}{d_{lower} - d_{upper}} \quad \text{(Equation 4.3)}$$

where F_d is diffusive flux at the middle of two sampling depths (written as d) in pmol CH_4 cm^{-2} soil d^{-1}. $[CH_4]_{lower}$ and $[CH_4]_{upper}$ are CH_4 concentrations in soil at lower and upper sampling depths in nmol CH_4 L^{-1} soil, d_{lower} and d_{upper} are the lower and upper gas sampling depths in cm, and D_a is the effective diffusion coefficient of CH_4 in cm^2 soil s^{-1}. In our case, diffusive fluxes were calculated for four discrete soil layers, namely 0-5 cm, 5-10 cm, 10-30 cm and 30-70 cm. The central depths of derived diffusive fluxes were 2.5, 7.5, 20 and 50 cm.

CH_4 net turnover rate T_d was calculated from the difference of diffusive fluxes in the upper and lower soil layers divided by the thickness of the soil layer between two depths (Equation 4.4, Goldberg *et al.*, 2008):

$$T_d = \frac{F_{d,upper} - F_{d,lower}}{d_{upper} - d_{lower}} \quad \text{(Equation 4.4)}$$

where T_d is the net turnover rate in pmol CH_4 cm^{-3} soil d^{-1}, $F_{d,upper}$ and $F_{d,lower}$ are diffusive fluxes at upper and lower depths in pmol CH_4 cm^{-2} soil d^{-1}, d_{upper} and d_{lower} are depths of diffusive fluxes for the upper and lower layer. As this step requires diffusive fluxes of two soil layers as input, three turnover rates could be derived in a soil profile, with central depths of 5, 13.75 and 35 cm.

4.3.5 Methanotrophic activity and isotopic fractionation of ^{13}C during CH_4 oxidation

We adopted the method of von Fischer *et al.* (2009) to calculate methanotrophic activity. This one-dimensional steady state model considers diffusive gas transport and methane oxidation, assuming no CH_4 production and, consequently, no CH_4 supply for oxidation from sub-layers. At steady state, the relationship between gas concentration at the upper and lower sampling depth in a semi-infinite soil is described as

$$[\mathrm{CH_4}]_{d,lower} = [\mathrm{CH_4}]_{d,upper} \cdot exp(-\Delta d \sqrt{\frac{P_g \cdot \mu}{D_a}}) \qquad \text{(Equation 4.5)}$$

Where $[CH_4]_{d,lower}$ and $[CH_4]_{d,upper}$ are the CH_4 concentrations at the lower sampling depth *d,lower* and upper sampling depth *d,upper*, respectively, in nmol CH_4 L^{-1} soil air, Δd is the thickness of soil layer between upper and lower sampling depth, in cm, μ is methanotrophic activity in s^{-1}. Rearranging this equation to solve for methanotrophic activity μ, we find

$$\mu = \frac{D_a \cdot (ln\frac{[\mathrm{CH_4}]_{d,lower}}{[\mathrm{CH_4}]_{d,upper}})^2}{P_g \cdot \Delta d^2} \qquad \text{(Equation 4.6)}$$

Thus, the methanotrophic activity μ at lower sampling depth depends on the CH_4 concentrations at the lower and upper sampling depths, $[CH_4]_{d,lower}$ and $[CH_4]_{d,upper}$, respectively, CH_4 diffusivity D_a and air-filled porosity P_g at the lower sampling depth, and the thickness of the soil layer Δd in cm (depth difference between the lower sampling depth *d,lower* and the upper sampling depth *d,upper*).

The methanotrophic activity μ is determined for each discrete layer using measurements at every two adjacent sampling depths. For the soil layer 0-5 cm, $[CH_4]_{d,upper}$ is the CH_4 concentration of ambient air and *d,upper*=0. Subsequently, μ at 5-10 cm is determined from CH_4 concentrations at 5 and 10 cm depths, with a thickness of the soil layer Δd=5 cm. μ at 30 and 70 cm depths are determined in the same way.

The heavier C isotope of methane, $^{13}CH_4$, diffuses more slowly than the lighter isotope, $^{12}CH_4$, from atmosphere into the soil and from surface soil to subsoil, with a theoretical diffusion fractionation factor value of 1.0195 ($\alpha_{tr}=D_{a,12}/D_{a,13}$) (Mason and Marrero, 1970; Chanton *et al.*, 2005). We calculated the isotopic fractionation factor of $^{13}CH_4$ during methane oxidation (α_{ox}) from measured $\delta^{13}CH_4$ profiles at the forest

plot in Project I during the dry season, using the Raleigh distillation approach (Steady-state diffusion-consumption model) (Reeburgh *et al.*, 1997; Maxfield *et al.*, 2008). Step-by-step determination of α_{ox} is provided in the supplement (Equations C6-C15). The discrimination against $^{13}CH_4$ in oxidation results in an enriched ^{13}C signature in soil CH_4.

4.3.6 Modeling profile distribution of CH_4 based on seasonal diffusivity and methanotrophic activity

CH_4 oxidation in soil profiles was evaluated for the dry season and rainy season separately, considering distinct rainfall pattern and soil moisture content. First, seasonal averages of CH_4 diffusive fluxes (Equation 4.3), effective diffusion coefficients (Equation 4.1), air-filled porosities and CH_4 concentrations were calculated for sampled depths of each land use, using combined datasets of Project I and Project II. The sampling date in January 2015 was excluded in calculating means for the dry season because of days of heavy rains. Based on these seasonal means, methanotrophic activity of each soil layer was determined (Equation 4.6) for dry and rainy seasons. The relative decrement of CH_4 diffusive flux, effective diffusion coefficient and methanotrophic activity from the dry season to rainy season were calculated.

Second, based on these seasonal averaged variables, CH_4 concentrations in soil profile were simulated up to 70 cm depth using a diffusion-oxidation model (Equation 4.5). Simulations were done for four discrete soil layers, with methane concentration in ambient air as input for the first layer. Sensitivity of simulated CH_4 distribution to diffusivity was tested by assigning the diffusivity of a layer to the whole profile, with layer specific methanotrophic activity. Similarly, the effect of methanotrophic activity on CH_4 distribution was tested by assigning a constant value from a discrete layer to the whole profile, with layer specific diffusivity.

Third, in order to compare the seasonal contributions of CH_4 diffusion and oxidation in CH_4 uptake, isotopic fractionation of $^{13}CH_4$ during diffusion and oxidation were introduced into diffusion-oxidation model (Equations 4.7-4.9), and verified with field-measured $\delta^{13}CH_4$ profiles. The forest plot and old rubber plantation plot in Project I were modeled, using plot specific parameters for the dry season, while for rainy season averaged parameters from the combined dataset were used (due to limitation of the model, discussed in 4.5.3). Thus, in addition to changes in CH_4 concentration profile, the shift in the $\delta^{13}C$ of CH_4 from the dry season to the rainy season due to changes in CH_4 diffusivity and oxidation could be predicted for each

land use. Diffusion-oxidation model incorporated isotopic fractionations is as follows:

From the measured CH_4 concentration and isotope ratios of $^{13}CH_4$ in ambient air, the concentration of methane isotopologues [$^{12}CH_4$] and [$^{13}CH_4$] were calculated (Supplement Equations C6-C11), and their concentrations at sampled soil depths were predicted by applying fractionation factors to [$^{13}CH_4$] as

$$[^{12}\mathrm{CH_4}]_{d,lower} = [^{12}\mathrm{CH_4}]_{d,upper} \cdot exp(-\Delta d\sqrt{\frac{P_g \cdot \mu}{D_a}}) \quad \text{(Equation 4.7)}$$

$$[^{13}\mathrm{CH_4}]_{d,lower} = [^{13}\mathrm{CH_4}]_{d,upper} \cdot exp(-\Delta d\sqrt{\frac{P_g \cdot \mu/\alpha_{ox}}{D_a/\alpha_{tr}}}) \quad \text{(Equation 4.8)}$$

Where $[^{12}CH_4]_{d,lower}$ and $[^{12}CH_4]_{d,upper}$, $[^{13}CH_4]_{d,lower}$ and $[^{13}CH_4]_{d,upper}$ are corresponding concentrations of methane at lower sampling depth *d,lower* and upper sampling depth *d,upper* in nmol CH_4 L^{-1} soil air, Δd is the thickness of the soil layer, α_{tr} is the fractionation factor of ^{13}C in CH_4 diffusion with a value of 1.0195, α_{ox} is the fractionation factor of ^{13}C in CH_4 oxidation determined from section in 4.3.5 (Equation C6-C15). These simulations were done for the four discrete soil layers, where the prediction from the bottom of one layer was used as the input for its lower layer.

At each sampling depth *d*, $\delta^{13}CH_4$ can be calculated from predicted $[^{12}CH_4]_d$ and $[^{13}CH_4]_d$ according to the delta notation as

$$\delta[^{13}\mathrm{CH_4}]_d = \left(\frac{\frac{[^{13}\mathrm{CH_4}]_d}{[^{12}\mathrm{CH_4}]_d}}{\frac{[^{13}\mathrm{CH_4}]_{Standard}}{[^{12}\mathrm{CH_4}]_{Standard}}} - 1\right) \cdot 1000 \quad \text{(Equation 4.9)}$$

Where $[^{13}CH_4]_{Standard}$ / $[^{12}CH_4]_{Standard}$ is ratio of ^{13}C to ^{12}C in Vienna Pee Dee Belemnite (VPDB) with value 0.0112375.

4.3.7 Statistical analysis

Statistical analysis was performed using SAS University Edition/SAS Studio (SAS Institute Inc., US), and graphs were prepared using OriginPro 9.0 (OriginLab, Northampton, MA). The land-use effect on CH_4 concentration profiles was analyzed using the combined datasets. Levels of hierarchy sampling were adjusted to account for the different sampling layouts in the two projects (Figure C3). Mixed models were used to test land use effects on CH_4 concentration, soil temperature, WFPS, air-filled porosity, total porosity, effective diffusion coefficient, and derived diffusive flux, turnover rate and methanotrophic activity in soil profiles. No variables were

transformed, and the residuals from the mixed model were assessed with Shapiro-Wilk normality test and skewness of histograms.

Means of these properties were compared using LSMEANS and SLICE statement under the MIXED procedure. Land use, measurement date, sampling depth, all two-way interactions and three-way interactions were set as fixed effects in the initial model. Each sampling level was crossed with the sampling date and set as random effect, which resulted in three levels of random effects in the initial model. A random effect was removed from the model when the variance was estimated to be zero. To account for temporal autocorrelation between sampling dates and spatial autocorrelation between sampling depth within a profile, gas profiles were defined as subjects in repeated measurements, and an anisotropic spatial power model [type=SP(POWA) (Date Depth) in MIXED procedure of SAS], was chosen as the spatio-temporal covariance structure. Three-way interactions and two-way interactions (except interaction of land use and depth) were removed one by one from the initial model when they were not significant in F tests of fixed effects, respecting the principle of marginality.

The land-use effect and its interaction with diffusion coefficient were added to the regression model of diffusive flux in order to identify the factors for the difference in CH_4 diffusive fluxes between land uses. The Land-use effect on the relationship between CH_4 diffusivity and air-filled porosity was also tested.

4.4 Results

4.4.1 Dynamics of CH_4 concentration, temperature, moisture and diffusivity in soil profiles

CH_4 concentrations in soil air were lower than the concentration in ambient air, and the difference between ambient air and soil air was usually larger in the dry season than in the rainy season (Figure 4.2). Although the means of CH_4 concentrations were higher at each depth in soils under rubber plantation than soils under forest, the difference was only statistically different at 5 cm and 70 cm depths (Table 4.1). CH_4 concentration decreased with increasing soil depth in natural forest, and the concentrations at 5 cm and 10 cm were significantly higher than concentrations at 30 cm and 70 cm. A similar pattern of decreasing CH_4 concentrations with depth was observed in rubber plantations.

Soils under rubber plantation had higher water-filled pore space than forest soils at all four sampling depths (Figure 4.2c, d), but there was a significant interaction between land use, sampling depth and sampling date. Soil temperature was significantly higher

under rubber than under forest at all sampling depths, but the difference between land uses and between depths within an individual land use was less than 1 ℃ (Figure 4.2e, f).

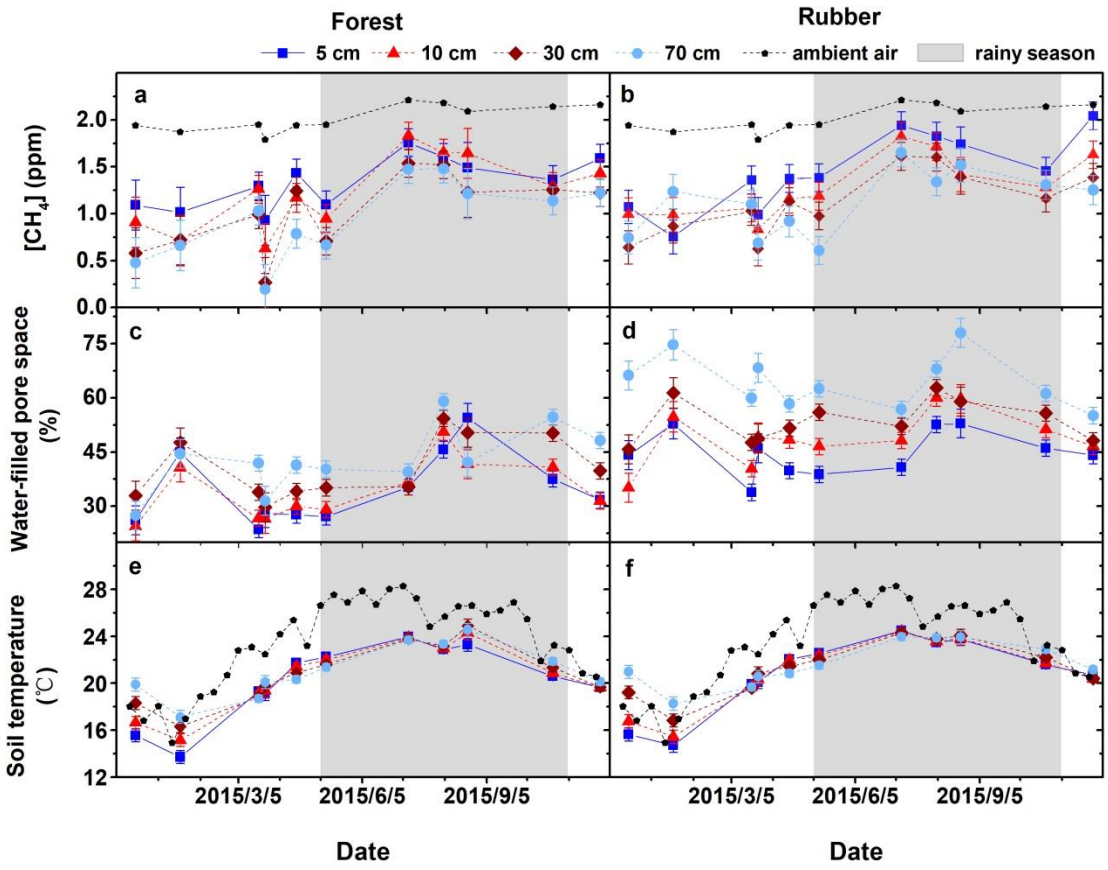

Figure 4.2 Dynamics of CH_4 concentration, water-filled pore space and temperature in soil profiles under forest and rubber plantations and ambient air. Means are least-square means from the three-factorial full model; error bars are standard errors; from combined dataset of Project I and Project II.

As a key factor controlling gas transport in soil, the average diffusive coefficient of CH_4 in forest soils was higher than in soils under rubber plantations at all four sampling depths (Table 4.1). Similarly, air-filled porosity was higher in forest soils than in soils under rubber plantations, corresponding to the lower soil moisture (WFPS) under forest soils compared to soils under rubber plantations (Figure 4.2, Table 4.1). For both diffusive coefficient and air-filled porosity, the land-use effect and sampling-depth effect were significant, while the three-way interaction of land use, sampling-depth and date was significant only for air-filled porosity. Total porosity was derived from bulk density, and the means comparison showed that forest soils had a wider range of porosity than soils under rubber plantations but there were no significant differences between them (Table 4.1).

4.4.2 Dynamics of CH_4 diffusive flux, turnover rate and methanotrophic activity

CH_4 diffusive flux, turnover rate and methanotrophic activity varied between sampling dates, but the top 10 cm soils were the major active layers in both natural forest and rubber plantation (Figure 4.3).

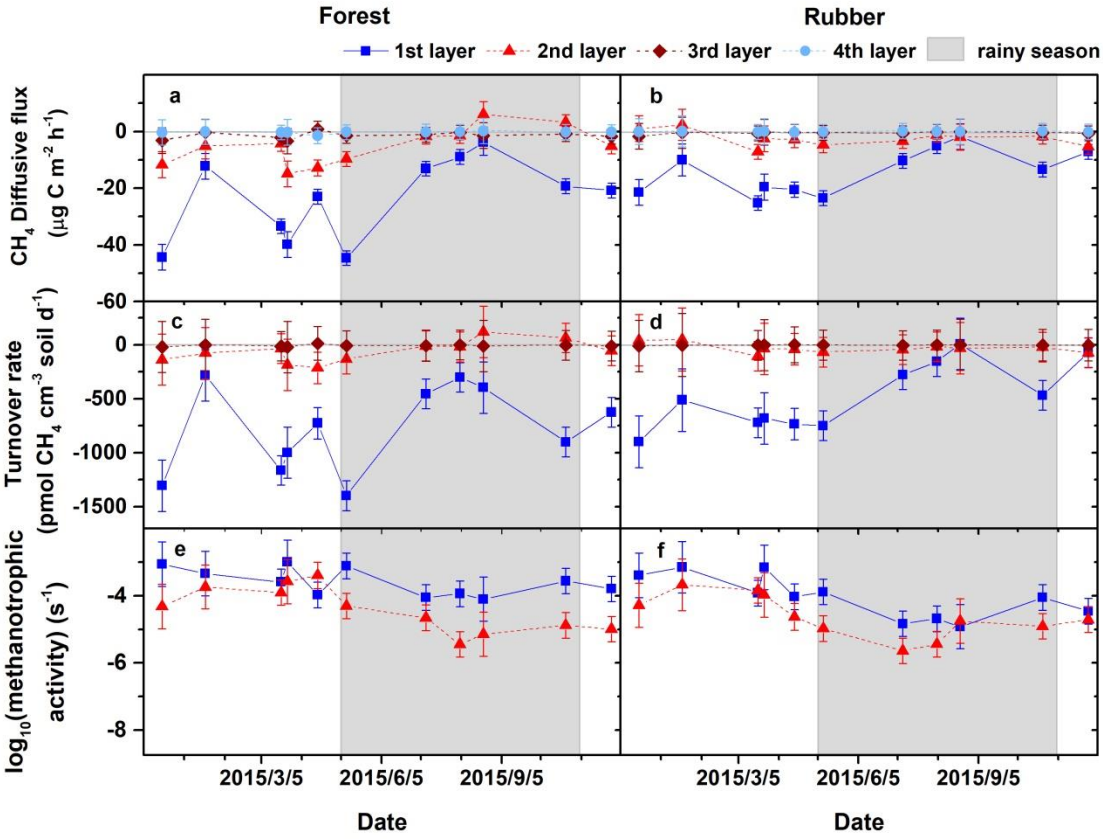

Figure 4.3 Dynamics of CH_4 diffusive flux, turnover rate and methanotrophic activity ($1og_{10}$ transformed) in forest and rubber plantation soil layers. The center depths for calculated diffusive fluxes were 2.5, 7.5, 20 and 50 cm respectively, and for turnover rate were 5, 13.75 and 35 cm respectively. Methanotrophic activity was determined for sampling depth at 5 and 10 cm, means for 30 and 70 cm were not presented here due to the limitation of calculation method. Reported values were least-square means and standard errors from three-factorial full model.

