

The transition from arable lands to rubber tree plantations in northern Thailand impacts weed assemblages and soil physical properties

M. NEYRET¹, H. ROBAIN¹, A. DE ROUW¹, B. SOULILEUTH², K. TRISOPHON³, K. JUMPA⁴ & C. VALENTIN¹

¹Institute of Ecology and Environmental Sciences (IEES-Paris), IRD, SU, CNRS, INRA, Paris Diderot, Paris Est Créteil, Bondy, France, ²Institute of Ecology and Environmental Sciences (IEES-Paris), IRD, SU, CNRS, INRA, Paris Diderot, Paris Est Créteil, Vientiane, Laos, ³Land Development Department, Regional Office 6, Chiang Mai, Thailand, and ⁴Land Development Department, Central Office, Bangkok, Thailand

Abstract

In South-East Asia, rapid land use changes in recent decades have raised concerns for biodiversity and soil conservation. Weeds provide many ecosystemic services for soil protection and support biodiversity, and could mitigate the negative effects of intensification. We investigated the changes in weed assemblages and weed–soil interactions on a chronosequence from annual crops to mature rubber tree plantations. We sampled five fields for each of four land uses in mountainous northern Thailand (rainfed upland rice, maize, young rubber tree (RT) intercropped with maize, and mature RT). We characterized weed assemblages (abundance, richness) and soil properties (bulk density, water, carbon and nitrogen content). Rice had the most diverse and abundant weed assemblages. Weed assemblages differed between (i) rice, (ii) maize and young RT with maize and (iii) mature RT. Soil water content was the highest in mature RT. Other soil properties varied strongly within and among fields, and did not vary significantly among land uses. Water and nitrogen content increased overall with living soil cover but decreased with weed species richness in mature RT. Such interactions could provide a basis for sustainable weeding practices favourable to soil and biodiversity conservation.

Keywords: Soil conservation, rubber tree, weed community, land cover, soil erosion, South-East Asia

Introduction

In recent decades, economic development in mountainous South-East Asia led to a rapid transition from subsistence to market-oriented crops, related to a transformation of low-input farming systems to medium- or high-input production with increased use of chemicals (Riwthong *et al.*, 2015). Although such changes have occurred worldwide, in South-East Asia, they have occurred at an unprecedented scale, threatening biodiversity and environmental resources (Rerkasem *et al.*, 2009; Fox *et al.*, 2014).

These trajectories in mountainous areas have been well described. Traditionally, in northern Thailand, shifting cultivation was the most common production system, relying on long fallow periods; rainfed rice was one of the main staple food (Wangpakapattanawong *et al.*, 2016). From the

1970s, demographic and economic growth caused the replacement of traditional shifting cultivation by more intense cash monocultures, such as maize (Fox & Vogler, 2005). Continuous cultivation and the expansion of croplands into previously forested areas led to severe environmental degradation (Wangpakapattanawong *et al.*, 2016), and to new policies encouraging the development of tree plantations, thought to protect soil and biodiversity. In particular, the expansion of rubber tree (RT) in non-traditional areas has been strongly encouraged due to high financial incentives (Fox & Castella, 2013). However, these plantations also have severe effects on soil conservation: while in young plantations the soil is often protected by intercrop or understorey, mature plantations are usually clean-weeded. Most studies investigating the impact of RT plantations on soil and biodiversity compared monocultures with lightly disturbed environments such as secondary forests (Liu *et al.*, 2015), or with other tree crops such as teak or palm tree (Guillaume *et al.*, 2016). They found that in flat areas, RT monocultures

Correspondence: M. Neyret. E-mail: margot.neyret@upmc.fr
Received September 2017; accepted after revision June 2018

decrease insect, bird and plant species richness and soil quality compared to forests (Beukema *et al.*, 2007), but are similar to or have slightly higher biodiversity and soil conditions than other tree plantations (Gnanavelrajah & Shrestha, 2007; Guillaume *et al.*, 2016). Various studies found that in mountainous areas tree plantations increased overland flow and sediment loss (Ribolzi *et al.*, 2017) and overall exacerbated soil degradation (Janeau *et al.*, 2003; Podwojewski *et al.*, 2008; Valentin *et al.*, 2008; Paiboonvorachat & Oyana, 2011). The processes and social implications of such trajectories have been discussed elsewhere (Fox & Castella, 2013; Ahrends *et al.*, 2015). However, the environmental impacts of the agricultural transition from annual crops to rubber tree plantations (changes in the main crop and associated practices; transition from open fields to closed canopy) at small scale are still largely unknown, especially in terms of plant diversity.

