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RESEARCH ARTICLE

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Converting forests into rubber plantations weakened the soil CH_4 sink in tropical uplands

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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 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

1 | 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 (Ahrends et al., 2015; Fox, 2014; Sarathchandra et al., 2018; Warren-Thomas, Dolman, & Edwards, 2015). 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, Castella, Ziegler, & Westley, 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 evaportranspiration and resulting in water shortages in dry season (Tan et al., 2011), and decrease of carbon sequestration in aboveground biomass (Kotowska, Leuschner, Triadiati, & Hertel, 2016; Yang et al., 2016) and in soil (de Blécourt, Brumme, Xu, Corre, & Veldkamp, 2013), as well as lowering of ecosytem carbon stocks if compared with swidden agriculture (Blagodatsky, Xu, & Cadisch, 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, Smith, Christensen, James, & Clark, 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 (Dalal & Allen, 2008; Ishizuka et al., 2005; Veldkamp, Koehler, & Corre, 2013; Werner et al., 2006), 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 (Hassler et al., 2015; Pendall et al., 2010; Veldkamp, Purbopuspito, Corre, Brumme, & Murdiyarso, 2008).

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; Fang et al., 2010; Gütlein, Gerschlauer, Kikoti, & Kiese, 2018; Werner et al., 2006). 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 (Ishizuka, Tsuruta, & Murdiyarso, 2002; Le Mer & Roger, 2001). Soil chemical properties, such as nitrogen input and status, are further known to have a range of possible interactions with CH_4 processes (Bodelier & 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 & 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.

2 | MATERIALS AND METHODS

2.1 | 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 1). The altitude decreases from the northwest to the south, ranging from 539- to

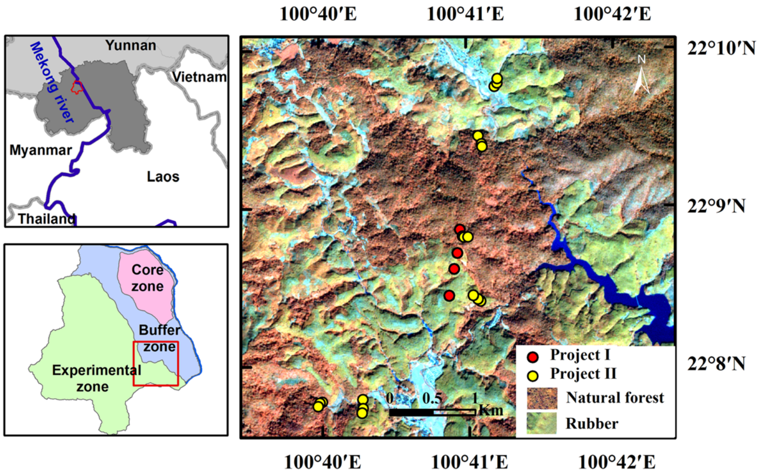

FIGURE 1 Location map of the transects in two projects in the Naban River Watershed National Natural Reserve [Colour figure can be viewed at wileyonlinelibrary.com]

2,304-m a.s.l. Annual air temperature was 22.30 ± 0.58°C, and annual precipitation was 1,157 ± 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 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.

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 S1a). 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 S1b). 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, Hänsel, Brumme, Corre, & Veldkamp, 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.

2.2 | 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°C 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 & 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°C before determining mineral nitrogen in the lab as detailed in Goldberg et al. (2017).

Site characteristics of the two projects are shown in Tables S1 and S2.

2.3 | 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, Blagodatsky, Xu, and Cadisch (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.

2.4 | 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 S2). The temporal autocorrelation in repeated measurements of CH_4 fluxes over the same chamber was addressed by comparing and selecting proper covariance structures (Figure S2). 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 | RESULTS

3.1 | 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 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 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} hr^{-1}, respectively (Table 1).