Table 4.1 Least-square means and standard errors of CH_4 concentration, temperature and water-filled pore space in soil profiles under forest and rubber plantations (from combined dataset of Project I and Project II)

Depth	CH_4 (ppm)		Soil temperature (°C)		Water-filled pore space (%)		Total porosity (m^3 m^{-3})		Air-filled porosity (m^3 m^{-3})		Effective diffusion coefficient (cm^2 s^{-1})	
(cm)	Forest	Rubber	Forest	Rubber	Forest	Rubber	Forest	Rubber	Forest	Rubber	Forest	Rubber
5	1.31^{aA}	1.45^{aB}	20.17^{aA}	20.83^{aB}	34.66	44.35	0.60^{aA}	0.60^{aA}	0.40	0.33	0.0223^{aA}	0.0111^{aB}
10	1.23^{aA}	1.28^{bA}	20.46^{bA}	20.98^{aB}	34.47	48.94	0.56^{abA}	0.59^{aA}	0.38	0.30	0.0209^{aA}	0.0087^{abB}
30	1.04^{bA}	1.13^{cA}	20.76^{cA}	21.35^{bB}	40.34	53.65	0.54^{bA}	0.55^{aA}	0.33	0.26	0.0147^{bA}	0.0065^{bB}
70	0.99^{bA}	1.12^{cB}	20.98^{cA}	21.64^{cB}	42.80	64.44	0.51^{bA}	0.54^{aA}	0.30	0.19	0.0113^{bA}	0.0046^{bB}
Standard error	0.06	0.05	0.14	0.14	1.52	1.52	0.02	0.02	0.01	0.01	0.0017	0.0017

* Least-square means sharing no common lower-case letter represent significant difference between depths within an individual land use; means sharing no common upper-case letter denote significant difference between forest and rubber plantation at same depth.

Diffusive fluxes of CH_4 from ambient air into surface soil (0-5 cm) were significantly higher in natural forest than in rubber plantations, with mean diffusive fluxes of -23.8±1.0 and -14.4±1.0 ug C m^{-2} h^{-1}, respectively (Figure 4.4, Table C1). Subsoil layers had much lower diffusive fluxes compared to surface soil, and there were no significant differences between natural forest and rubber plantations in soils below 10 cm depth.

Turnover rate showed a similar trend in that only the topsoil (0-10 cm) was significantly different between natural forest and rubber plantations, with average turnover rates of -793±54 and -451±55 pmol CH_4 cm^{-3} soil d^{-1}, respectively (Figure 4.4, Table C1). The turnover rate fluctuated around zero in subsoil and there were no significant differences between natural forest and rubber plantations.

Methanotrophic activity was highest in the surface soil (0-5 cm) and decreased by approximately an order of magnitude in the sampled subsequent soil layers. Forest soils at 0-5 cm exhibited significantly higher methanotrophic activity than corresponding soils under rubber plantations (Table C1). Calculated averaged methanotrophic activities at deeper soil layers (30 and 70 cm) were not reliable because some profiles had higher methane concentration at 70 cm than at 30 cm.

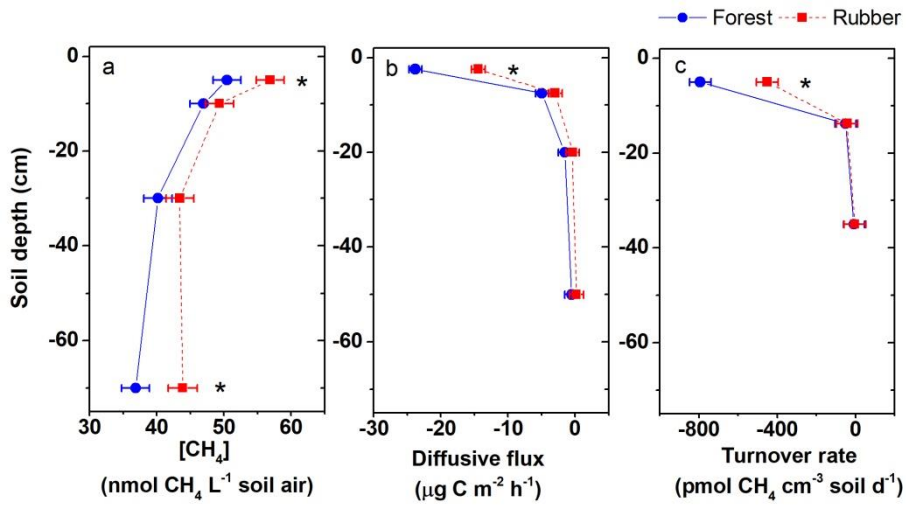

Figure 4.4 Average CH_4 concentration in soil air (a), diffusive flux (b), and turnover rate (c) at different soil layers for forest and rubber plantations (least-square means from combined dataset of Project I and Project II, error bars are standard error). * represents significant difference in comparison between natural forest and rubber plantation at individual depths ($p<0.05$); comparisons between depths within an individual land use are shown in Table C1.

4.4.3 Factors affecting CH_4 uptake rate in soils under forest and rubber plantations

Diffusivity alone explained 32% of variation in CH_4 fluxes for the surface 0-5 cm soil (Figure 4.5a). In the regression of diffusive fluxes and diffusivity for surface soil (0-5 cm), adding the land-use effect and interaction with diffusivity showed that both were not significant. Thus confirming that CH_4 diffusive fluxes decreased in a similar manner with diffusivity in forests and rubber plantations (quadratic function with same slope values), i.e. the more negative CH_4 fluxes from forest soils corresponded to higher diffusivity compared to soils under rubber plantations (Figure 4.5a). Further, the contrast in CH_4 diffusivity between surface soils (0-5 cm) under natural forests and rubber plantations was due to the higher and wider range of air-filled porosity in forest soils than in soils under rubber plantations (Figure 4.5b).

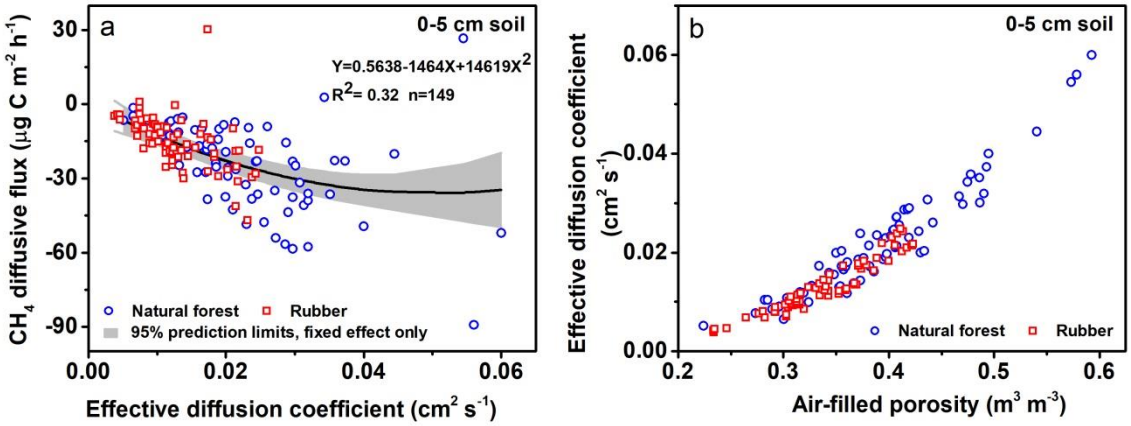

Figure 4.5 a) Relationship of CH_4 diffusive fluxes and effective diffusion coefficients for 0-5 cm soil depth, n=149; b) contrast of effective CH_4 diffusion coefficient and air-filled porosity between forest soils and soils under rubber plantations. Effective CH_4 diffusion coefficients were calculated from total porosity and air-filled porosity and corrected for temperature effects using Equation 4.1 and 4.2, see details in section 4.3.4.

4.4.4 Effect CH_4 diffusivity and methanotrophic activity on seasonality of CH_4 profiles

From the dry season to the rainy season, the CH_4 diffusive flux changed from -28.7 to -20.1 μg C m^{-2} h^{-1} and from -18.1 to -12.2 μg C m^{-2} h^{-1} for surface 0-5 cm soil under forest and rubber plantation, respectively (Table 4.2). The effective CH_4 diffusion coefficients decreased by 27.6%~35.7% and 17.1%~37.6% for soils under forests and rubber plantations, respectively (Table 4.2). A strong decrease in methanotrophic activity from the dry to the wet season occurred in soils at 5-10 cm depth in both

forests and rubber plantations, i.e. by 99.6% and 83.3%, respectively, while activity in the surface 0-5 cm soil decreased only by 23.2% and 38% for forests and rubber plantations, respectively.

By testing the CH_4 profile distribution using the seasonal averaged methane diffusivities of individual depths (Table 4.2), we found that, in both the dry season and the rainy season, CH_4 concentrations in the soil were not sensitive to the difference in diffusivities at different depths (Figure C4). In contrast, when a constant rate of methanotrophic activity (μ) was used across all depths, with depth-specific diffusivity, CH_4 distribution strongly varied depending on specific value of methanotrophic activity. For example, CH_4 concentration quickly decreased to nearly zero at 40-50 cm when methanotrophic activity of 5 cm was applied across all depths, while the decline of CH_4 concentration was more gradual when methanotrophic activity at 30 or 70 cm was used across all depths (Figure C5). Because the methanotrophic activity at 10 cm depth largely reduced in the rainy season in both land uses, the simulated decrement of CH_4 concentration with depth became gradual when the methanotrophic activity from 10 cm depth was used (Figure C5).

Table 4.2 Decline of CH_4 uptake rate, diffusivity and methanotrophic activity from the dry season to the rainy season in soils under forests and rubber plantations (Combined dataset, Project I and Project II, calculated as decrement from dry to rainy season and then divided by the value in dry season, %)

Land use	Depth (cm)	CH_4 diffusive flux ($\mu g\ C\ m^{-2}\ h^{-1}$)			Effective diffusion coefficient ($cm^2\ s^{-1}$)			Methanotrophic activity (s^{-1})		
		Dry season	Rainy season	Uptake Decrement (%)	Dry season	Rainy season	Decrement (%)	Dry season	Rainy season	Decrement (%)
Forest	5	-28.7	-20.1	29.9	0.0279	0.0182	34.9	3.35E-04	2.74E-04	18.2
Forest	10	-8.4	-1.8	79.0	0.0249	0.0160	35.7	4.68E-05	1.64E-07	99.6
Forest	30	-1.5	-1.0	34.4	0.0176	0.0121	31.2	2.95E-06	2.08E-06	29.5
Forest	70	-0.6	-0.2	73.2	0.0127	0.0092	27.6	4.42E-07	5.96E-08	86.5
Rubber	5	-18.1	-12.2	32.7	0.0146	0.0115	20.7	1.23E-04	7.57E-05	38.5
Rubber	10	-4.4	-2.7	37.8	0.0114	0.0077	32.8	6.69E-05	1.12E-05	83.3
Rubber	30	-0.6	-0.4	37.9	0.0085	0.0053	37.6	9.20E-07	6.61E-07	28.2
Rubber	70	-0.2	0.0	109.5	0.0048	0.0040	17.1	9.00E-10	4.12E-08	-

4.4.5 Seasonality of isotopic signatures of soil CH_4 and indication on processes

Soil CH_4 profiles in dry season sampling were enriched in ^{13}C compared to $\delta^{13}CH_4$ in ambient air, with larger enrichment in deeper soil layers in both forest and rubber

plots from Project I (Figure 4.6a). In top 30 cm soil layers, the enrichment by $^{13}CH_4$ was larger in the forest plot than in plots under rubber plantations, corresponding to higher CH_4 uptake by the forest soil. However, in the rainy season, soil CH_4 was less enriched than in the dry season, and $\delta^{13}CH_4$ in forest soil profiles shifted more strongly to the less enriched direction than in young rubber and old rubber profiles (Figure 4.6b). The mid-age rubber plot had a few extremely depleted $^{13}CH_4$ signatures in the topsoil, i.e. -69.6‰ and -57.6‰ at 5 and 10 cm depth in rainy season sampling (Figure 4.6b). The $\delta^{13}CH_4$ profiles of the forest plot were similar to the signature in ambient air in rainy season sampling.

Based on the $\delta^{13}CH_4$ profiles of the forest plot in the dry season, the estimated fractionation factor of ^{13}C in CH_4 oxidation (α_{ox}) was 1.0292 ± 0.0015 (n=12) (see detailed calculations in supplementary Equations C6-C15). Subsequently, this fractionation factor was applied in simulating CH_4 concentrations (Equation 4.5) and $\delta^{13}CH_4$ profiles (Equation 4.7-4.9) in the dry and rainy season, with the assumption of no CH_4 production in the soil.

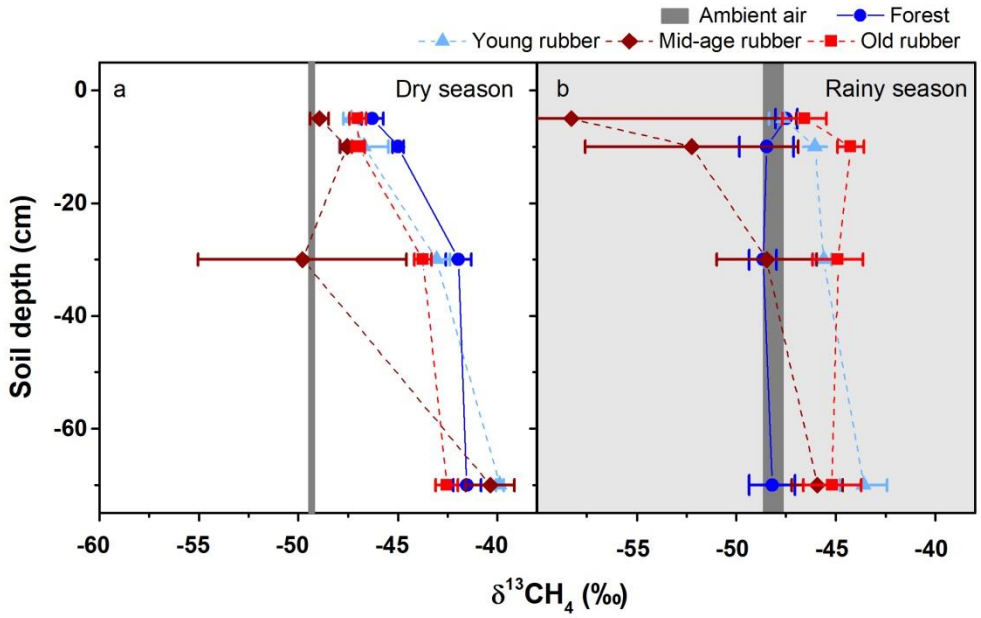

Figure 4.6 $\delta^{13}CH_4$ profiles of the forest plot and rubber plots at different age in Project I, sampled during the dry season (a) and during the rainy season (b).

Simulations of CH_4 concentrations and $\delta^{13}CH_4$ profiles in the dry season yielded good predictions for both forest and old rubber plots except 70 cm depth (Figure 4.7, solid black lines). As a result of decreased CH_4 diffusivity and CH_4 oxidation in the rainy season, both forest and rubber plots showed that, while CH_4 concentration increased

from dry season to rainy season (Figure 4.7a, c, from black lines to color lines), $\delta^{13}CH_4$ shifted to less enriched values (Figure 4.7b, d, from black lines to color lines).

After accounting for differences in ambient air between dry and rainy season, the measured shifts of $\delta^{13}CH_4$ of the four sampling depths from dry to rainy season sampling were 2.4, 4.7, 7.9 and 7.9‰ for forest and 0. 8, -1.5, 2.4 and 3.9 ‰ for rubber plantations, respectively. When rainy season averaged parameters were used in the simulation, the predicted shifts in the $\delta^{13}CH_4$ profile of the forest plot were not enough to capture the measured shift (Figure 4.7b, blue dash line vs blue symbols). In contrast, the predicted shifts in the $\delta^{13}CH_4$ profile of the old rubber plot were slightly larger than the measured differences (Figure 4.7d, red dash line vs red symbols).

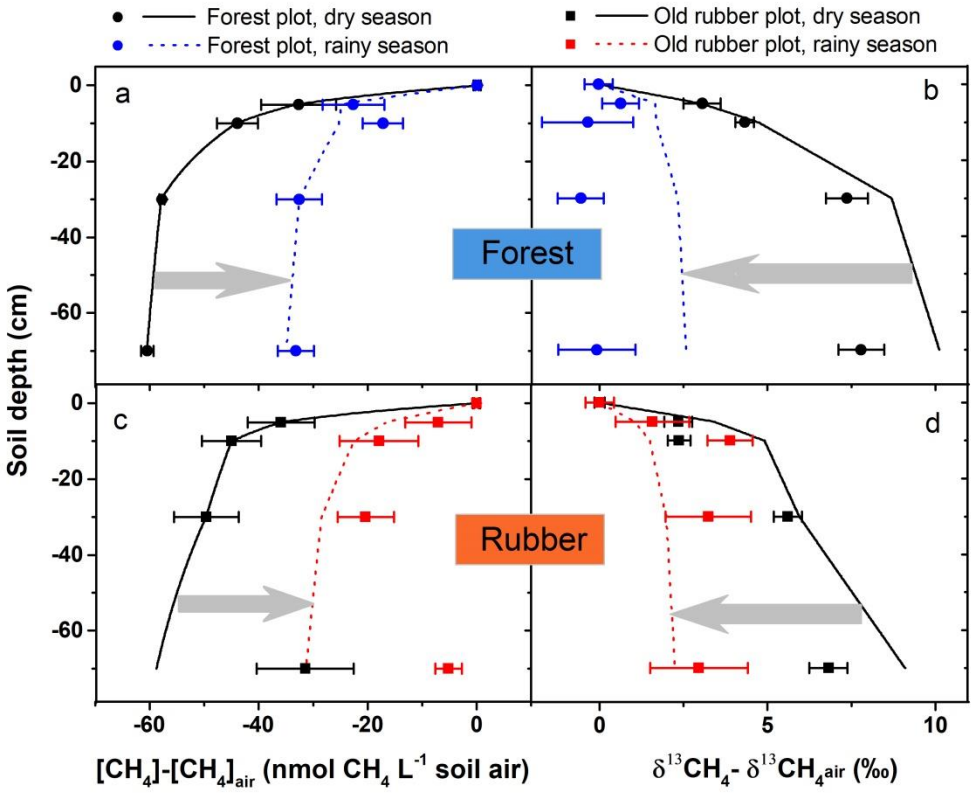

Figure 4.7 Predictions of CH_4 concentrations (Equation 4.5) and $\delta^{13}C$ of CH_4 in the soil profile using a 1D diffusion-consumption model (Equation 4.7-4.9). To account for the $^{13}CH_4$ differences in ambient air between seasons, predicted CH_4 concentrations and $\delta^{13}CH_4$ values were obtained by subtracting corresponding values in ambient air. Lines are simulations; symbols and error bars are means and standard errors from field measurements.