Weeds are often very competitive and can severely reduce crop yield and decrease the production quality. In intense agricultural systems, weeds are now mostly managed by herbicides, which have been a key element in increasing crop production. Yet weeds provide diverse services in the agroecosystem (Jordan & Vatovec, 2004). Although few studies investigated specifically the impact of weeds on soil erosion, it seems reasonable to assume that similarly to other plant covers, weeds support soil fertility and favour erosion control (Durán Zuazo & Pleguezuelo, 2008). Plants at ground level reduce splash erosion and reduce runoff velocity (Seitz *et al.*, 2016). Roots reduce runoff and erosion by increasing soil shear strength and favouring infiltration (Janeau *et al.*, 1999); they also enhance soil stability by direct meshing of soil aggregates (Durán Zuazo & Pleguezuelo, 2008). However, agricultural intensification worldwide has strongly modified weed communities, leading to the appearance of herbicide-resistant weed species and to the decrease in weed diversity and associated benefits (Jordan & Vatovec, 2004). In Europe, rare species have been replaced by generalist species (Storkey *et al.*, 2012) that tend to be more harmful to crops. Although such studies remain limited in South-East Asia, they tend to demonstrate a strong impact of land use (Storkey *et al.*, 2012) and herbicides on weed assemblages, potentially affecting erosion control.

The aim of this study was to investigate the effect of agricultural trajectories and land use change on the interactions between weed assemblages and soil physical characteristics in sloping cultivated areas of north Thailand, before the start of the monsoon season. By land use, we mean the crop or assemblage of crops and associated farming practices during the year preceding sampling. We focused on four land uses along the transition from annual crops to mature rubber tree (RT) plantations: upland rice and maize, followed by young RT plantations with maize intercrop and finally mature RT monocultures. We hypothesized that (i) cash crops (maize and rubber trees) are more intensively

managed and have poorer soil and lower biodiversity compared to upland rice fields; and (ii) the transition from annual, open-field crops to closed canopy in mature plantations leads to changes in plant communities' species composition, resulting in variations in plant–soil interactions. We investigated four main soil properties, related to soil susceptibility to erosion and crop growth: (i) soil water content, which is important regarding plant growth as well as soil structure and hydraulic response; (ii) soil bulk density, which determines porosity and thus infiltration rates; (iii) carbon content, which impacts aggregate stability and (iv) nitrogen content, which is essential to plant growth. We used quantitative statistical methods to investigate the relations between these characteristics and weed community properties: (i) the proportion of soil covered by living plants, (ii) litter biomass, (iii) weed species richness and (iv) living biomass.

Material and methods

Study sites

Environmental conditions. Study sites were located in Huai Lang, Wiang Kaen district, northern Thailand (100°27'E, 20°00'N, Figure 1). Fields cultivated by smallholders cover most of the area. In the year before the sampling, daily average temperature varied from 6.2 to 30.9 °C, with an average of 24.4 °C. Total rainfall between March 2015 and March 2016 was 1346 mm, mostly falling during the rainy season (April to November: 90% of total precipitations, Figure S1).

During the sampling period, mean temperature was 26.9 °C (daily minimum 17.0 °C, maximum 39.7 °C). Six rainfall events were recorded in February and March, with a cumulative height of 6.7 mm. The Antecedent Precipitation Index (API), which is a proxy of soil water content (Descroix *et al.*, 2002) and is proportional to the sum of daily precipitation amount for previous days, was under 0.1. This indicates that soil water content was not dependent on previous rains and was decreasing from evapotranspiration and drainage. Rainfall erosivity (EI₃₀/monthly rainfall, with EI₃₀ the monthly erosivity index, calculated as proposed by Renard *et al.* (1997) according to the Revised Universal Soil Loss Equation) was the highest in April in 2015 and April and June in 2016 (Figure S1).

Soils belonged to Alfisols with clay to clay-loam texture and were classified in three main soil series: Muak Lek, Wang Saphung and Tha li, discriminated mostly on their texture and depth (Figure 1 and Table 1, Jumpa (2012)).