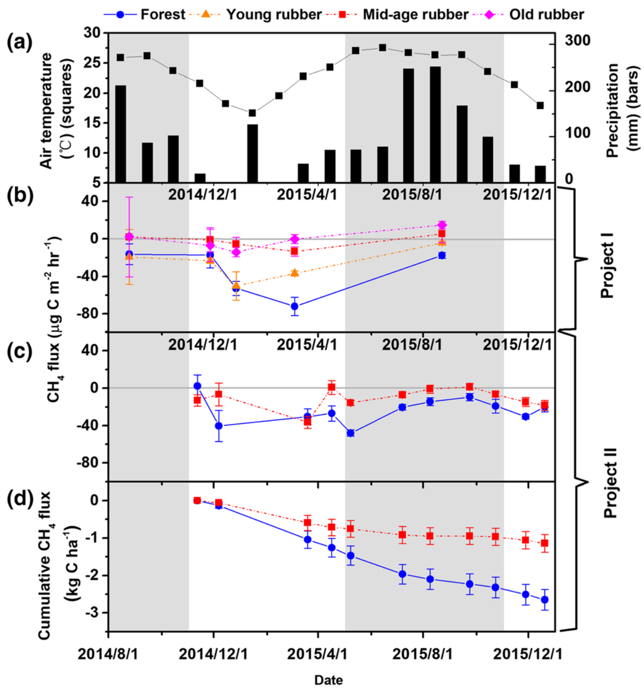

FIGURE 2 Climate conditions and dynamics of CH_4 fluxes during 2014 and 2015. Climate conditions (a), soil surface CH_4 fluxes measured in Project I (b) and in Project II (c), and cumulative CH_4 fluxes in Project II (d). Shaded parts of graphs represent rainy season. Negative CH_4 flux means CH_4 uptake; 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 [Colour figure can be viewed at wileyonlinelibrary.com]

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 1 and Figure 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 S3).

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

3.2 | 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 = .59 in Project I and r = .33 in Project II) than for soil temperature (Table 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), land use was not a significant fixed effect in the

TABLE 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

Projects I and II	Land use	CH_4 flux (μg C m^{-2} hr^{-1})	*n*
	Natural forest	$-27.2 \pm 3.4^{a*}$	310
	Rubber	-10.4 ± 2.6^{b}	341
Project II	Land use	Cumulative CH_4 flux (kg C ha^{-1} yr^{-1})	*n*
	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 ($p < .05$).

TABLE 2 Pearson correlation coefficients between CH_4 flux and soil temperature and moisture measured on multiple dates. First controlling variables are shown in bold

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

*Significant correlation at α = .05 level.

TABLE 3 Means and range of water-filled pore space in Project I and Project II [Colour table can be viewed at wileyonlinelibrary.com]

Projects	Land use	Mean ± standard error	Range (min–max)	*n*
Water-filled pore space (0–12 cm, %)				
Project I	Natural forest	$28.8 \pm 1.0^{a*}$	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($p < .05$).

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 S4) 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 and Table 4). According to the applied regression models (Figure 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.

3.3 | 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

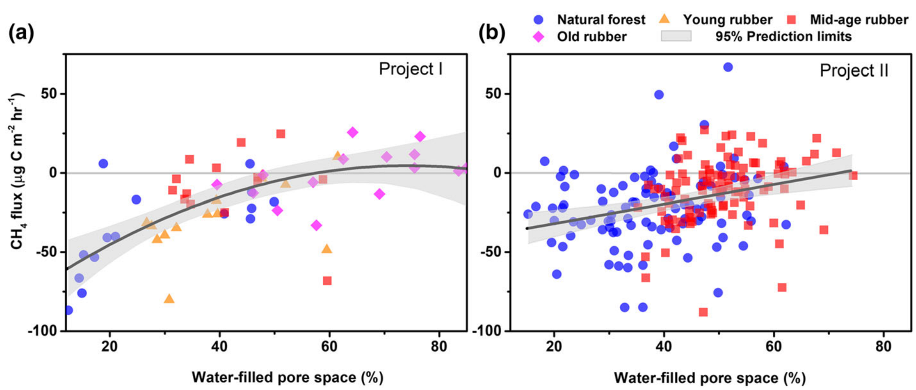

FIGURE 3 CH_4 flux regression model with water-filled pore space for Project I (a) and Project II (b). Regression lines and prediction limits were estimates from the model with only fixed effects, with model $y = -88.7744 + 2.5147\,x - 0.0169\,x^2$, R^2 = 0.39, and n = 60 for Project I and $y = -44.3421 + 0.6166\,x$, R^2 = 0.34, and n = 198 for Project II, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 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		

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 4). At a given WFPS, an increase in nitrate content led to a decrease of the CH_4 flux (Figure 4).