4.5 Discussion

4.5.1 Aerated topsoil predominantly responsible for CH_4 oxidation

The study demonstrated that the aerated topsoil was mainly responsible for CH_4 uptake, with 0-5 cm and 5-10 cm depth soil accounting for 78% and 16% of total profile uptake for forest, and 82% and 17% for rubber plantation, respectively (Figure 4.3, Figure 4.4, Table C1). Similar localizations of predominant CH_4 oxidation have been observed in the top centimeters of mineral soils or Ah horizons in temperate and Mediterranean forests *in situ* (Koschorreck and Conrad, 1993; Rosenkranz *et al.*, 2006). Higher potential CH_4 uptake and peak methanotrophic activity were found at a depth of 5-10 cm in boreal and pristine temperate forests, due the presence of organic layers (Amaral and Knowles, 1997; Price *et al.*, 2004) which were absent in our case. A soil core experiment demonstrated that gas diffusion between atmosphere and soil was faster than CH_4 oxidation (Koschorreck and Conrad, 1993). Considering the small difference in CH_4 diffusivities within the soil profile (Table 4.1, Table 4.2), and CH_4 distribution being not very sensitive to diffusivities at different depths (Figure C4) in our study, the localization of the main CH_4 oxidation activity in the upper part of the soil profile supports the hypothesis that methanotrophic activity controls profile CH_4 distribution stronger than diffusivity.

Although CH_4 oxidation in subsoil was observed in some studies, i.e. in temperate beech forest (Butterbach-Bahl and Papen, 2002), the weak CH_4 uptake by soils below 20 cm depth in our study (Figure 4.4b, Table C1) is similar to observed low or absence of methanotrophic oxidation activity in other forest studies (Koschorreck and Conrad, 1993; Kiese *et al.*, 2003; Price *et al.*, 2004). In our study, CH_4 concentrations at 30 and 70 cm could be as low as 0.14 and 0.22 ppmv during the dry season, but the average CH_4 concentrations at these two depths during the dry season were 1.02 and 0.90 for forest, and 0.97 and 0.94 ppmv for rubber plantations, respectively. These concentrations are above the limitation of the CH_4 supply for the growth of the methanotrophic population (<0.5 ppmv) (Koschorreck and Conrad, 1993), suggesting that a very low methanotrophic activity in subsoil (Table 4.2) is still possible despite limited supply of CH_4. O_2 availability strongly influenced the fraction of methanotrophic oxidation of produced CH_4 in a humid tropical forest (Teh *et al.*, 2005), suggesting that low O_2 and periodic anoxia have restricted methanotrophs in the subsoil.

While we could clearly demonstrate that methanotrophic activity controls soil profile CH_4 distribution stronger than diffusivity in both seasons and for both land-use types,

the hypothesis that the relative importance of physical diffusion and biological oxidation depends on the season and land use was not supported.

4.5.2 WFPS regulates gas diffusion and is responsible for major differences in CH_4 sinks between land uses

The hypothesis that the differences in WFPS between forests and rubber plantations result in different CH_4 diffusivities, as well as controlling CH_4 uptake by soils, was confirmed. Consistent with a weakened CH_4 sink in converted rubber plantations observed in a previous study using the chamber method (Lang *et al.*, 2019), the concentration gradient method used here demonstrated that the average CH_4 uptake at 0-10 cm depth under rubber plantations was reduced by 39% over the measurement period compared to that of forest soils (Table C1). Our study explicitly quantified the changes of CH_4 diffusivities throughout the soil profile, and demonstrated that higher WFPS led to the lower CH_4 diffusivities in soils under rubber plantations. CH_4 diffusivities in soils under rubber plantations were only about half of those in forest soils (Table 4.1, Table 4.2), which resulted in a 56% decline in CH_4 uptake by surface soils (0-5 cm) under rubber plantations (Table 4.1, Figure 4.4b).

The temporal variation of CH_4 oxidation in 0-5 cm surface soil was jointly controlled by diffusivity and methanotrophic activity. CH_4 Diffusivity alone explained 32% of variation in CH_4 oxidation, and land-use effect was not significant in the regression linking CH_4 flux with diffusivity (Figure 4.5a). From the dry season to rainy season, the relative decrement of CH_4 diffusivity in 0-5cm layer was larger in forest than in rubber plantations, but the relative change in methanotrophic activity in forest was smaller (Table 4.2). Considering the different ranges of WFPS and CH_4 diffusivity under two land uses in our study, one can conclude that soils under rubber plantation were wetter and more likely moved towards low diffusivity extremes than forest soils. Therefore, the effects of CH_4 diffusivity and methanotrophic activity on CH_4 oxidation likely differ at low WFPS in forest and at high WFPS in rubber plantations. A similar dependency on soil moisture range was observed in an arable land and in a semiarid steppe where low soil moisture during summer restricted CH4 oxidation (Dobbie and Smith, 1996; Wolf *et al.*, 2011), while the temperate woodland nearby the arable land was more limited by gas transport because of high soil moisture (Dobbie and Smith, 1996).

As a primary control on CH_4 oxidation in the soil, gas diffusivity is controlling the supply of atmospheric CH_4 and O_2 for methanotrophic oxidation (Smith *et al.*, 2018). Without an adequate replenishment of depleted substrates, especially O_2, at low gas

diffusivity the oxidation rate of CH_4 could become restricted (Ridgwell *et al.*, 1999). Considering that gases diffuse approximately 10^4 times slower in water than in air (Tang and Riley, 2014), increasing soil moisture not only greatly reduces the connectivity of the air pore-network in the short term, but continuing wet conditions could create anaerobic sites changing redox conditions and hence favoring methane production (Luo *et al.*, 2013).

As a primary factor regulating soil aeration and gas diffusivity, WFPS was frequently identified as main reason for the variation in CH_4 fluxes in tropical forests and rubber plantations (Werner *et al.*, 2006; Itoh *et al.*, 2012; Hassler *et al.*, 2015; Lang *et al.*, 2019). At our sites, WFPS was high, especially during the rainy season (average WFPS at 0-5 cm were 37.8±1.6% and 45.2±1.2% for forest and rubber plantation, respectively), and WFPS was negatively correlated with methanotrophic activity ($r=-0.34$ $p<0.01$, $n=150$, 0-5 cm soil). Compared to the thresholds of volumetric water content, i.e. below 38% as net CH_4 sink and above 43% as a net CH_4 source in a temperate landscape (Kaiser *et al.*, 2018), the high WFPS during the rainy season in our study indicates that the soils shifted towards the low diffusivity extreme during episodes of water saturation, not only limiting activities of methanoptrophs but also favoring methanogens.

In addition to soil moisture, other soil properties including compaction, soil texture, and local-scale variability could also affect the soil-gas diffusion coefficient (Moldrup *et al.*, 2013). Bulk density is considered an easily measurable proxy for soil compaction and is commonly used in determining the total porosity of soils (Antille *et al.*, 2015). However, in our study, the total porosities of soils under rubber plantations were not significantly different from those of forest soils (Table 4.1). Although soil under rubber plantations was often more clayey than forest soil, it was not the decisive factor for higher WFPS under rubber plantations compared to forest as demonstrated in Lang *et al.* (2019). Fine textured soils may play an important role in microenvironment formation for microbial activity of CH_4 oxidation and production (Ishizuka *et al.*, 2002). However, the reasons for the contrasting WFPS between forest and rubber plantations in our case were more complex than only changes in soil texture in determining CH_4 diffusivities (Figure 4.5b). Therefore, the weakened CH_4 uptake by soils under converted rubber plantations was likely due to an altered soil water regime.

The reasons why the soil water regime differs between rubber plantations and tropical forests remain unclear so far based on available studies on water budgets and soil water usage. Although rubber monoculture has a distinct single-storey canopy

structure and lacking an understorey layer compared to forest, literature reports on water input and loss in the two land uses are inconsistent. Zhu *et al.* (2018) measured a lower throughfall, the major rainfall input, in rubber plantations than in forest in Xishuangbanna (54% vs 76% of total rainfall), contradicting the higher throughfall in rubber plantation than lowland rainforest observed in a Malaysian study by Zulkifli *et al.* (2003). Stem flow was very low in both rainforest and rubber plantation, accounting for less than 2% of rainfall (Zulkifli *et al.*, 2003). Water vapor trapped by forest canopy from prevailing winter fog could contribute about 5% of annual precipitation in Xishuangbanna (Liu *et al.*, 2004), while the single-storey canopy structure and the open space between tree rows in rubber plantations is expected to trap less water vapor than forest. Comparisons of surface runoff in the two land uses also showed inconsistent results, i.e. surface runoff in rubber monoculture was 3-33 times the runoff in forest (Wu *et al.*, 2001; Zhu *et al.*, 2018), but annual runoff was 367 mm in rubber plantation compared to 565 mm in forest in another study (Tan *et al.*, 2011). A few studies reported rubber monoculture had higher evapotranspiration rates than forest resulting in depletion of soil moisture and discharge to the catchment (Guardiola‐Claramonte *et al.*, 2008, 2010; Tan *et al.*, 2011; Giambelluca *et al.*, 2016). However, this is not consistent with our observations of a higher soil moisture content under rubber trees. Recently, low transpiration rates were measured in rubber stands under humid tropical climate (Niu *et al.*, 2017), while evapotranspiration varied substantially in tropical forest types (Tanaka, 2008). In view of these contrasting findings, more detailed studies are needed to understand how land-use conversion changes the soil water regime.

The mechanism of weakened CH_4 uptake in converted rubber plantations is largely governed by changes in gas diffusivity, caused by an altered soil-water regime during land-use conversion; while within the soil profile of an individual land use, methane concentration distribution was more sensitive to the biological control (methanotrophic activity) than the physical control (gas diffusivity).

4.5.3 Insights from modeling seasonal variation of soil $\delta^{13}C$-CH_4

When CH_4 in soil is at sub-atmospheric concentration and net CH_4 fluxes occur mostly as CH_4 uptake, neither the chamber method nor the gradient method can determine the extent of CH_4 production in a profile with net CH_4 uptake. However, using stable isotope $^{13}CH_4$ measurements and incorporating ^{13}C carbon fractionation factors into the one-dimensional methane diffusion-oxidation model, we were able to simulate the profile distribution of $\delta^{13}CH_4$ and reveal the contribution of the two processes to the seasonal shift in methane uptake (Figure 4.7). For example, both CH_4

diffusivity and methanotrophic activity decreased in the rainy season, resulting in higher CH_4 concentration in the profile compared to dry season (Figure 4.7 a, c). The lower CH_4 diffusivity in the rainy season would result in less depleted ^{13}C signature in soil CH_4, while lower methanotrophic activity would lead to less enriched ^{13}C signature during CH_4 oxidation. Therefore, the fractionations of $^{13}CH_4$ during diffusion and oxidation would less in rainy reason, shifting ^{13}C signature of soil CH_4 closer to the signature in ambient air. The model used in this study could predict this shift in ^{13}C signature both land-use types except for subsoil at 70 cm depth (Figure 4.7b, d).

The discrepancy between the simulation and field measurements at lower soil depths in the rainy season could be due to two reasons. First, methane was likely produced in deeper soil layers during wet periods and served as substrate for methane oxidation in upper layers. The forest plot had a higher CH_4 concentration at 10 cm than at 5 cm depth, and the old-rubber plot had the highest CH_4 concentration at 70 cm depth in the rainy season sampling (Figure 4.7a, c), thus supporting the proposed subsoil CH_4 source. In addition, the lower $\delta^{13}CH_4$ (less enriched signature) in subsoil than in the upper layers, i.e. at 30 and 70 cm depths of the old rubber plots in the rainy season sampling (Figure 4.6b, Figure 4.7d), did not support CH_4 oxidation in subsoil using CH_4 substrate from the upper layers. A second reason for the mismatch between model and measurements could be that produced CH_4 has an isotopic signature different from that coming from the atmosphere and thus affecting the $\delta^{13}C$ of the CH_4 residuals in the soil. Although the dominant vegetation in natural forest and rubber plantations is composed of C3 plants, as confirmed by $\delta^{13}C$ in litter samples collected from soil surface (-30.96±0.15‰ vs -29.72±0.08‰ for the forest plot and old-rubber plot, difference -1.24‰), the $\delta^{13}C$ differences in soil organic carbon between the two land uses were larger than the differences in litter, with differences of -2.71‰, -4.57‰, -4.67‰ and -4.12‰ for the four sampled depths. The acetoclastic pathway is likely the main pathway for methane production in these upland soils without long periods of water saturation. Considering the range of carbon fractionation factor from 1.021 to 1.034 for the acetoclastic pathway (Fey *et al.*, 2004), the heavier ^{13}C in soil carbon under rubber plantations in this study is likely to result in a smaller shift of ^{13}C in CH_4 remaining in the soil.

Estimations of the isotopic fractionation factor (kinetic isotopic effect, a_{ox}) of methane oxidation in tropical forest soils are scarce (Teh *et al.*, 2006). To our knowledge, only a few studies estimated the carbon isotopic fractionation factor from soil probes measured under field conditions (Reeburgh *et al.*, 1997; Maxfield *et al.*, 2008). The estimated carbon fractionation factor of methane oxidation was 1.0292±0.0015

(n=12) from the forest plot, which is slightly higher than reported values from temperate forest soils using soil probes (1.0211-1.0250) (Reeburgh *et al.*, 1997; Maxfield *et al.*, 2008), and static chambers *in situ* (1.0181±0.0004) (Snover and Quay, 2000). When a lower fractionation factor of diffusion (a_{tr}) is used in estimating a_{ox} (Equation C6-C15) instead of the theoretical value 1.0195, for example, a_{tr}=1.013±0.003 determined from air-filled pores of tundra soil under filed condition (Preuss *et al.*, 2013), or a_{tr}=1.0178±0.0009 estimated from a glass beads column (De Visscher *et al.*, 2004), then the estimated a_{ox} at our site is closer to the estimations for the temperate forest mentioned above, with values of 1.0226±0.0015 or 1.0275±0.0015, respectively. When incubating soils under very high CH_4 concentration (CH_4 165-3800 ppm, O_2 as in ambient air 21%), the estimated a_{ox} ranged from 1.0102 to 1.0225 and varied depending on the CH_4 concentration and oxidation rate in a humid tropical forest (Teh *et al.*, 2006). However, considering soil CH_4 at sub-atmospheric concentration (except a few profiles sampled at wet conditions) and the top 10 cm soil as active layer for CH_4 oxidation, the dependency of a_{ox} on CH_4 concentration was not likely in our case. Chanton *et al.* (2008) found that a_{ox} decreased nonlinearly with increasing CH_4 concentration rate from incubating land-fill cover soil. Our estimated CH_4 uptake rate was at their very low end, thus our estimation of a larger a_{ox} is reasonable if methanotrophs in aerated forest soils have a similar dependency on the CH_4 oxidation rate.

The extreme depleted $\delta^{13}CH_4$ signature measured in the mid-age rubber plot at a specific date and depth (Figure 4.6) can be attributed to CH_4-producing termite activity, because termites emit CH_4 highly depleted in $^{13}CH_4$ (Sugimoto *et al.*, 1998), while the hydrogenotrophic pathway that is producing highly depleted $^{13}CH_4$ is not likely the dominate pathway for upland soil.

4.5.4 Importance and outlook

This study clarified the mechanisms of CH_4 diffusion and oxidation in natural forest and rubber plantations in tropical uplands, and revealed CH_4 production in subsoil under wet conditions, although the net flux resulted in a CH_4 sink. Warren-Thomas *et al.* (2015) estimated 4.3-8.5 million ha of rubber expansion are needed to meet the projected demand for natural rubber by 2024, and average precipitation is projected to increase 1.5% by 2050 under different representative climate change scenarios (Zomer *et al.*, 2014). In response to these land-use and climate change scenarios, CH_4 uptake by tropical upland soils is likely to continue to decline in the future. Recent studies on rubber agroforestry have shown intercropping could improve the soil physical properties, promoting soil water infiltration and recharge groundwater (Jiang

et al., 2019; Zhu *et al.*, 2019b). Furthermore, reducing herbicide use in weed management also had positive effects on soil structure and infiltration (Liu *et al.*, 2016), which may improve soil aeration and CH_4 uptake in rubber plantations.

Reliable estimations of land-use change impact on the soil function as a CH_4 sink requires an in depth understanding of the physical and biological controlling factors. In the upland areas where soil CH_4 concentrations are well below the ambient air concentration, high-affinity methanotrophs are more dominant than low-affinity methanotrophs (Dunfield, 2007). The composition and size of the methanotrophic community may shift with land-use change and management (agrochemicals, i.e. fertilization, herbicide, pesticide, etc.) (Shukla *et al.*, 2013). To characterize the land-use change impact on CH_4 processes, more advanced approaches, such as isotope labeling and molecular analysis of the incorporated labeled isotope in microbial biomass could be used in future to determine the structure of methanotrophic and methanogens communities and their activities (Knief *et al.*, 2003; Chowdhury and Dick, 2013).

4.6 Conclusions

The function of soils as a methane sink was weakened when converting natural forest into rubber plantations in tropical upland soils. This prominent land-use change effect was due to an altered soil water content, which subsequently reduced the gas diffusivity and methane consumption in the soil. Methane uptake was limited to the top 10 cm depth. Gas diffusivity controlled the seasonal dynamics of CH_4 uptake similarly for soils under natural forest and rubber plantations, and the larger relative decline in CH_4 uptake from the dry to rainy season occurred at 5-10 cm than at 0-5 cm depth for both land uses. We estimated a carbon fractionation factor for CH_4 oxidation from soil air sampled at different soil depths in the dry season. By introducing this factor into the one dimensional diffusion-oxidation model, the actual distribution of CH_4 and $\delta^{13}CH_4$ in the dry season could be reproduced, while simulating conditions in the rainy season clearly revealed CH_4 production in subsoil, suggesting that measured surface net flux or concentration gradient methods are insufficient on their own for characterizing the processes controlling methane turnover in tropical upland soils during the rainy season. Quantitatively separating the relative contribution of CH_4 production from gas transport and CH_4 oxidation requires taking the methane production and the carbon isotopic signature of substrates into account.