Farming practices. Upland rice was the most widespread subsistence crop, while maize and rubber tree (RT) were the main cash crops. Maize and upland rice were grown in monoculture. Rotations usually involved alternation between maize (1–3 yr) and rice (1–2 yr). Maize and rice were

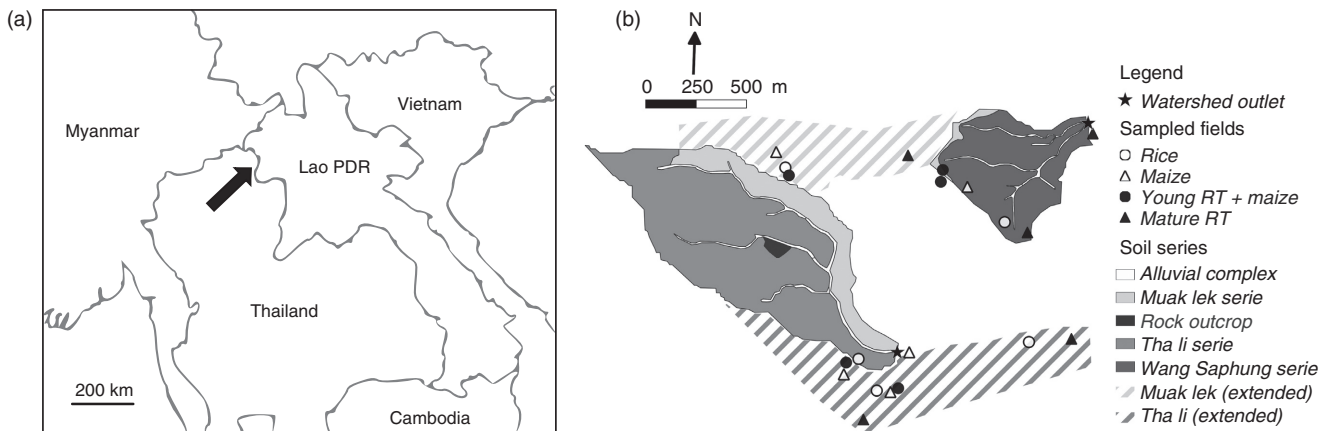


Figure 1 Situation of the study area. (a) Location of Huai Lang study site. (b) Plots location in the study area. Right: catchment dominated by mature RT plantations. Left: catchment dominated by annual crops. Soil series were taken adapted from Jumba (2012), and hatched areas represent areas where soil series was not identified, and was extrapolated from known soil distribution in the catchments.

Table 1 Characterization of soil series (adapted from Jumba (2012)).

Series name (abbrev.)	USDA classification	Texture	Soil depth	Soil pH
Muak Lek Series (MI)	Ultic Haplustalfs	Clayey-skeletal	Shallow	5.5–6
Tha Li Series (TI)	Ultic Haplustalfs	Clayey-skeletal	Medium	5.5–7
Wang Saphung Series (Ws)	Typic Haplustalfs	Fine, clay-loam	Deep	5.5–6.5

harvested during October and November, respectively. All the RT plantations in the area belong to the first rubber cycle. Young RT (2–3 yr old) had an average tree girth at 130 cm height of 15 cm (\pm standard deviation 4 cm), while mature RT (8–15 yr old) tree girth was 55 ± 10 cm. Mature RT were tapped during the rainy season.

Glyphosate was the most common herbicide, used in 79% of the fields. Up to three different herbicides per field (including atrazine, gramoxone, metsulfuron-methyl and chlorimuron-ethyl) were sprayed up to three times a year. All fields except one were fertilized. Farmers used herbicide-resistant varieties of maize which allowed them to use herbicides after maize germination. Table 2 summarizes the various practices reported by field owners for the crop preceding sampling. Field preparation occurred from April to June: crop residues in upland rice and maize fields were burnt before seeding, with a few exceptions. The steep slopes did not permit ploughing, and soil was mostly left undisturbed, except for occasional manual surface hoeing.

Vegetation sampling

We sampled five fields for each of four land uses in March 2016, before the start of clearing and tapping operations. We alternated the different land uses randomly to avoid potential bias due to sampling time. One 100 m² square

(henceforth ‘field’) was set in each field, at a location representative of the whole field.

Characterization of plant cover

Five 1 m² squares (henceforth ‘plots’) were randomly selected within the field for plant cover and soil characterization (Figure 2).

We identified all living plants in each plot to measure plant density and species richness. We separated the above-ground biomass in each plot into living (i.e. green) weeds, dead weeds and crop residues. Samples were oven-dried at 50 °C for 48 h. Dead weeds and crop residues were weighed separately and then pooled to estimate total litter biomass.

We took pictures from 150 cm above each plot after removal of the litter to measure soil cover by living weeds. Images were corrected for perspective deformation using GIMP (Gnu Image Manipulation Program) software, and living soil cover was measured by colour thresholding using Fiji (Fiji Is Just ImageJ) software (Schindelin, 2012).