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 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 S5). 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.

3.4 | 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

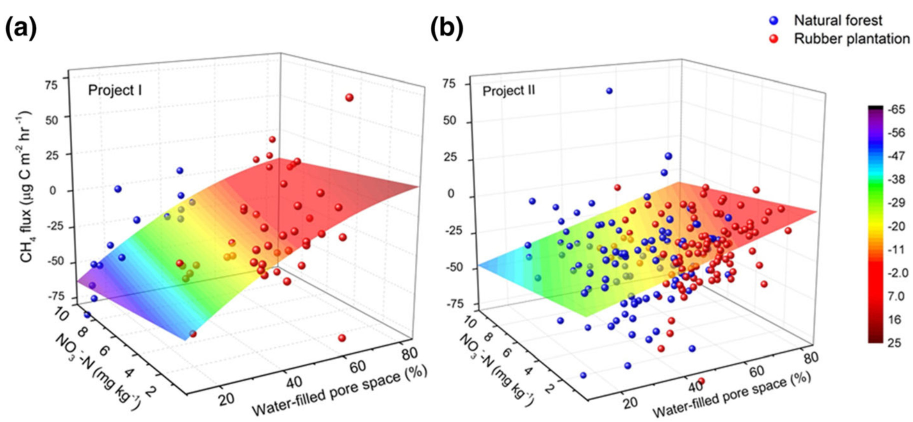

FIGURE 4 Simulated CH_4 flux surface (*z*) using water-filled pore space (*x*) and soil nitrate content (NO_3^-–N, *y*) as explanatory variables for Project I (a) and for Project II (b). Fitted equation of CH_4 flux was $z = -63.6152 + 1.6474\ x - 0.00791\ x^2 - 1.5548\ y$, $R^2 = 0.55$, and $n = 60$ for Project I and $z = -35.5297 + 0.5124\ x - 1.7177\ y$, $R^2 = 0.36$, and $n = 198$ for Project II [Colour figure can be viewed at wileyonlinelibrary.com]

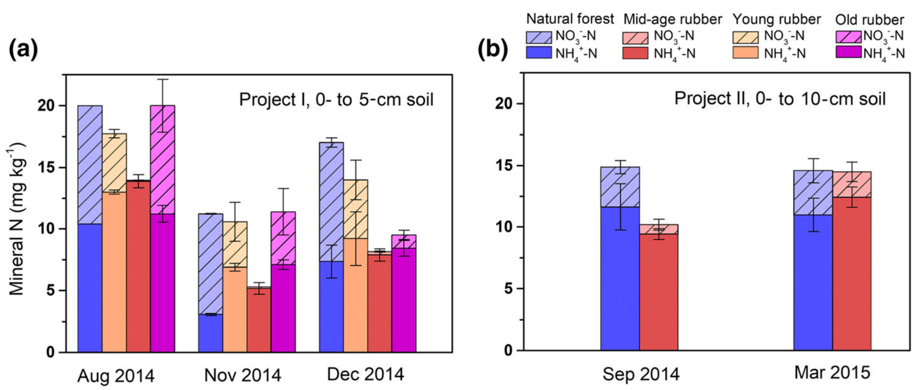

FIGURE 5 Mineral N content in topsoil under natural forests and rubber plantations of different age at different sampling dates in Project I (a) and in Project II (b). Error bars are standard error; in (a), *n* = 3 except natural forest on first two dates where composite sample was analyzed, and in (b), *n* = 9 [Colour figure can be viewed at wileyonlinelibrary.com]

flux (r = .43). As an independent variable, soil clay content explained only 18.6% variation of cumulative CH_4 flux (Figure 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 (Tables 4 and S2), 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 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.