The weakened CH_4 sink function in soils under rubber monoculture exerts a negative effect on the global CH_4 budget and climate change, given the large extent of rubber

plantation**s** worldwide. More sustainable cultivation approaches, such as rubber agroforestry that also improve soil structure and aeration are needed to mitigate this negative impact.

Chapter 5 General discussion

5.1 Overview

This thesis assessed the impact of converting natural forest into rubber plantations on soil CO_2 emission and soil CH_4 sink in the tropical uplands. It focused on the methodological gaps in quantifying the temperature effect on soil CO_2 fluxes considering moisture interference (Chapter 2); statistically addressing the confounded controlling factors of CH_4 fluxes and land use change, and identifying the pathway of interactions between mineral nitrogen and CH_4 processes using chamber measured fluxes (Chapter 3); methane diffusion and oxidation processes in soil profiles were investigated using measured concentration gradient and $\delta^{13}CH_4$ profiles (Chapter 4). The estimation of an isotopic ^{13}C fractionation factor of CH_4 oxidation using soil probes *in situ*, and incorporating this factor into modeling the seasonality of CH_4 profiles were rarely studied so far in tropical upland soils. Therefore this study is novel and provides insights of dynamics of methane diffusion, oxidation and production processes and pointed out the direction for future studies.

In this discussion, the mechanisms of soil moisture regulating the seasonality of soil CO_2 fluxes is discussed firstly, as well as the applicability of the improved method in quantifying the temperature effect on soil CO_2 fluxes with consideration of moisture interference. Second, the control and mechanisms of land use change effect on soil CH_4 sink function is investigated, including the relative control by gas diffusivity and methanotrophic activity, and interactions with mineral nitrogen. Subsequently, the implication of isotopic modeling approach in differentiating CH_4 processes is discussed. Because of the important role of soil moisture on soil CO_2 and CH_4 fluxes in this assessment, the possible reasons for higher soil moisture in converted rubber plantations are discussed. Last but not least, the overall impact of converting natural forest into rubber plantations on soil carbon fluxes in the context of large-scale land conversions in Southeast Asia is discussed.

5.2 Interference of soil moisture on seasonality and temperature sensitivity of soil respiration

Although soil temperature mainly drives the seasonality of soil respiration, continuously high soil moisture in the rainy season could suppress soil respiration when moisture is exceeding the optimal range. Under the tropical monsoon climate, intensive rainfall events overlap with high soil temperature in the rainy season, thus soil respiration rate is expected to be high at high soil temperature when soil moisture

is optimal. The observed parabolic relationship between soil moisture and soil respiration confirmed the suppression of soil respiration under periodical wet condition in both forests and rubber plantation (Figure 2.4). This decline of soil respiration rate by excessive soil water, facilitated by clayey soil texture, can be due to water barriers in the soil pore network that limit O_2 diffusion into soil (Silver *et al.*, 1999), or due to inhibition of diffusion of respired CO_2 diffuse out of the soil in the short term (Sotta *et al.*, 2004). According to the Structure-dependent Water-Induced Linear reduction (SWLR) model, gas diffusivity in porous soil media is a function of soil water and porosities (Moldrup *et al.*, 2013). Although the diffusivities of O_2 and CO_2 were not explicitly determined for the soil respiration study (Chapter 2), the CH_4 diffusivities in soil profiles determined in Chapter 4 supported the statement that high soil moisture reduces gas diffusivities in the soil (Figure 4.5). The tipping points of soil respiration caused by changes in soil moisture were lower in forest and young rubber plantation than in mature rubber plantations, suggesting the gradual interference of soil moisture from young rubber plantation to older rubber plantations.

Quantifying the combined effect of soil temperature and soil moisture on soil respiration is still a challenge. By using the mixed effect model (LME), the differences in relative importance of soil temperature and soil moisture helped to explain the difference in patterns of soil respiration between land uses during wet periods of the rainy season. For example, soil temperature predominately controlled the soil respiration rate (relative importance 0.62 ± 0.05, Table 2.4, Figure 2.2) at the forest plot, and low soil moisture that was mostly under its tipping point (at WFPS 38.4%). Therefore, both soil temperature and moisture had positive effects on soil respiration on forest site, keeping it high during wet periods of rainy season. In contrast, the relative importance of soil temperature on soil respiration were only 0.34 ± 0.08 and 0.21 ± 0.10 for young and mature rubber plantation plots, respectively. Although their tipping points of soil moisture were mostly higher (at WFPS 37.8% and 51.6%), high soil moisture under rubber exerted a negative effect on respiration rate during wet period of the rainy season, thus explaining the decline of respiration rate while soil temperature was high (Table 2.4, Figure 2.2). This interference of high soil moisture on soil respiration rate could mask the temperature effect especially during the rainy season. The improved approach in this study demonstrated the necessity of accounting for the moisture effect in determining the temperature sensitivity of soil respiration.

Neglecting the interference of soil moisture would result in underestimation of temperature sensitivity of soil respiration (Q_{10}) for both forest and rubber plantations. Q_{10} were compared using a two parameter exponential approach and a linear mixed

effect model (Table 2.6). Both two parameter exponential method and LME method in this study estimated higher Q_{10} values for forest compared to rubber plantations. Q_{10} estimations in the literature using two parameters exponential method also observed tendency of higher Q_{10} values in forest than in rubber plantations, i.e. 2.08-3.09 for forest and 1.33-2.26 for rubber plantations (Sha *et al.*, 2005; Fang and Sha, 2006; Wu *et al.*, 2014). However, these estimates were all smaller than the corresponding values obtained from LME method in this thesis. This difference confirmed that temperature sensitivity of soil respiration was underestimated if moisture effect was not accounted for. Moreover, according to the definition of temperature sensitivity, the higher Q_{10} values in forest than in rubber plantations suggested that forest is likely to respire more CO_2 from soils than rubber plantations in response to a warming climate. More studies are needed to understand the mechanisms, such as the effect of soil organic matter quality on the kinetics of mineralization.

Improving the estimation of temperature sensitivity could help reducing the uncertainty in predicting soil CO_2 emissions in response to climate change. It has been well established that soil respiration rate declines under water stress or when soil is too wet (Moyano *et al.*, 2012), but the knowledge gap of the interactive effect of soil temperature and moisture on soil respiration is still limiting the predictions of CO_2 emission and feedbacks to climate change (Meyer *et al.*, 2018). As a key parameter in carbon cycle models and in coupled climate change-carbon cycle models, a common practice is using fixed Q_{10} values estimated from exponential function with soil temperature and further modify the respiration function for the dependency on soil moisture (Friedlingstein *et al.*, 2006). As illustrated in this study, Q_{10} was underestimated using the exponential function without accounting for moisture interference, thus using a lower temperature sensitivity might underestimate warming-induced carbon loss.

5.3 From surface net CH_4 flux to underlying processes in the soil profile

The net CH_4 fluxes measured by chambers and fluxes determined by concentration gradient method both confirmed that converting natural forest into rubber plantations weakened the soil function as CH_4 sink (Chapter 3 and 4). Soil moisture was identified as decisive controlling factor of CH_4 fluxes apart from a confounded texture effect, thus responsible for the reduced CH_4 uptake in rubber plantations (Chapter 3). This was further confirmed by the regulation of soil moisture on gas diffusivities in soil media (Chapter 4). Location of CH_4 oxidation in the profile was concentrated in the top 10 cm mineral soil, and methanotrophic activity controlled profile CH_4 distribution more than diffusivity within an individual land use. The isotopic

fractionations of $^{13}CH_4$ in diffusion and oxidation were incorporated into a diffusion-oxidation model to describe the seasonality of $^{13}CH_4$ distribution in soil profiles. The simulations matched the CH_4 concentration and isotopic signature-$\delta^{13}CH_4$ profiles in the dry season, however, the differences between simulated and observed $\delta^{13}CH_4$ profiles in the rainy season revealed CH_4 production in subsoil.

The net CH_4 flux is the balance between CH_4 oxidation by methanotrophs and CH_4 production by methanogens, jointly regulated by abiotic and biotic factors that control gas diffusion, activities of methanotrophs and methanogens in the soil (Le Mer and Roger, 2001). Converting natural vegetation systems into agricultural systems could change soil structure, soil hydraulic and other physical properties that affect physical diffusion and in consequence the availability of substrate CH_4 and O_2 for oxidation (Castaldi *et al.*, 2006). Management of converted agricultural system, such as applying mineral fertilizers, can interfere with CH_4 processes via different pathways, such as alleviating N limitation for the growth of methanotrophs, inhibiting CH_4 oxidation under aerobic condition due to competition with ammonia oxidizer, and inhibiting CH_4 production under anaerobic condition because of competition with nitrate reducers (Bodelier, 2011; Tate, 2015), and applying herbicide might affect the microbial communities in general. The altered soil water regime in converted rubber plantations mediated soil aeration, which may change the soil redox potential and affect the interactions between CH_4 processes and mineral nitrogen.

5.3.1 Control of gas diffusion on CH_4 oxidation

Induced changes in soil structure and physical properties during land use conversion, such as compaction and soil water content, could affect gas diffusivities in the soil (Castaldi *et al.*, 2006). As a proxy of soil compaction, bulk density of all sampling sites, and determined total porosity in this thesis showed no significant difference between forest and rubber plantations (Table 2.2, Table B2, Table 4.1). The CH_4 diffusivities determined at four sampled depths in this thesis were lower in soils under rubber plantations compared to forest (Table 4.1, Table 4.2), but this contrast was predominately driven by altered soil water content and air-filled porosities (Table 3.3, Table 4.1). Although de Blécourt *et al.* (2014) found higher bulk density in older rubber plantations at 0-10 cm depth on the terraces, considering the relative small area of terraces to the area of entire plantation, the compaction due to tapping activity seems rather limited.

The CH_4 diffusivities of soils under rubber plantation were only half that of forest

soils (Table 4.1, Table 4.2), predominantly caused by the contrasting WFPS between the two land uses, and mainly explained the weakened CH_4 sink in rubber plantations (Figure 4.5). Gas diffusivity is a primary control on CH_4 oxidation in the soil, controlling the supply of atmospheric CH_4 and O_2 for methanotrophic oxidation (Smith *et al.*, 2018). Without an adequate replenishment of depleted substrates, especially O_2 that is used not only by plant roots but also by aerobic microbial processes, the oxidation rate of CH_4 becomes restricted at low gas diffusivity (Ridgwell *et al.*, 1999). O_2 concentrations in the topsoil decreased significantly with increasing rainfall in upland forests in the humid tropics (Silver *et al.*, 1999), and very low CH_4 concentration (<0.5 ppmv) in the soil could limit CH_4 supply for the growth of the methanotrophic population (Koschorreck and Conrad, 1993). In this studied tropical uplands, CH_4 concentrations at 30 and 70 cm depth could be as low as 0.14 and 0.22 ppmv during the dry season, but the averaged concentrations were about half of atmospheric concentration during the rainy season. Methanotrophic activities in the subsoil were very low (Table 4.2), and the simulation of methanotrophic activity effect suggested that methanotrophic activity controlled CH_4 distribution in the profile more than gas diffusivities (Figure C5). Therefore, the low CH_4 oxidation in subsoil is more likely limited due to the supply of O_2 rather than CH_4.

Land use change mediated CH_4 sink by altering soil water content and CH_4 diffusivities in this studied tropical upland soils. Considering that the diffusion rate of gases, including O_2, is 10^4 slower in soil water than their diffusion in air (Tang and Riley, 2014; Neira *et al.*, 2015), increasing soil moisture not only greatly reduced the connectivity of the air pore-network in the short term, but continuing wet conditions could create anaerobic sites and change redox conditions favoring methane production when degraded organic carbon is available (Luo *et al.*, 2013). This might be the mechanism explaining the CH_4 production in subsoil of rubber plantations where soil moisture was constantly high.

Land use change may induce other structural changes that affect CH_4 oxidation without greatly changing gas diffusivity, such as reduction of macro-porosity, formation of anaerobic microsites favoring CH_4 production in fine textured soil (Castaldi *et al.*, 2006). Quantifying the effect of converting forest into rubber plantations on soil structure and contribution to CH_4 sink require further studies.

5.3.2 Control of methanotrophic activity on CH_4 oxidation

In this thesis, methanotrophic activities were calculated for discrete soil layers, using a diffusion-oxidation model (von Fischer *et al.*, 2009) with measured CH_4

concentration and calculated diffusivities at each sampling depth. This indirect estimation of methanotrophic activity allowed to separate the effects of physical diffusion and biological activity on CH_4 uptake. The main localization of CH_4 oxidation was in the top 10 cm of mineral soil and comprised more than 90% of CH_4 uptake in the soil profile (Figure 4.4, Table C1). The averaged methanotrophic activities in forest soils at 0-5 cm depth were significantly higher than the activities in the soils under rubber plantations (Table C1). During the transition from the dry season to rainy season, a greater decline of methanotrophic activity occurred at 5-10 cm depth than at 0-5 cm depth under both land uses (Table 4.2), suggesting that increased water-filled porosity in the rainy season greatly restricted the activity of methanotrophs at 5-10 cm depth. The simulation of the methanotrophic activity effect on CH_4 distribution in soil profile showed that biological activity played a more important role than gas diffusivity in controlling CH_4 oxidation within soil profiles.

The relationship between environmental factors and methanotrophic activity was evaluated in the most active 0-5 cm surface soils. Unlike the arid systems, where the activity of methanotrophs is restricted by water stress and methanotrophic activity positively correlated to soil moisture (von Fischer *et al.*, 2009), a negative correlation between WFPS and methanotrophic activity was observed in this study (Chapter 4), suggesting that high soil moisture exerted a negative effect on methanotrophic activity in the tropical upland soils. Optimum soil moisture range also applies to CH_4, and high moisture above the optimum could change a CH_4 sink into a net CH_4 source, i.e. soil was a net CH_4 sink when volumetric water content was below 38% and became a net CH_4 source when moisture was above 43% in a temperate landscape (Kaiser *et al.*, 2018). However, due to the large temporal variation of CH_4 fluxes and characteristics of monsoon climate, both positive and negative CH_4 fluxes were observed at WFPS below the threshold estimated from our regression (WFPS at 57.6 and 73.8 for Project I and Project II, Figure 3.3). Therefore, the duration of high moisture in the tropical system during the rainy season should be considered in addition to optimal moisture range for CH_4 processes. The average soil temperature of our studied forest and rubber plantations was around 20 ℃ (Table 4.1), which has very limited effect on methanotrophic activity because it is close to the range of optimum temperature (25-35 ℃) for maximum CH_4 consumption (Mohanty *et al.*, 2007).

In short, methanotrophic oxidation was limited to 0-10 cm topsoil and sensitive to soil moisture. High moisture in rainy season resulted in substantially reduced methanotrophic activity at 5-10 cm depth. Methanotrophic activity controls distribution of CH_4 oxidation in soil profile more than diffusivity.

5.3.3 Interactions between mineral nitrogen and CH_4 oxidation and production

Based on the observed differences in soil mineral nitrogen content between forest and rubber plantations, and the relationship with CH_4 fluxes and the main controlling factor-WFPS, the mechanisms explaining their interactions in this studied tropical upland soils and the role of land use changes are discussed and summarized at below.

At aerobic conditions, methanotrophic ammonia oxidation can compete for active sites on monooxygenase (MMO) in methanotrophs, producing toxic intermediate products, such as hydroxylamine (NH_2OH) and nitrite (NO_2^-), thus inhibiting CH_4 oxidation (Dobbie and Smith, 1996). Adding ammonium to the topsoil of a temperate forest inhibited CH_4 consumption both *in situ* and *in vitro*, but the extent of inhibition differed at soil depths, supporting the inhibition pattern by competition between ammonia and methane for monooxygenase and toxic effect of nitrite (Schnell and King, 1994). A similar inhibition effect was observed in a tree plantation in tropical lowland only during the dry period (Weitz *et al.*, 1999). In this thesis, ammonium was the dominant mineral nitrogen form and the content in forest soils was comparable to rubber plantations (Table 2.2, Figure 3.5). Considering the better aeration in forest soils than in soils under rubber plantations, the inhibition of CH_4 oxidation by ammonium is not likely one of reasons for lower CH_4 oxidation in converted rubber plantations.

At periodical anaerobic conditions, methanogens are favored to produce CH_4 using substrates such as acetate-methyl or acetate-carboxyl (acetoclastic pathway), or CO_2 and H_2 (hydrogenotrophic pathway) (Le Mer and Roger, 2001; Conrad, 2005). In competing for electrons, methanogens are less favored compared to nitrate reducers, and sulphate (SO_4^{2-}) and ferric iron (Fe^{3+}) reducers that often appear in tropical soils (Chidthaisong and Conrad, 2000). Nitrate was preferably reduced in this sequential reduction process under anoxic conditions, and the low redox potential was needed to initiate the methanogenesis in addition to the presence of CH_4 precursors in the soil (Peters and Conrad, 1996). In the meantime, nitrates reduces to toxic compounds (NO_2^-, NO and N_2O) that greatly inhibit the activity of methanogens (Bodelier, 2011; Butterbach-Bahl, 2013). A recent study by Fan *et al.* (2020) showed that as an effective electron acceptor, adding nitrate could enhance anaerobic CH_4 oxidation in incubated rice paddy soils. Compared to the forest soils, the lower nitrate content was corresponding to higher WFPS and smaller CH_4 uptake in rubber plantations in this study. The positive effect of nitrate on CH_4 uptake suggested in covariate analysis (Figure 3.4, Table B5) supports the mechanism stating that higher nitrate content could competitively inhibit CH_4 production under wet conditions.

Nitrogen limitation is another mechanism explaining the stimulated CH_4 uptake in nitrogen adding experiments, as well as in explaining the positive correlation between nitrogen content and CH_4 uptake. In nitrogen limited soil, adding nitrogenous fertilizer could relieve N limitation of cell growth and increase the activity of methanotrophs, or interfere with the synthesis of the involved enzymes in CH_4 oxidation, or promote the population of the nitrifiers (ammonium oxidizer) that are also able to oxidize CH_4 because of ammonia monooxygenase (AMO) (Bodelier and Laanbroek, 2004). However, nitrogen limitation theory was not often supported by N adding experiments. Although there was stimulated CH_4 uptake at low dose of nitrogenous fertilizer in forest and tree plantation systems (Koehler *et al.*, 2012; Geng *et al.*, 2017), more studies showed a negative impact of N addition on CH_4 uptake, i.e. CH_4 uptake was reduced by more than 20% after applying nitrogenous fertilizer in tree-based systems (Zhang *et al.*, 2012; Zheng *et al.*, 2016). In tropical systems, the negative correlations between nitrate and CH_4 fluxes in a lowland forest, between ammonium and CH_4 fluxes in the organic layer of a montane forest (Veldkamp *et al.*, 2013), and between CH_4 fluxes and mineral N content in reference forest, jungle rubber, rubber monoculture and oil palm plantation were interpreted as N limitation (Hassler *et al.*, 2015). However, this negative correlation could be also due to the inhibition of CH_4 production by nitrate reducers especially under wet conditions, as discussed in the preceding paragraph.

In interpreting the interactions and mechanisms between CH_4 fluxes and mineral nitrogen, soil moisture needs to be considered and a proper statistical analysis could assist the interpretation (Chapter 3). Fertilization is a common practice in agricultural systems to improve the productivity. Compared to natural reference systems, CH_4 uptake in fertilized agricultural systems was less than a half of the uptake in reference systems (Dobbie *et al.*, 1996; Chan and Parkin, 2001b). Hence, this general difference is not likely due to N limitation.

Other management practices, such as spraying herbicide glyphosate to clear the understory vegetation and sulfur powder to control mildew and anthracnose diseases in rubber monoculture, may affect soil faunal diversity but showed no significant changes in soil microbial community composition and function up to mature stage (Li *et al.*, 2016; Singh *et al.*, 2019). Well-designed experiments on herbicide and sulfur control on methanotrophs and methanogens and resulted changes in CH_4 fluxes are lacking. Therefore such effects are much less studied and hardly to be separated from other main controlling factors.

5.3.4 Implications of modeling CH_4 and $\delta^{13}CH_4$ profiles

Modeling the distribution of CH_4 in soil profiles determined the location of CH_4 oxidation and explained the relative control of gas diffusion and methanotrophic activity on CH_4 uptake. The diffusive flux and turnover rate suggested the active CH_4 oxidation predominantly occurred in the top 10 cm mineral soil in both forest and rubber plantations (Figure 4.4). The land use mediated CH_4 sink was affected more via changes in gas diffusivities than in methanotrophic activity. A similar location of maximal CH_4 oxidation has been observed in temperate and boreal forests (Koschorreck and Conrad, 1993; Amaral and Knowles, 1997). Such estimations in soil profiles *in situ* are largely missing for heterogeneous tropical forest and plantation systems. A few studies in humid tropical forests measured soil CH_4 concentrations above that of the atmospheric concentration and soils acted as a net CH_4 source (Silver *et al.*, 1999; Teh *et al.*, 2005). The CH_4 profiles measured in a tropical primary forest and a disturbed land use in Sumatra (Ishizuka *et al.*, 2002) suggested a decline of CH_4 concentrations with increasing soil depth but the number of observations were insufficient to account for large spatial and temporal variations.

Adding the isotopic fractionation effect in modeling $^{13}CH_4$ revealed CH_4 production in subsoil during the rainy season (Figure 4.7). When CH_4 in soil is at sub-atmospheric concentration and net CH_4 fluxes are mostly negative (CH_4 uptake), neither the chamber method nor the gradient method can differentiate the CH_4 production from the net CH_4 uptake. The discrimination of $^{13}CH_4$ in CH_4 oxidation results in enriched ^{13}C signature in soil residual CH_4 (Coleman *et al.*, 1981), while slower diffusion of $^{13}CH_4$ than $^{12}CH_4$ from atmosphere into soils leads to depleted ^{13}C signature in soil CH_4 (De Visscher *et al.*, 2004). Adding these fractionation effects into the one-dimension diffusion-oxidation model, simulated control of gas diffusivity and methanotrophic activity on $^{13}CH_4$ distribution matched the observations in the dry season. However, although the averaged CH_4 concentration profiles were at sub-atmospheric concentration in rainy season, the ^{13}C fractionation by diffusion and oxidation was not sufficient to explain the observations in forest soils and subsoil of rubber plantation, suggesting that the model assumption became invalid at wet conditions and CH_4 production also contributed to changes in $\delta^{13}CH_4$ in the soil.

To estimate the exact fraction of CH_4 production and oxidation in net CH_4 uptake, analyzing the isotopic carbon composition of CH_4, precursors of CH_4 and CO_2 are needed (Teh *et al.*, 2006). Alternative approaches such as isotope labeling, combining with inhibitor to methanotrophs or methanogens, and molecular analysis of incorporated labeled isotope in microbial biomass, could be used in future to

characterize the land use change impact on CH_4 processes (Knief *et al.*, 2003; Chowdhury and Dick, 2013). The composition and size of the methanotrophic community may shift with land use change and management (agrochemicals, i.e. fertilization, herbicide, pesticide, etc.) (Shukla *et al.*, 2013). Determining the structure of methanotrophic and methanogens communities and their activities could reveal how land use change induces alters CH_4 fluxes at microbial level.

5.4 Altered soil water regime in converted rubber plantations

Soil moisture in rubber plantations was higher than in forest soils in this thesis. This large difference explained the suppression of soil respiration in rubber plantations during the wet periods of rainy season and weakened soil CH_4 sink in rubber plantation. This difference in soil moisture was based on sufficient spatial replicates at landscape level with different soil textures (Table 3.3, Table 4.1). In addition, this difference in soil moisture between natural forest and rubber plantations was proved not exclusively be due to a confounded texture effect (Figure 3.6). However, the observations in this thesis contradicted somewhat results of a water-balance study, which found rubber plantations depleting soil moisture (Guardiola‐Claramonte *et al.*, 2008). Rubber trees have been reported as "Water pumps" and "Big drinkers", and their large scale expansion at the expense of rainforest is considered as one of the reasons contributing to more frequent and severe regional droughts (Qiu, 2009; Tan *et al.*, 2011). Therefore, the water usage and budget of rubber trees and native forest from literature are discussed at below in order to understand the potential reasons for the higher observed soil moisture under rubber plantations.

The transpiration rate of rubber trees was actually not very high for a tropical tree crop (<3 mm d^{-1}) (Carr, 2011). For example, the mean transpiration rate was 1.3 mm d^{-1} from mature stands growing under humid tropical climate in Indonesia (Niu *et al.*, 2017), 2-2.4 mm d^{-1} under tropical monsoon climate in Cambodia (Kobayashi *et al.*, 2014), and maximum at 2.4 mm d^{-1} in drought-prone of northeast Thailand (Isarangkool Na Ayutthaya *et al.*, 2011). The sap fluxes of rubber trees showed less active transpiration during the dry season than the rainy season (Kobayashi *et al.*, 2014), especially the leaf shedding of rubber trees in the middle of dry season reduced transpiration (Priyadarshan and Clément-Demange, 2004), but significantly increasing uptake of deep soil water only occurs during new leaf flushing (Guardiola‐Claramonte *et al.*, 2008). Dry season evapotranspiration from tropical forests in Thailand and adjacent regions considerably different between forest types, ranging from 0.6 mm d^{-1} to 5.9 mm d^{-1} (Tanaka, 2008). In addition, because of lacking direct comparison between forest and rubber plantations using same method, whether rubber plantations lose

more water through transpiration or evapotranspiration is still unclear.

Rainforest canopy could trap water vapor from the prevailing winter fog, contributing about 5% of annual precipitation in rainforest in Xishuangbanna (Liu *et al.*, 2004). In contrast, intensively managed rubber monoculture has one story structure, open spaces between tree rows and leaf shedding phenomenon, thus water harvest from fog drip is expected to be low. The reduced presence of heavy fog from late January to April in the region was believed the consequence of replacing rainforest with rubber plantation at large scale (Wu *et al.*, 2001).

Surface runoff in rainforest was around one third of runoff in rubber monoculture (Wu *et al.*, 2001), and cumulative infiltration in rainforest was higher than infiltration in rubber plantations (Chen *et al.*, 2019), suggesting less contribution to deep drainage and recharge to the groundwater in rubber plantations. Contrary to higher soil moisture and no significant compaction in rubber monoculture from this thesis, Chen *et al.* (2019) observed soil compaction in old rubber monoculture but correspond to slightly lower soil moisture compared to rubber intercropping and rainforest.

In summary, available studies on water usage and balance could not explain observed higher soil moisture in rubber plantations than in natural forest. From field observations, remaining natural forest at similar altitude of rubber plantations is often located on steep slopes, which may facilitate soil water flow in forest. Furthermore, in contrast to the growth of understory vegetation in forest, the understory in rubber plantations is regularly cleared with herbicide, which may reduce the infiltration of soil water in rubber plantations. Slightly tilt terraces (de Blécourt *et al.*, 2014) can reserve more water than slopes during the rain events, and tapping activity is likely to compact soils on the terraces. Observed stagnation of water on terraces after rain events is likely due to poor soil structure and low infiltration. However, there is a lack of information how different the infiltration between forest and the slopes between rubber tree rows is. To resolve the reasons for contrasting soil moisture in forest and rubber plantations, further studies need to cover all components of water cycles in both reference forest and rubber plantations.

5.5 Overall land use change impact on gaseous carbon fluxes from soil

CO_2 respired from forest soils tends to be higher, and less likely suppressed during wet periods in rainy season compared to soils under rubber plantations in tropical uplands. The annual soil CO_2 flux in forest was 20% higher than the flux in mature rubber monoculture (Table 2.3). Similar lower respiration rates were observed in

rubber plantations than reference forests in tropical upland in Xishuangbanna (15% and 23%) (Lu *et al.*, 2009; Goldberg *et al.*, 2017). However, there was no consistent trend to comparisons in tropical lowlands (Ishizuka *et al.*, 2002; Hassler *et al.*, 2015). The chronosequence studies suggested that soils respire the least amount of CO_2 in young rubber plantations, and respiration rates slowly increase in older plantations (Lang *et al.*, 2017; Gao *et al.*, 2019). This dynamic of soil respiration rate was partly due to the litterfall production, which requires 9-10 years to reach the maximum production in a rubber plantation (Mandal and Islam, 2008). The decline of soil organic carbon in topsoil stabilizes around 20 years after establishing rubber plantations (de Blécourt *et al.*, 2013), consistent with recovery of soil respiration rate. The high correlation between cumulative CO_2 fluxes and organic carbon content in topsoil of forest and rubber plantations at different age (Chapter 2), agree with the linkage between spatial variability of soil respiration and soil carbon content (Ferréa *et al.*, 2012). Therefore, despite the land use change effect on seasonality of soil respiration, the annual emissions of CO_2 and dynamics of CO_2 fluxes are largely depending on the dynamic of ant litter input and soil organic carbon content.

Converting natural forest into rubber plantations generally tends to reduce soil carbon content in topsoil (Blagodatsky *et al.*, 2016), while the substantial carbon stocks in deep soils remain stable (Borchard *et al.*, 2019). For example, soil carbon content in topsoil decreased by 13-23% during conversion of forest to rubber monoculture in Xishuangbanna (Guo and Gifford, 2002; de Blécourt *et al.*, 2013) and by 30% in sandy soil in Ghana (Chiti *et al.*, 2014). This relative decline of soil carbon content and aforementioned reduction of soil respiration rate are of similar magnitude, confirming the importance of mineralization of soil organic matter in annual CO_2 emissions from soils.

Converting natural forest into intensively managed rubber monoculture weakened the soil CH_4 sink, with annual CH_4 uptake reduced by 58.4% in this study (Table 3.1). Similar decrease in CH_4 uptake was observed in other converted tree crop plantations, such as rubber monoculture, oil palm and cacao agroforestry in tropical lowlands in Indonesia (Veldkamp *et al.*, 2008; Hassler *et al.*, 2015). A meta-analysis showed that changing land uses from a natural system to a cultivated system in upland increased CH_4 fluxes by 14 μg CH_4 m^{-2} h^{-1} (McDaniel *et al.*, 2019), and the net CH_4 uptake in managed systems was only 40% of the uptake in undisturbed control sites in tropical seasonal-dry systems in Africa (Castaldi *et al.*, 2006). The reasons why agricultural practices negatively affect the CH_4 uptake by soils include applying nitrogenous fertilizers, alteration in soil porosity and structures, induced shift in microbial communities, etc. (Castaldi *et al.*, 2006). In this thesis, altered soil moisture,

difference in mineral nitrogen and soil texture were identified in contributing to the weakened CH_4 sink in converted rubber plantations. Compared to the soil respiration process, the predominate factors and mechanisms for weakened CH_4 uptake in converted agricultural systems are far more complex and vary largely between systems and climate zones.

Although the global warming potential of CH_4 is high (34 times of CO_2 in 100-year time horizon), the CH_4 uptake was two orders of magnitude smaller than CO_2 respired from soils. For example, the annual CO_2 fluxes were 8.48 ± 0.71 and 6.75 ± 0.79 Mg C ha^{-1} yr^{-1} (Chapter 2), and the annual CH_4 fluxes were −2.41 ± 0.28 and −1.01 ± 0.23 kg C ha^{-1} yr^{-1} for forest and mature rubber (Chapter 3), respectively. Converting CH_4 uptake to CO_2 equivalent carbon unit considering the global warming potential of CH_4, the soil carbon emitted from soil respiration were 103 and 199 times of methane carbon oxidized by soils. Aerated soils are the only known biological CH_4 sink, this soil function is still of importance to mitigate anthropogenic greenhouse gas emissions. In addition, higher soil respiration rate relates to faster turnover of organic matter and nutrients in the soil, as well as biomass production, which not necessarily means larger carbon emission from the system, on the contrary, soil respiration could serve as a bioindicator of soil health (Bastida *et al.*, 2008). In forest, high soil respiration rate is coupled with high biomass production that contribute to accumulation in biomass carbon.

Overall, converting forest into rubber plantations reduced the soil aeration and weakened the function as CH_4 sink; the CO_2 emissions from soils under rubber plantation depended on the age of the plantation and the dynamics of soil carbon in topsoil. Therefore, this land use conversion has a negative effect on CH_4 sink function and likely negatively affect soil health. The overall impact of this land conversion on carbon dynamics requires comprehensive assessments covering carbon stocks and carbon fluxes.

5.6 Contribution and outlook

From a methodological perspective, this study addressed: (1) the interference of soil moisture on estimating the temperature sensitivity (Q_{10}) of soil respiration; (2) confounded land use effect and soil texture, which is intrinsically related to the main controlling factor-soil moisture; (3) using covariate analysis with consideration of main controlling factor to identify the pathway of interactions between mineral nitrogen and CH_4 processes; (4) determination of isotopic carbon fractionation factor in CH_4 oxidation using $\delta^{13}CH_4$ profiles *in situ*, and applying it in modeling the control

of gas diffusivities and methanotrophic activity on CH_4 and $\delta^{13}CH_4$ distribution in soil profiles.

The high soil moisture masked the temperature effect on soil respiration during wet periods of the rainy season. This study addressed the inference of soil moisture and estimated higher values of temperature sensitivity (Q_{10}) than other studies in the region. This study explicitly addressed the confounded factors between soil moisture, soil texture and land use type, which was missing in the assessments conducted in the region (Ishizuka *et al.*, 2002; Werner *et al.*, 2006). Without addressing this limitation of the space-for-time approach in land use change assessment, understanding of induced changes in controlling factors and mechanisms would be limited. In addition, because spatial replicates at landscape level in this study covered a wide range of clay content, the land use change effect was able to be disentangled from confounded texture effect. This implies that a sufficient number of spatial replicates covering a wide range of gradients are crucial in reliably assessing land use change impact.

The covariate analysis in this study demonstrated the necessity of considering all major controlling factors when interpreting the interaction between CH_4 processes and mineral nitrogen, because the effect of mineral nitrogen is not independent from physical factors that regulate the entry of CH_4 and O_2 into the soil (Bodelier, 2011). The positive effect of nitrate on CH_4 uptake and high soil moisture supported the pathway of competitive inhibition by nitrate reducers under wet conditions. The nitrogen limitation theory can be verified through nitrogen adding experiments. Considering mineral nitrogen form and status change fast, more frequent mineral nitrogen sampling would help identifying the pathways of interactions between CH_4 processes and mineral nitrogen N.

The isotopic ^{13}C fractionation factor (α_{ox}) in methane oxidation was estimated using $\delta^{13}CH_4$ profiles *in situ* in this study. It is an essential parameter in separating CH_4 production from net CH_4 uptake, but α_{ox} is seldom reported for tropical forest soils (Teh *et al.*, 2006). Although estimated α_{ox} in this study is slightly higher than reported values in temperate forests and humid tropical forests (Reeburgh *et al.*, 1997; Teh *et al.*, 2006; Maxfield *et al.*, 2008), our estimated value of α_{ox} is considered reasonable (discussion 4.5.3). Knowing this fractionation factor allowed to simulate the effect of CH_4 diffusivity and methanotrophic activity on ^{13}C signature of CH_4 in soil profiles. The simulation in the rainy season revealed CH_4 production when soil CH_4 was at sub-atmospheric concentration. The one-dimension diffusion-oxidation model became insufficient to predict $\delta^{13}CH_4$ distribution in soil profiles under wet conditions, thus measuring ^{13}C signature of soil CO_2 and acetate (or dissolved organic carbon) and

adding a CH_4 production component into the model would provide better understanding of the fraction of CH_4 production in net CH_4 uptake for tropical upland soils. Isotope labeling of methane is another option to separate and quantify the fraction of CH_4 production and oxidation.

Soil CH_4 sink function is weakened in rubber plantations, exerting a negative impact on the soil GHG budget. Soil CO_2 fluxes are generally lower in rubber plantations than in forest, but the dynamics largely depends on organic carbon content in the topsoil. Low soil respiration rate and reduced soil aeration in rubber plantations, indicate a negative impact on soil heath. Given the extensive rubber expansion in the last two decades, and the projected increasing demand for natural rubber, sustainable cultivation and effective mitigation strategies are needed to counter the negative impacts by rubber monoculture.

Recent studies have shown that rubber intercropping systems and agroforestry have positive effects on soils properties and ecosystem functions. A review by Zhu *et al.* (2019b) showed that rubber agroforestry reduced the surface runoff, soil, organic carbon and related nutrients losses by 58%, 65%, 9% and 50%, respectively, and lowered pollutants from herbicide and pesticide by 49% on average. Rubber agroforestry also improved soil physical properties, promoting soil water infiltration and recharge groundwater (Jiang *et al.*, 2019; Zhu *et al.*, 2019a), which may have positive effects on soil aeration and CH_4 uptake in rubber plantations. Change of current weed management is another option to increase infiltration and reducing runoff (Liu *et al.*, 2020).

This study contributed in assessing the land use change impact on two gaseous carbon fluxes, to develop mitigate strategies to counter the negative impact of this conversion, comprehensive assessments on carbon stocks and dynamics, as well as on other ecosystem services are needed. A number of rubber intercropping trials have been conducted to mitigate negative environmental impacts by rubber monoculture, but the adoption rate by stallholder farmers are rather low. Integrating permanent plants into rubber plantations needs to be highly profitable or labor extensive to be adopted on a large scale (Langenberger *et al.*, 2017).