The cumulative CH_4 fluxes negatively correlated to soil organic carbon content (0–10 cm) for Project II, but the correlation (r = −.35, p = .15, n = 18) was not significant.

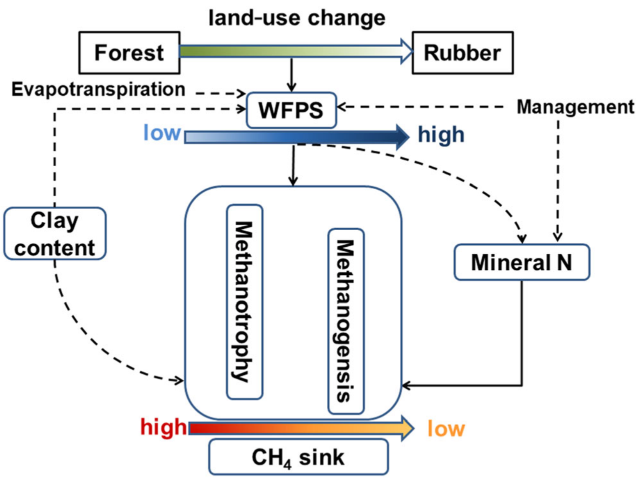

FIGURE 7 The impact of land-use change, soil texture, and management on soil function as atmospheric CH_4 sink. Solid lines show statistically confirmed effects, and dashed lines are other effects tested and discussed in our study. Converting natural forest into rubber plantation weakened the soil function 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 [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

4.1 | 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 1 and Figures 2 and 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 (Chan & Parkin, 2001; Dobbie & Smith, 1996) 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

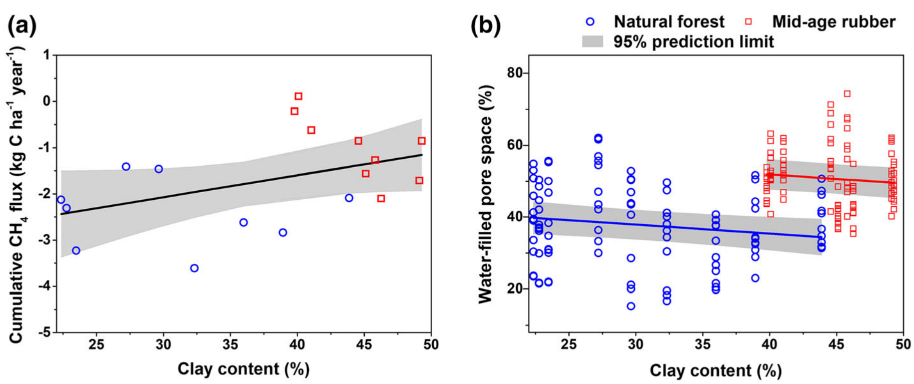

FIGURE 6 Texture effect on CH_4 flux and water-filled pore space in Project II. Regression between clay content and cumulative CH_4 flux (a) and between clay content and water-filled pore space (b). Gray shading represents 95% prediction limit. In (a), each point of annual cumulative CH_4 fluxes was 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 [Colour figure can be viewed at wileyonlinelibrary.com]

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.

4.2 | 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 and Figure 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, Zimmermann, Karbin, Hagedorn, & Niklaus, 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, Wijesuriya, Dissanayake, Karunaratne, & Herath, 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 (Hassler et al., 2015; Ishizuka et al., 2002; Werner et al., 2006). 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 6b). 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, Chamen, Tullberg, & Lal, 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 S2). 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 & 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 (Giambelluca et al., 2016; Tan et al., 2011), 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, Röll, Meijide, Hendrayanto, & Hölscher, 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.

4.3 | 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 4 and Table S5). 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 & 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 (Geng et al., 2017; Koehler et al., 2012), 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 S5). 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.

5 | 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 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.

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CONFLICT OF INTERESTS

The authors declare no conflict of interests.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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