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Appendixes

Appendix A

Appendixes to Chapter 2, “Seasonal differences in soil respiration and methane uptake in rubber plantation and rainforest”, Lang et al., 2017

Table A1 Reported annual soil CO_2 and CH_4 fluxes in the Southeast Asia

NO	Source	Land use, age (years, if rubber)	Annual soil CO_2 flux ($MgCha^{-1}yr^{-1}$)	Annual soil CH4 flux ($kgCha^{-1}yr^{-1}$)	Q_{10}	Method	Average air temperature (℃)	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[g]	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)	Rainofrest	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[a]	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[a]	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[a]	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[a]	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.?N 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[c], 1.22[d]	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[c], 1.77[d]	LI-6400					0.78		0-60
2		Rubber, 19	11.96	n.d.	2.37[c], 1.44[d]	LI-6400					0.83		0-60
2		Rubber, 33	11.09	n.d.	2.26[c], 1.10[d]	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[e]	263.4±67.1[f]	
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[e]	331.4±34.1[f]	
3		Rubber, 7-16	16.09±1.40	-0.29±0.12	n.d.	Static chamber, GC					2.8±0.4[e]	198.4±32.5[f]	
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[e]	182.9±10.8[f]	
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[e]	186.19±11.0[f]	
4		Rubber, 14-17	16.52±1.32	-0.93±0.35	n.d.	Static chamber, GC					2.0±0.3[e]	172.6±23.8[f]	
Sumatra, Indonesia.													
5	Ishizuka *et al.* (2002)	Rainforest P1	5.55±1.35[b]	-1.86±0.76[b]	n.d.	Static chamber, GC		2060		1.09 °S, 102.10 °E	3	0.19	
5		Rainforest P2	8.21±2.36[b]	0.37±2.18[b]	n.d.	Static chamber, GC				1.09 °S, 102.10 °E	-	-	
5		Logged over forest L1	5.72±1.54[b]	-0.39±0.46[b]	n.d.	Static chamber, GC				1.06 °S, 102.16 °E	3.5	0.24	
5		Logged over forest L2	7.10±2.05[b]	-1.54±0.85[b]	n.d.	Static chamber, GC				1.09 °S, 102.11 °E	4.5	0.65	
5		Rubber	6.53±2.32[b]	-1.12±0.46[b]	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;

[a]: annual flux value were calculated from reported annual average flux by multiplying time; [b]: annual flux value were calculated from reported annual average flux by multiplying time, mean±std; [c]: dry season, [d]: rainy season; [e]: $kgCm^{-2}$, [f]: gNm^{-2};

[g]: LCi-SD is open chamber respiration system, LI-series are closed chamber system.

Appendix B

Appendixes to Chapter 3, "Converting forests into rubber plantations weakened the soil CH_4 sink in tropical uplands", Lang et al., 2019

Table B1 Site characteristics

	Site	Land use	Latitude	Longitude	Altitude (m a.s.l)	Slope (degree)	Aspect	Age (years)
Project I	Mandian	Natural forest	22º8′51.5″N	100º40′56.7″E	859	35	Northwest	-
		Young rubber	22º8′42.6″N	100º40′55.6″E	848	35	Southeast	9
		Mid-age rubber	22º8′36.5″N	100º40′54.2″E	822	15	South	17
		Old rubber	22º8′26.3″N	100º40′52.1″E	798	15	South	30
Project II	Mandian	Natural forest	22º7′45.9″N	100º39′58.8″E	724	25	Northeast	-
		Mid-age rubber	22º7′43.6″N	100º40′16.4″E	673	20	Northwest	18
	Manlü	Natural forest	22º8′48.5″N	100º40′58.4″E	784	25	Northwest	-
		Mid-age rubber	22º8′25.0″N	100º41′3.8″E	704	20	South	23
	Manfei	Natural forest	22º9′24.0″N	100º41′5.9″E	665	25	Northwest	-
		Mid-age rubber	22º9′47.1″N	100º41′12.5″E	614	25	Southwest	17

Table B2 Soil properties of plots in Project I and Project II

Project I	Site	Land use	Bulk density (g cm^{-3})	Sand (%)	Silt (%)	Clay (%)	Total C (%)	Total N (%)	C/N Ratio	pH
0-15 cm soil	Mandian	Natural forest	0.92±0.01	15	41	44	2.09	0.22	9.3	4.2
		Young rubber	0.98±0.02	27	31	42	1.46	0.13	11.2	3.3
		Mid-age rubber	0.96±0.01	15	31	54	2.15	0.14	15.0	4.3
		Old rubber	1.04±0.02	13	32	55	2.49	0.19	13.3	4.4
Project II	Site	Land use	Bulk density (g cm^{-3})	Sand (%)	Silt (%)	Clay (%)	Total C (%)	Total N (%)	C/N Ratio	pH
0-10 cm soil	Mandian	Natural forest	1.26±0.03	43±5	27±4	30±1	2.9±0.1	0.26±0.02	10.9±0.3	6.2±0.2
		Mid-age rubber	1.22±0.03	28±1	30±1	42±2	2.9±0.2	0.23±0.01	12.3±0.4	4.7±0.1
	Manlü	Natural forest	1.05±0.03	33±3	28±1	40±2	2.5±0.2	0.27±0.01	9.5±0.9	4.7±0.1
		Mid-age rubber	1.11±0.01	29±2	24±0	48±2	2.5±0.1	0.22±0.01	11.3±0.3	4.6±0.1
	Manfei	Natural forest	1.26±0.02	63±0	14±0	23±0	2.6±0.1	0.24±0.01	10.6±0.3	5.6±0.1
		Mid-age rubber	1.21±0.02	36±3	20±1	44±2	2.1±0.2	0.17±0.01	11.7±0.6	5.4±0.1

Note: In Project I, Bulk density (mean ± standard error) was calculated from 3 samples; in project II, all reported properties were mean±standard error, reported Bulk density was averaged from 27 measurements, other properties were from 6 samples.

Table B3 CH_4 flux and annual cumulative flux means and standard errors from natural forest and rubber plantation at site and slope position level in Project II

Effect	Land use	Site	CH_4 flux (ug C m^{-2} hr^{-1})	n (CH_4 flux)	Annual cumulative CH_4 flux (kg C ha^{-1} yr^{-1})	n (Annual flux)
Land use*Site	Natural forest	Mandian	-22.5 ±3.5	99	-2.16 ±0.48	9
		Manfei	-24.2 ±3.5	98	-2.60 ±0.50	8
		Manlü	-23.9 ±3.5	98	-2.56 ±0.50	8
	Mid-age rubber	Mandian	-9.3 ±3.5	99	-0.80 ±0.48	9
		Manfei	-7.3 ±3.5	99	-1.09 ±0.48	9
		Manlü	-15.5 ±3.5	99	-1.14 ±0.48	9
Effect	Land use	Slope position	CH_4 flux (ug C m^{-2} hr^{-1})	n (CH_4 flux)	Annual cumulative CH_4 flux (kg C ha^{-1} yr^{-1})	n (Annual flux)
Land use*Slope Position	Natural forest	Lower	-27.2 ±3.8	98	-2.74 ±0.46	8
		Middle	-19.9 ±3.8	98	-2.14 ±0.46	8
		Upper	-23.7 ±3.8	99	-2.42 ±0.44	9
	Mid-age rubber	Lower	-9.0 ±3.8	99	-0.91 ±0.44	9
		Middle	-9.9 ±3.8	99	-0.60 ±0.44	9
		Upper	-13.3 ±3.8	99	-1.50 ±0.44	9

Note: statistical comparison of the slice Land use*Site and Land use*Slope position were not shown because these two-way interactions were not significant fixed effects in the model.

Table B4 Comparison of CH_4 flux regression models with linear WFPS and quadratic WFPS explanatory terms

Project I		Linear WFPS	Quadratic WFPS
	AIC	544.5	541.7
	Significance in F test Pr>F, WFPS	<.0001	0.0012
	Significance in F test Pr>F, $WFPS^2$	-	0.0304
	Variance from random and residual effects	539.08	496.98

Project II		Linear WFPS	Quadratic WFPS
	AIC	1794.9	1796.7
	Significance in F test Pr>F, WFPS	<0.0001	0.6957
	Significance in F test Pr>F, $WFPS^2$	-	0.6925
	Variance from random and residual effects	524.3	516.2

Table B5 Comparison of CH_4 flux model with and without covariate (standardized variables as input, Maximum likelihood method)

		Covariate						
Project I		WFPS model	Total N (0-15cm)	NH_4^+-N (0-5cm)	NO_3^--N (0-5cm)	Total C (0-15cm)	Clay% (0-15cm)	pH (0-15cm)
	Sum of variances	0.5971	0.597	0.5825	0.5715	0.5675	0.5454	0.5584
	AIC	145	147	145.5	144.4	144	141.7	143.1
	F test fixed effects, Pr>F							
	Covariate	-	0.9191	0.2290	0.1101	0.0854	0.0219	0.0483
	WFPS	0.0010	0.0038	0.0005	0.0690	0.0004	0.0022	0.0003
	$WFPS^2$	0.0297	0.0577	0.0170	0.3970	0.0095	0.0257	0.0089
		Covariate						
Project II		WFPS model	Total N (0-10cm)	NH_4^+-N (0-10cm)	NO_3^--N (0-10cm)	Total C (0-10cm)	Clay% (0-10cm)	pH (0-10cm)
	Sum of variances	0.8901	0.8828	0.8886	0.8617	0.8899	0.8898	0.8879
	AIC	534.7	533.3	535.7	530.2	535.7	536.7	535.5
	F test fixed effects, Pr>F							
	Covariate	-	0.0655	0.3078	0.0109	0.3037	0.9619	0.2616
	WFPS	0.0001	0.0033	0.0002	0.0012	0.0004	0.0002	0.0002

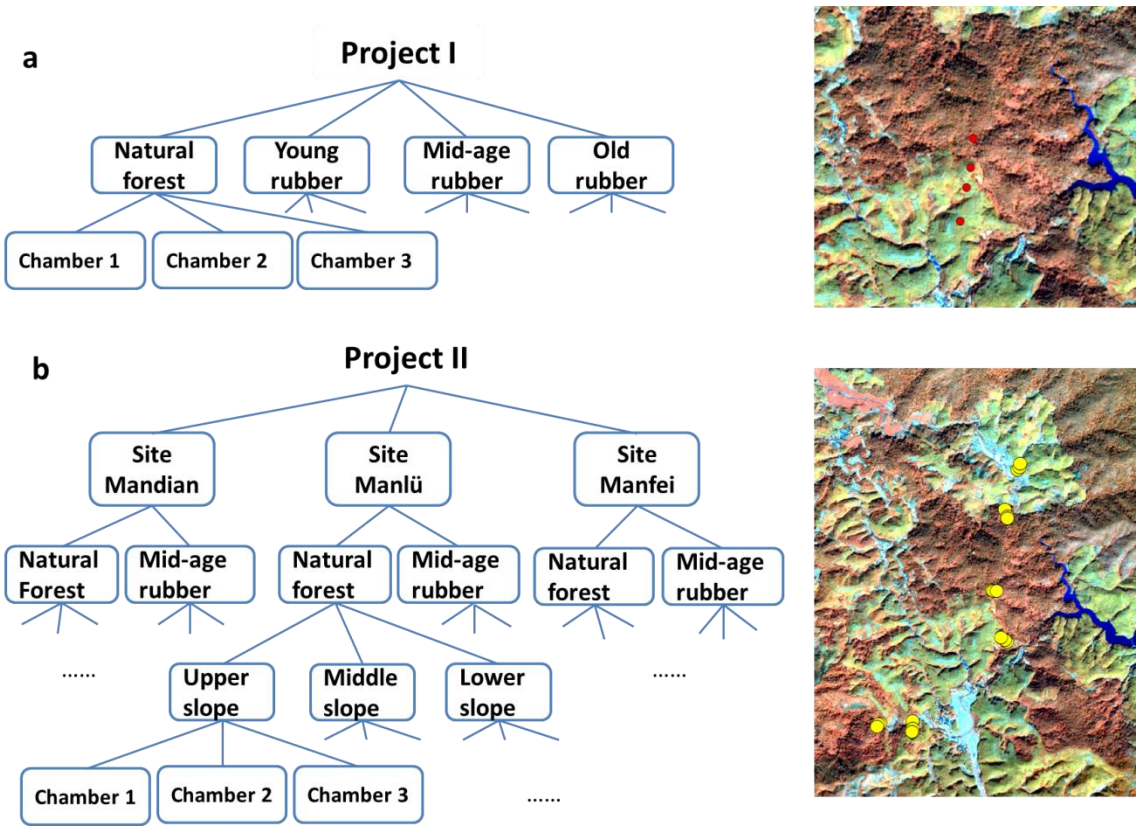

Figure B1 CH_4 flux sampling layout in Project I (a) and Project II (b)

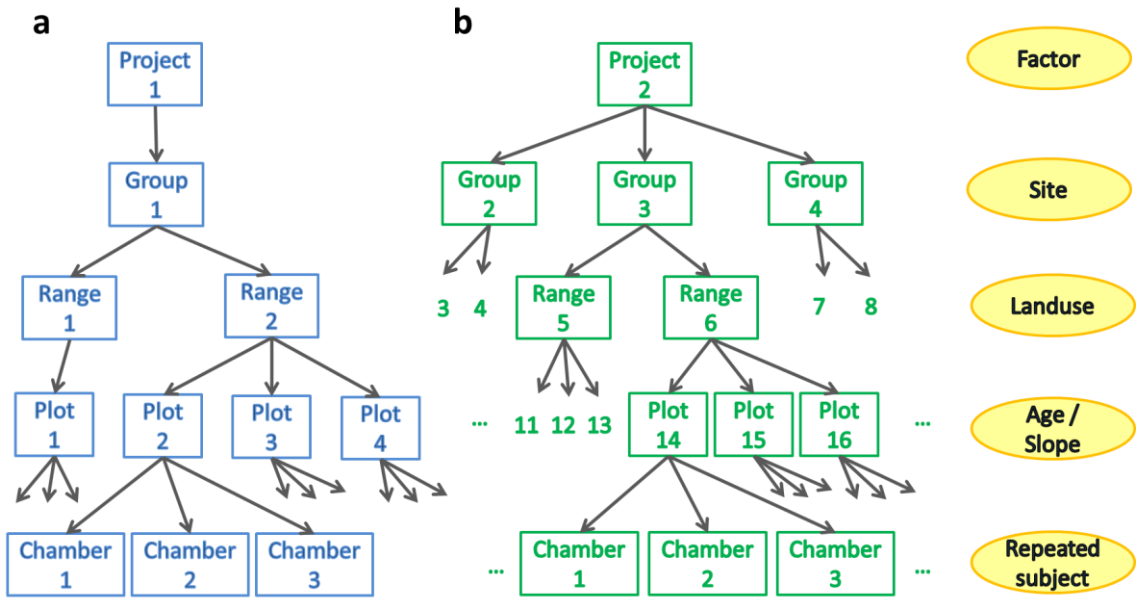

Figure B2 Setting levels for comparing means of CH_4 flux using joint datasets (a and b showed the physical unit and the right part showed the factor at each level of sampling). Levels were set as follows: at site level, the natural forest plot and three rubber plots in Project I were treated as a paired group, corresponding to the level of three sites in Project II, where each site contained a paired group of natural forest and rubber plantation. Two ranges were nested under each paired group, with one range in forest land use and the other in rubber plantation land use. Plots were further nested under ranges, with one plot nested under forest land use and three plots nested under rubber plantation in Project I, and three plots nested under each range in Project II. Three rubber plots under the range in Project I represent rubber age effect, while three plots under each range in Project II indicate slope position effect. As sub-samples and repeated subjects, three chambers at each plot were nested under plot level.

Covariance structure defines how two repeated measurements related to each other, and how correlation between two measurements on the same subject changes over time (temporal autocorrelation). In this study, we tested covariance structures including default variance component (VC), compound symmetry (CS), spatial power (SP(POW)) and unstructured (UN), detailed explanation and mathematical expression can be found in SAS user guide (SAS Institute Inc. 2009).

SAS Institute Inc. 2009. *SAS/STAT ® 9.2 User's Guide, Second Edition*. Cary, NC: SAS Institute Inc. Page 3954-3968.

Appendix C

Appendixes to Chapter 4, "Mechanism of methane uptake in profiles of tropical soils converted from forest to rubber plantations", Lang et al., 2020

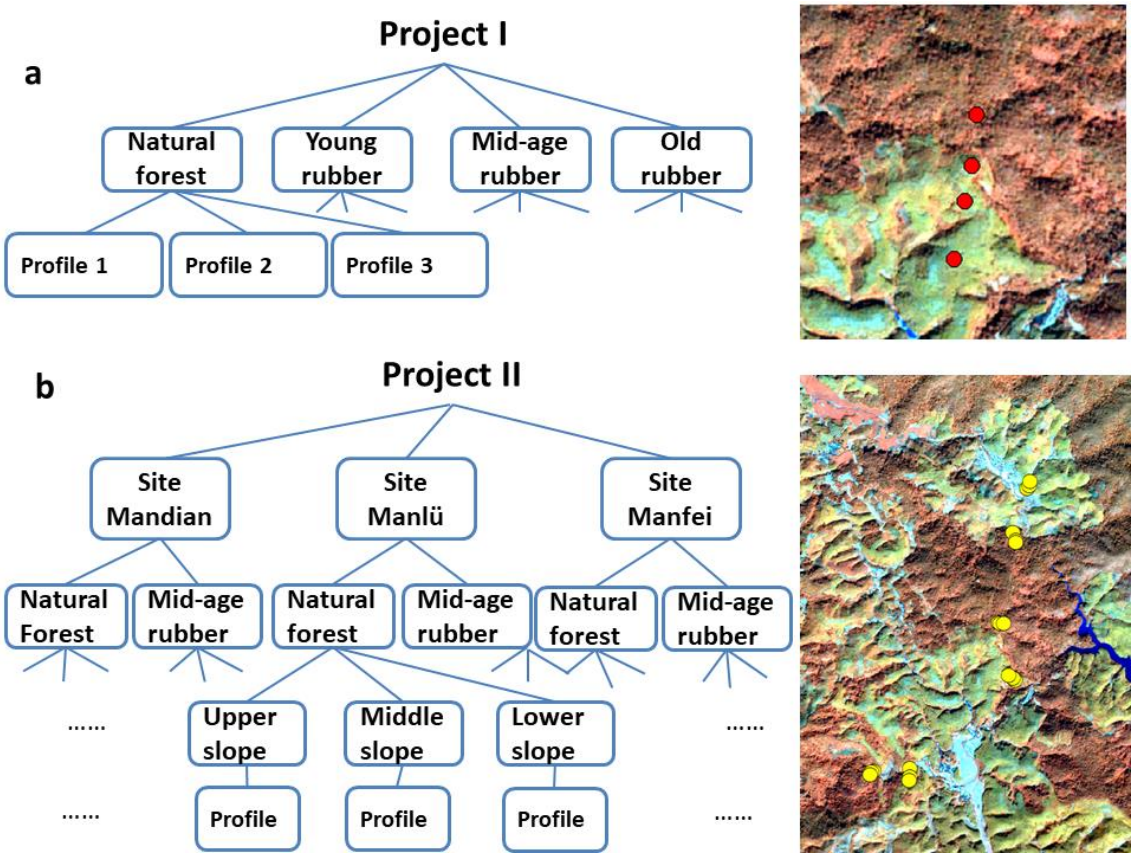

Figure C1 Sampling layout in Project I (a) and in Project II (b)

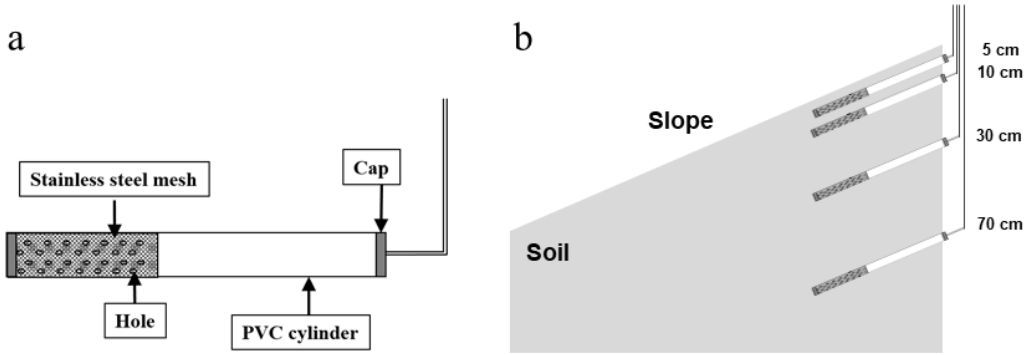

Figure C2 Structure of a soil gas sampler (a) and installation in a soil profile (b). Structure (a) has been illustrated in Goldberg *et al*. (2017)

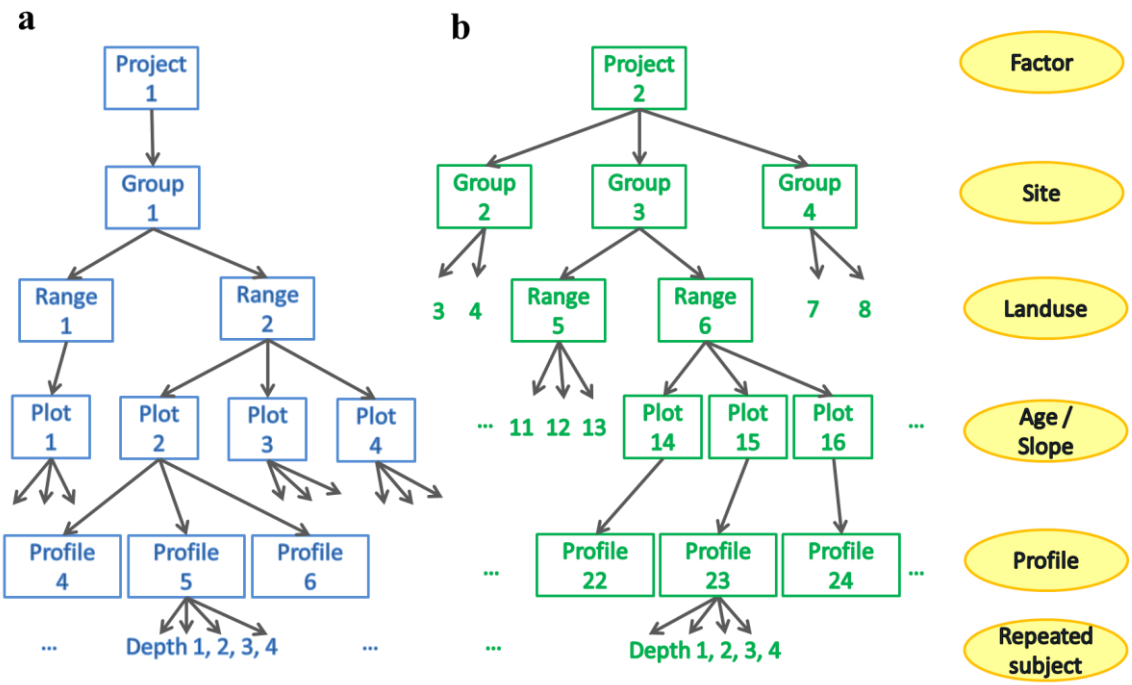

Figure C3 Setting of levels for comparing means of CH_4 concentration using combined datasets (a and b showed the physical sampling unit and the right part showed the factor at each level of sampling)

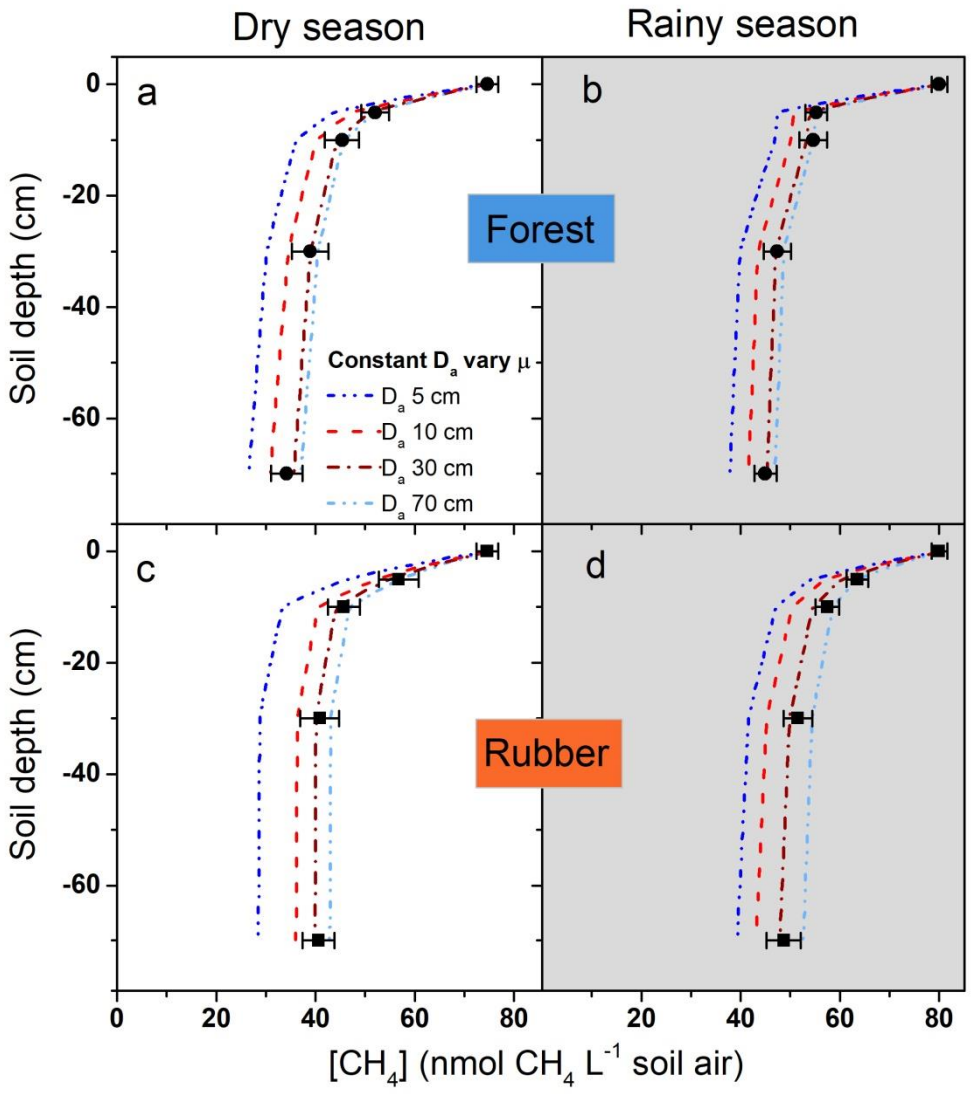

Figure C4 The effects of effective CH_4 diffusion coefficients (D_a) from different depths on seasonal CH_4 concentration profiles: D_a effect on the profile of forest in the dry season (a) and in the rainy season (b), D_a effect on the profile of rubber in the dry season (c) and in the rainy season (d). CH_4 concentrations were simulated with depth specific methanotrophic activity but keeping D_a from one depth as constant for the simulation throughout 0-70 cm soil. Symbols are seasonal averaged CH_4 concentrations from combined dataset of Project I and Project II.

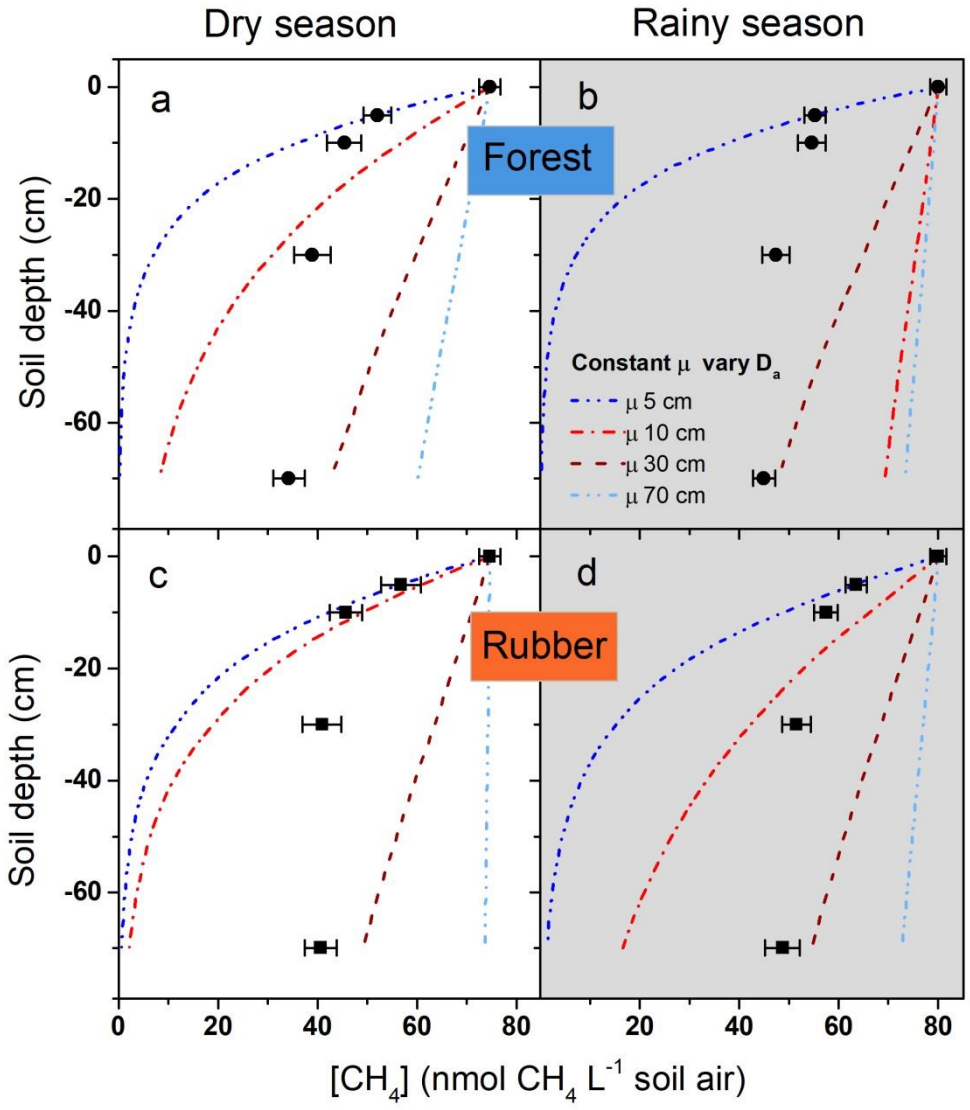

Figure C5 The effects of methanotrophic activities (μ) from different depths on seasonal CH_4 concentration profiles: μ effect on the profile of forest in the dry season (a) and in the rainy season (b), μ effect on the profile of rubber in the dry season (c) and in the rainy season (d). CH_4 concentrations were simulated with depth specific diffusivity but keeping μ from one depth as constant for the simulation throughout 0-70 cm soil. Symbols are seasonal averaged CH_4 concentrations from combined dataset of Project I and Project II.

Table C1 Average CH_4 concentration in soil air, diffusive flux, turnover rate and methanotrophic activity at different soil layers for forest and rubber plantation (least square means from combined dataset of Project I and Project II, and errors are standard errors)

Depth	CH_4 (nmol CH_4 L^{-1} soil air)		Diffusive flux (ugC m^{-2} h^{-1})		Turnover rate (pmol CH_4 cm^{-3} soil d^{-1})		$log_{10}(u)$ (s^{-1})	
	Forest	Rubber	Forest	Rubber	Forest	Rubber	Forest	Rubber
1st layer	50.5 ± 2.1^{aA}	56.9 ± 2.1^{aB}	$-23.8 \pm 1.0^{aA*}$	-14.4 ± 1.0^{aB}	-793 ± 54^{aA}	-451 ± 55^{aB}	-3.6 ± 0.1^{aA}	-4.1 ± 0.1^{aB}
2nd layer	47.0 ± 2.1^{aA}	49.4 ± 2.1^{bA}	-4.9 ± 1.0^{bA}	-3.0 ± 1.0^{bA}	-51 ± 54^{bA}	-44 ± 55^{bA}	-4.4 ± 0.1^{bA}	-4.7 ± 0.1^{bA}
3rd layer	40.2 ± 2.1^{bA}	43.5 ± 2.1^{cA}	-1.5 ± 1.0^{cA}	-0.4 ± 1.0^{bcA}	-7 ± 54^{bA}	-3 ± 55^{bA}		
4th layer	36.9 ± 2.1^{bA}	43.9 ± 2.1^{cB}	-0.5 ± 1.0^{cA}	0.2 ± 1.0^{cA}				

* Least-square means sharing no common lower-case letter represent significant difference between depths within individual land use, means sharing no common upper-case letter denote significant difference between forest and rubber plantation at same depth.

The center depths for calculated diffusive fluxes were 2.5, 7.5, 20 and 50 cm respectively, and for turnover rate were 5, 13.75 and 35 cm respectively. Methanotrophic activity was determined for sampling depth at 5 and 10 cm, means for 30 and 70 cm were not presented here due to the limitation of calculation method. Reported values were least-square means and standard errors from three-factorial full model.

Step-by-step calculating effective diffusion coefficient in soil media

Total soil porosity was calculated from bulk density (Equation C1),

$$P_t = 1 - \frac{BD}{2.65}$$

Equation C1

where P_t is total soil porosity in m^3 void m^{-3} soil, *BD* is bulk density in g cm^{-3}, 2.65 is the density of quartz.

Air-filled soil porosity was calculated from total porosity and volumetric water content using Equation C2,

$$P_g = P_t - P_{vmw}$$

Equation C2

where P_g is air-filled soil porosity in m^3 soil air m^{-3} soil, P_t is total porosity, and P_{vmw} is volumetric water content in m^3 water m^{-3} soil.

Pressure p is required in correcting temperature and pressure effect on diffusion coefficient in free air. To account for the effect by altitude and seasonal temperature changes on pressure, barometric equation is used in calculating p (Equation C3),

$$p = p_0 \cdot (1 - \frac{0.0065 \cdot H}{T_{air}})^{5.255876113}$$

Equation C3

where p is air pressure at temperature T and altitude H, p_0 is 101325 Pa, H is altitude in m a.s.l., T_{air} is air temperature in K.

The diffusion coefficient of CH_4 in free air was 0.1952 cm^2 s^{-1} (Massman, 1998). Correction of the temperature and air pressure effect on diffusion coefficient in free air was applied using Equation C4 (Massman, 1998),

$$D(T, p) = D(0, 1) \cdot \frac{p_0}{p} \cdot (\frac{T}{T_0})^{\alpha}$$

Equation C4

where $D(T, p)$ is the CH_4 diffusion coefficient at temperature T in K and air pressure p in pa, $D(0, 1)$ is the CH_4 diffusion coefficient in free air under standard temperature T_0 and pressure p_0, T_0 is 273.15 K and p_0 is 101325 pa, α is a constant with a suggested value of 1.81.

Effective diffusion coefficient in soil media was further determined using Structure-dependent Water-induced Linear Reduction model (SWLR) (Moldrup *et al.*, 2013) (Equation C5),

$$D_a = D(T, p) \cdot P_g^{1+C_m \cdot P_t} \cdot (\frac{P_g}{P_t})$$

Equation C5

where D_a is effective diffusion coefficient in soil in cm^2 s^{-1}, $D(T, p)$ is temperature and

pressure corrected diffusion coefficient in free air calculated from Equation C4, P_g is air-filled porosity in m^3 soil air m^{-3} soil, P_t is total soil porosity in m^3 void m^{-3} soil, and C_m is media complexity factor with a suggested value of 2.1 for intact soil.

Step-by-step determining the fractionation factor of $^{13}CH_4$ in methane oxidation

The isotopic fractionation factor of $^{13}CH_4$ in methane oxidation process was determined from measured $\delta^{13}CH_4$ profiles at the forest plot in Project I in dry season sampling, using Raleigh distillation approach (Steady-state diffusion-consumption model) (Reeburgh *et al.*, 1997; Maxfield *et al.*, 2008).

(1) Determine isotopologues of CH_4

Isotope ratio of $^{13}CH_4$ in delta notation is presented as

$$\delta^{13}\mathrm{CH_4} = (\frac{R_{sample}}{R_{standard}} - 1) \cdot 1000$$

Equation C6

where $\delta^{13}CH_4$ is the isotope ratio of the ^{13}C in CH_4 in ‰, $R_{standard}$ is ratio of ^{13}C to ^{12}C in Vienna Pee Dee Belemnite (VPDB) with value 0.0112375. R_{sample} is the ratio of $^{13}CH_4$ to $^{12}CH_4$ in the gas sample, rearrange Equation S6, R_{sample} can be calculated from measured $\delta^{13}CH_4$ with the Equation C7

$$R_{sample} = (\frac{\delta^{13}\mathrm{CH_4}}{1000} + 1) \cdot R_{standard}$$

Equation C7

To determine the concentrations of the isotopologues of CH_4, firstly the mole fractions of $^{13}CH_4$ and $^{12}CH_4$ are calculated using the following equations (Maxfield *et al.*, 2008)

$$X^{13}C = \frac{R_{sample}}{1 + R_{sample}}$$

Equation C8

$$X^{12}C = \frac{1}{1 + R_{sample}}$$

Equation C9

where $X^{13}C$ and $X^{12}C$ are mole fraction of $^{13}CH_4$ and $^{12}CH_4$ in the gas sample (dimensionless).

Then the concentrations of heavy and light CH_4 in each gas sample, [$^{13}CH_4$] and [$^{12}CH_4$], can be obtained by multiplying the mole fractions of isotopologue of CH_4 with measured CH_4 concentration in the gas sample (Equations C10 and C11),

$$[^{13}\mathrm{CH_4}] = [\mathrm{CH_4}] \cdot X^{13}C$$

Equation C10

$$[^{12}\mathrm{CH_4}] = [\mathrm{CH_4}] \cdot X^{12}C$$

Equation C11

[$^{13}CH_4$], [$^{12}CH_4$] and [CH_4] are in nmol CH_4 L^{-1} soil air.

(2) Determine fractionation factor of ^{13}C in methane oxidation

If use *k* represents the methane oxidation rate constant, according to Raleigh distillation approach (diffusion-consumption model at steady-state) (Reeburgh *et al.*, 1997; Maxfield *et al.*, 2008), when assuming [CH_4] at bottom of soil layer approaches to zero, solved *k* from the differential equation is

$$k = D_a \cdot [ln(\frac{[\mathrm{CH_4}]_d}{[\mathrm{CH_4}]_0})]^2$$

Equation C12

where D_a is effective diffusion coefficient of CH_4 in soil media, $[CH_4]_0$ and $[CH_4]_d$ are methane concentration at depths of 0 and *d* cm.

As Equation C12 holds true for both $^{12}CH_4$ and $^{13}CH_4$, methane oxidation reaction rate constants for $^{12}CH_4$ and $^{13}CH_4$ can be expressed as

$$k_{12} = D_{a,^{12}\mathrm{CH_4}} \cdot [ln(\frac{[^{12}\mathrm{CH_4}]_d}{[^{12}\mathrm{CH_4}]_0})]^2$$

Equation C13

$$k_{13} = D_{a,^{13}CH_4} \cdot [ln(\frac{[^{13}CH_4]_d}{[^{13}CH_4]_0})]^2$$

Equation C14

where $D_{a,^{12}CH_4}$ and $D_{a,^{13}CH_4}$ are effective diffusion coefficient for $^{12}CH_4$ and $^{13}CH_4$ in soil, $[^{12}CH_4]_0$ and $[^{12}CH_4]_d$ are concentrations of $^{12}CH_4$ at depths of 0 and *d* cm, and $[^{13}CH_4]_0$ and $[^{13}CH_4]_d$ are concentrations of $^{13}CH_4$ at depths of 0 and *d* cm.

According to the definition of isotopic fractionation (kinetic isotopic effect), and accounting for the fractionation in diffusion process using theoretical value of 1.0195 ($\alpha_{tr} = \frac{D_{a,^{12}CH_4}}{D_{a,^{13}CH_4}} = 1.0195$) (Mason and Marrero, 1970; Chanton, 2005), the fractionation due to methane oxidation by methanotrophs can be expressed as the ratio of k_{12} and k_{13} as

$$\alpha_{ox} = \frac{k_{12}}{k_{13}} = \frac{D_{a,^{12}CH_4}}{D_{a,^{13}CH_4}} \cdot [\frac{\ln\left(\frac{[^{12}CH_4]_d}{[^{12}CH_4]_0}\right)}{\ln\left(\frac{[^{13}CH_4]_d}{[^{13}CH_4]_0}\right)}]^2 = \frac{1.0195}{1} \cdot [\frac{\ln\left(\frac{[^{12}CH_4]_d}{[^{12}CH_4]_0}\right)}{\ln\left(\frac{[^{13}CH_4]_d}{[^{13}CH_4]_0}\right)}]^2$$

Equation C15

$[^{12}CH_4]_0$ and $[^{13}CH_4]_0$ are calculated from measured $[CH_4]$ and $\delta^{13}CH_4$ of the ambient air sample, and $[^{12}CH_4]_d$ and $[^{13}CH_4]_d$ are calculated from measured $[CH_4]$ and $\delta^{13}CH_4$ of soil gas sample at depth *d*. α_{ox} is determined for four sampling depths, with the estimation at depth *d* using $[CH_4]$ and $\delta^{13}CH_4$ from ambient air and soil gas sampled at depth *d*.

The forest plot in Project I sampled in dry season had three gas profiles, the average of a total twelve estimations is used in further modeling.

Summary

Deforestation and agricultural expansion in the tropics have been a large source of anthropogenic greenhouse gas emissions and a threat for soil fertility loss due to intensification of agricultural usage. Large-scale conversion of natural forests to rubber plantations in Southeast Asia during past decades is one of those cases, making the region a deforestation and forest degradation hotspot. The impact of this land use change on fluxes of CO_2 and CH_4, two of the most important greenhouse gases (GHG), was assessed within the framework of two research projects dealing with sustainable rubber cultivation. Land use conversion could modulate soil CO_2 emissions and the balance between CH_4 oxidation and production via changing soil physical, chemical and biological properties. However, the impact of this conversion on soil CO_2 and CH_4 fluxes has not been sufficiently understood. This study was conducted in Xishuangbanna, Southwestern China - a representative area for recent rubber expansion into non-traditional growing areas. Aims were to quantify the impact of this land use change on soil CO_2 and CH_4 fluxes and to clarify mechanisms responsible for the differences between natural forests and rubber plantations.

In order to identify and quantify the controlling factors that determine GHG under different land uses, soil respiration rates were measured monthly for one year and CH_4 fluxes were measured during the rainy season in a forest, 9- and 22-year-old rubber monoculture and a 22-year-old rubber-tea intercropping system. A linear mixed effect model was used in studying soil temperature and moisture variations and temperature sensitivity (Q_{10}) of soil respiration (Chapter 2). The land use change impact on the ability of soils to function as CH_4 sink was assessed using combined datasets from two projects having complementary measurements. First, soil surface CH_4 fluxes measured by static chamber method were used to assess the land use change impact, with a focus on quantifying the main controlling factors. Confounded controlling factors and land use effects were disentangled, and the pathway of interactions between CH_4 processes and mineral nitrogen was identified (Chapter 3). Second, the concentration gradient method and one-dimensional diffusion-oxidation model were applied to quantify the vertical distribution of CH_4 uptake in soil profiles, and to separate the relative control by gas diffusivity and by methanotrophic oxidation on CH_4 uptake. This second part used CH_4 concentration profiles collected from soil probes at 5, 10, 30 and 70 cm depths for one year, and $\delta^{13}CH_4$ profiles sampled once in the rainy season and once in the dry season (Chapter 4).

Distinct different temporal patterns of soil respiration were observed on sites during most of the rainy season: forest maintained a high soil respiration rate, while soil

respiration in rubber plantations became suppressed (by up to 69%) during the most moist period in rubber plantations. Forest soils thus emitted the highest amount of CO_2 with an annual cumulative flux of 8.48 ±0.71 Mg C ha^{-1} yr^{-1}, compared to 6.75 ±0.79, 5.98 ±0.42 and 5.09 ±0.47 Mg C ha^{-1} yr^{-1} for mature rubber, rubber-tea intercropping, and young rubber, respectively. 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 interference of moisture effect on soil temperature, therefore, improved temperature sensitivity assessments when high soil moisture suppressed soil respiration under rubber plantations. Temperature sensitivity of soil respiration was higher for forest compared to rubber plantations, Q_{10} values were 3.1 for forest and 1.7, 2.2 and 2.4 for mature rubber, rubber-tea intercropping and young rubber respectively.

According to the static chamber method, soils under natural forest were stronger CH_4 sinks than soils under rubber plantations, with annual CH_4 fluxes of -2.41 ±0.28 kg C ha^{-1} yr^{-1} and -1.01 ±0.23 kg C ha^{-1} yr^{-1}, respectively. Water-filled pore space (WFPS) was the main factor explaining the differences between natural forests and rubber plantations, even reverting soils under rubber plantation temporarily from CH_4 sink into a CH_4 source during the rainy season in older plantations. Although soils under rubber plantations were more clayey than soils under natural forest, this was proved not to be the decisive factor driving higher soil moisture and lower CH_4 uptake in the former soils. Soil nitrate content was often lower under rubber plantations, while ammonium content was comparable between forests and rubber plantations. Adding nitrate content as a model covariate improved the explanation power of the CH_4 fluxes - WFPS regression, suggesting a positive effect of soil nitrate on CH_4 uptake.

Concentration gradients method showed that CH_4 consumption in 0-5 cm soil was significantly higher in natural forests than in rubber plantations, with a mean CH_4 flux of -23.8 ±1.0 and -14.4 ±1.0 ug C m^{-2} h^{-1} for forest and rubber plantations, respectively. The atmospheric CH_4 oxidized by top 10 cm soil accounted for 93% and 99% of total consumption for forest and rubber plantations, respectively. CH_4 diffusivity at four sampled depths were significantly lower in rubber plantation than in forest. This reduced CH_4 diffusivity, caused by altered soil water regime, predominately explained the weakened CH_4 sink in converted rubber plantations. From the dry season to the rainy season, methanotrophic activity at 5-10 cm soil depth strongly decreased by 99.6% and 83.3% for forest and rubber plantations respectively. Estimated isotopic fractionation factor for carbon due to CH_4 oxidation was 1.0292 ± 0.0015 (n=12). Modeling $^{13}CH_4$ distribution in soil profiles using a diffusion-oxidation model explained the observations in the dry season, but suggested CH_4 production in subsoil in the rainy season, which needs to be considered in future studies to fully explain

changes in CH_4 processes during land use transformation.

In summary, converting natural forests into rubber plantations tended to reduce soil CO_2 emissions, but this conversion substantially weakened CH_4 uptake by tropical upland soils. The altered soil water regime and conditions of soil aeration under converted rubber plantations appear to have a pronounced impact on processes of gaseous carbon fluxes from soils. Although reduced soil CO_2 emissions could mitigate the positive feedback of climate change, a weakened CH_4 sink function exerts a negative impact on the CH_4 balance in the tropics. The clarified mechanisms in this study could improve the regional budget of greenhouse gases emissions in response to land use change and climate change. To meet the increasing demand for natural rubber and counter the negative GHG effects induced by rubber monoculture, sustainable cultivation and effective mitigation strategies, such as rubber agroforestry, are needed.

Zusammenfassung

Die Rodung von Wäldern und die Ausbreitung der landwirtschaftlichen Nutzfläche in den Tropen haben einerseits einen großen Anteil an den anthropogenen Treibhausgasemissionen, zum anderen stellen sie eine Bedrohung für die Bodenfruchtbarkeit dar. Beispielhaft dafür ist die Umwandlung von naturnahen Wäldern zu Kautschukplantagen in Südost Asien in den letzten Jahrzehnten, das damit zu einem Hotspot für Waldrodung und Degradierung wurde. Der Einfluss dieser Landnutzungsänderungen auf CO_2 und CH_4, zwei der wichtigsten Treibhausgase (GHG), wurde innerhalb der zwei Forschungsprojekte untersucht, die sich mit dem nachhaltigen Kautschukanbau befassten. Landnutzungsänderungen konnten CO_2 Emissionen, sowie das Gleichgewicht zwischen CH_4 Oxidation und Produktion beeinflussen, indem sie physikalische, chemische und biologische Bodeneigenschaften veränderten. Der Einfluss hierbei auf CO_2 und CH_4 Flüsse ist jedoch unzureichend erforscht. Die hier präsentierten Studien wurden in Xishuangbanna im Südwesten Chinas durchgeführt, einemrepräsentativesnGebiet, in dem kürzlich der Kautschukanbau in nicht traditionelle Kautschuk-Anbaugebiete ausgeweitet wurde.. Die Ziele der Arbeit waren, den Einfluss der Landnutzungsänderungen auf die CO_2 und CH_4 Gasflüsse des Bodens zu quantifizieren, sowie die Mechanismen, und deren Unterschiede zwischen naturnahen Wäldern und Kautschukplantagen zu erklären..

Um die ausschlaggebenden Faktoren für diese Unterschiede zu identifizieren und zu quantifizieren, wurden die monatlichen Raten der Bodenatmung über den Zeitraum eines Jahres, sowie die CH_4 Flüsse während der Regenzeit gemessen. Alle Messungen fanden in naturnahem Wald, 9- und 22-jährigen Kautschuk Monokulturen, sowie in einer 22-jährigen Mischkultur von Kautschuk und Tee statt. Ein Modell mit gemischten linearen Effekten wurde genutzt, um die Variabilität der Bodentemperatur und -feuchte, sowie die Temperatursensitivität (Q_{10}) der Bodenatmung zu analysieren (Kapitel 2). Der Einfluss von Landnutzungsänderungen auf die Fähigkeit des Bodens als CH_4 Senke zu fungieren, wurde durch die Auswertung kombinierter Datensätze aus zwei Projekten mit sich ergänzenden Messungen bewertet. . Um den Einfluss der Landnutzungsänderung zu analysieren und die Haupteinflussfaktoren zu quantifizieren, wurden zuerst die CH4 Flüsse an der Erdbodenoberfläche mit der statischen Kammermethode gemessen. Störfaktoren wurden von den Landnutzungseffekten getrennt, und die Wechselwirkungen zwischen CH_4-Prozessen und mineralischem Stickstoff wurden identifiziert (Kapitel 3). In einem zweiten Schritt wurden die Konzentrationsgradientenmethode und ein eindimensionales Diffusions-Oxidationsmodel genutzt, um die vertikale Verteilung der CH_4 Aufnahme in

den Bodenprofilen zu quantifizieren, und die relative Kontrolle durch Gasdiffusionsvermögen und durch methanotrophe Oxidation bei der CH4-Aufnahme zu trennen. Dieser zweite Teil nutze CH_4 Konzentrationsprofile, die über den Zeitraum eines Jahres von Bodensensoren in 5, 10, 30 und 70 cm Bodentiefe erstellt wurden, sowie $\delta^{13}CH_4$ Profile, die je einmal in der Regen- und einmal in der Trockenzeit gemessen wurden (Kapitel 4).

Während des größten Teils der Regenzeit zeigten die Standorte deutliche verschiedene zeitliche Muster der Bodenatmung: : Im Waldstandort war die Respirationsrate konstant hoch, während sie in den Kautschukplantagen in der feuchtesten Periode reduziert war (um bis zu 69 %). Waldböden emittierten somit am meisten CO_2, mit einem jährlichen kumulativen Fluss von 8.48 ± 0.71 Mg C ha^{-1} a^{-1}, verglichen mit 6.75 ± 0.79, 5.98 ± 0.42 and 5.09 ± 0.47 Mg C ha^{-1} a^{-1} des ausgewachsenen Kautschuks, der Kautschuk und Tee Mischkultur und den jungen Kautschukplantagen. Die Bodentemperatur war der Hauptfaktor für die saisonale Variation der Bodenatmung.. Ein zusätzlicher quadratischer Bodenfeuchtigkeitsterm im Modell erklärte die Interferenz der Bodenfeuchte auf den Temperatureffekt und verbesserte die Analysen der Temperatursensitivität, da zeitweise hohe Bodenfeuchte die Bodenrespiration in Kautschukplantagen unterdrückte. Die Temperatursensitivität der Bodenrespiration war im Wald höher als in Kautschukplantagen. Die Q_{10} Werte für den Wald waren 3.1, wohingegen der ausgewachsene Kautschuk, die Kautschuk-Tee-Mischkultur, sowie due junge Kautschukplantage Q10 Werte von 1.7, 2.2 und 2.4 zeigten.

Laut Ergebnissen der statischen Kammermethode , waren Böden unter naturnahem Wald mit CH_4 Flüssen von -2.41 ± 0.28 kg C ha^{-1} a^{-1} stärkere CH_4 Senken als Böden unter Kautschukplantagen mit Flüssen von -1.01 ± 0.23 kg C ha^{-1} a^{-1}. Die Wassersättigung der Bodenporen (WFPS) war der Hauptfaktor, der die Unterschiede zwischen zwischen naturnahem Wald und Kautschukplantagen erklärte. Dieser Effekt konnte Böden unter älteren Kautschukplantagen in der Regenzeit sogar zeitweise von CH_4 Senken zu CH_4 Quellen transformieren. Es konnte gezeigt werden, dass, obwohl die Böden unter Kautschukplantagen höhere Tongehalte hatten als die Waldböden, dies nicht der entscheidende Faktor für höhere Bodenwassergehalte und niedrigere CH_4 Aufnahmen war. Die Nitratkonzentration in Boden der Kautschukplantagen war oft niedriger, während Ammoniumgehalte zwischen Wald und Kautschukplantagen vergleichbar waren. Nitratgehalt als zusätzliche Kovariable im Model verbesserte die Erklärungsstärke der CH_4 Fluss - WFPS Regression, was auf einen positiven Einfluss von Nitrat im Boden auf CH_4 Aufnahme schließen ließ.

Die Konzentrationsgradientenmethode zeigte, dass die CH_4 Aufnahme in 0–5 cm

Bodentiefe in den naturnahem Wäldern signifikant höher war als in den Kautschukplantagen. Die mittleren CH_4 Flüsse lagen bei -23.8±1.0 im Wald und bei -14.4±1.0 ug C m^{-2} h^{-1} in den Kautschukplantagen. Das atmosphärische CH4, das durch die obersten 10 cm der Böden oxidiert wurde, machte 93% bzw. 99% des Gesamtverbrauchs für Wald und Kautschukplantagen aus. Die Diffusität von CH_4 in den Kautschukplantagen war in allen vier beprobten Bodentiefen signifikant niedriger im Vergleich zum Wald. Diese verminderte Diffusionsfähigkeit, die durch Veränderungen im Wasserhaushalt verursacht wurde, erklärte in erster Linie die geringere CH_4 Aufnahme der konvertierten Kautschukplantagen. Die Aktivität der Methanotrophen in 5–10 cm Bodentiefe verringerte sich stark von der Trocken- zur Regenzeit und betrug 99.6% im Wald und 83.3% in den Kautschukplantagen. Der geschätzte Faktor der Isotopenfraktionierung für Kohlenstoff aufgrund der CH_4 Oxidation war 1.0292 ± 0.0015 (n=12). Die Modellierung der $^{13}CH_4$ Verteilung im Bodenprofil unter Verwendung eines Diffusions-Oxidationsmodells erklärte die Beobachtungen in der Trockenzeit, aber sagte für die Regenzeit eine Produktion von CH_4 im Unterboden voraus. Dies sollte in zukünftigen Studien beachtet werden, um die CH_4 Prozesse aufgrund von Landnutzungsänderungen vollständig erklären zu können.

Die Konvertierung von naturnahem Wald zu Kautschukplantagen verringerte tendenziell CO_2 Emissionen, schwächte aber gleichzeitig die CH_4 Aufnahme der tropischen Böden substanziell. Die veränderten Wasser- und Lufthaushalte der Böden von konvertierten Kautschukplantagen scheinen einen deutlichen Einfluss auf die Prozesse der gasförmigen Kohlenstoffflüsse von Böden zu haben. Obwohl reduzierte CO_2 Emissionen den positiven Feedbackmechanismus durch den Klimawandel verringern könnten, bedeutet eine verringerte CH_4 Aufnahmefunktion einen negativen Einfluss auf die CH_4 Bilanz in den Tropen. Die in dieser Studie erläuterten Mechanismenkönnten die regionale Budgetierung der Treibhausgasemissionen infolge der Landnutzungsänderungen sowie des Klimawandels verbessern. Nachhaltige Anbausysteme und wirksame Minderungsstrategien, wie Kautschuk-Agroforstsysteme, sind erforderlich, um die erhöhte Nachfrage nach Kautschuk zu decken und negativen Effekten der Kautschukmonokulturen auf Treibhausgaseemissionen entgegenzuwirken.

Understanding how land use change affects greenhouse gas emissions is important to develop mitigation strategies to counter the negative impact. This PhD thesis deals with the impact of converting forest into rubber plantations on soil CO_2 emission and CH_4 sink function, focuses on statistically quantifying the controlling factors of soil CO_2 and CH_4 fluxes, and modeling CH_4 processes within soil profiles to investigate the mechanism of changes in CH_4 sink.