Soil sampling

Soil water content was measured 13 times in each 1 m² plot, on a regular grid, using a TDR Delta Soil Moisture probe (depth of investigation: 10 cm, factory calibration for clayey

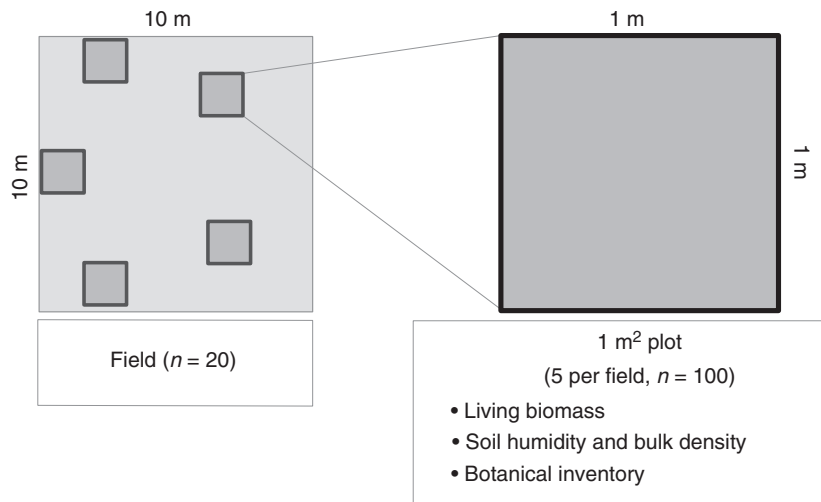


Figure 2 Sampling protocol.

soils) and then averaged. Topsoil was sampled once from each 1 m² plot using a 92 cm³ cylinder (5 cm height) to determine bulk density. An aliquot of the soil sample was then ground to 200 µm to measure C and N contents using a CHNOS Elemental Analyser Vario EL III (Elementar). As a result, we had five pseudo-replicates for soil water content, bulk density, C and N content in each of the 20 fields.

Data analyses

Statistical analyses were conducted using the R software (R Core Team 2017). We used linear models to investigate (i) variations of weed community characteristics (richness and abundance) and soil properties with land use and (ii) covariations between weeds and soil properties. For analyses at the 1 m² plot level, we used linear mixed models with random effects at the field level (function *lme*, package *NLME*, Pinheiro *et al.* (2017)) as a ‘site factor’ to take into account the non-independence of the five plots within each field (Zuur *et al.*, 2009). We hypothesized that the relationships between variables (i.e. the slopes) were similar among plots. Consequently, we only included random intercepts in the models.

R^2 , the explained variance of a model, is usually defined only for simple linear models to assess a model’s goodness-of-fit. Marginal R_m^2 and conditional R_c^2 are calculated as the proportion of variance explained, respectively, by fixed effects and by fixed and random effects. These two fitting criteria overcome most of the issues of R^2 calculation in mixed models (Nakagawa & Schielzeth, 2013). We used the implementation developed by Bartoń (2016) in the R package *MUMIN* (function *r.squaredGLMM*). Correlations were calculated using the *corr.test* function (PSYCH package, Revelle (2017)).

Our data showed very unbalanced species abundances (e.g. ubiquitous species vs. rare species) resulting in a sparse matrix (i.e. matrix containing many zeroes). To have a convenient

representation of site and individuals distance in ordination methods, we did a Hellinger transformation before analysis, as recommended by Legendre & Gallagher (2001):

$$y'_i = \sqrt{\frac{y_{ij}}{y_i}}$$

where y_{ij} is the abundance of species j in site i and y_i the total abundance in site i .

A principal component analysis of the Hellinger-transformed abundance data was then performed and we retained the 3 first dimensions accordingly to the relative variation of eigenvalues. Finally, the variation of plant communities between land uses was assessed using a between-class analysis (function *bca*, package *ADE4*, Dray *et al.* (2007)) to assess the variation of plant communities between land uses. This method allows a specific type of PCAiv (Principal Component Analysis with respect to Instrumental Variables) in which the explanatory variable is limited to one factor. The significance of the variations was addressed using a randomization-based test on 1000 repetitions.

Results

Variations of soil properties with land use

Most slopes were steep (> 40% in half of the fields) regardless of the land use ($P > 0.3$). Land uses were independent from position along the hillslope ($P > 0.4$, Table 2) and soil series (χ^2 independence test: $P > 0.7$), whose characteristics can be found in Table 1.

Bulk density was 1.3 g/cm³ (\pm standard deviation 0.1 g/cm³), without significant difference with land use ($P > 0.5$, Figure 3a). Soil water content was higher in mature RT plantation ($14.9 \pm 4.5\%$) than other land uses ($7.5 \pm 2.4\%$,

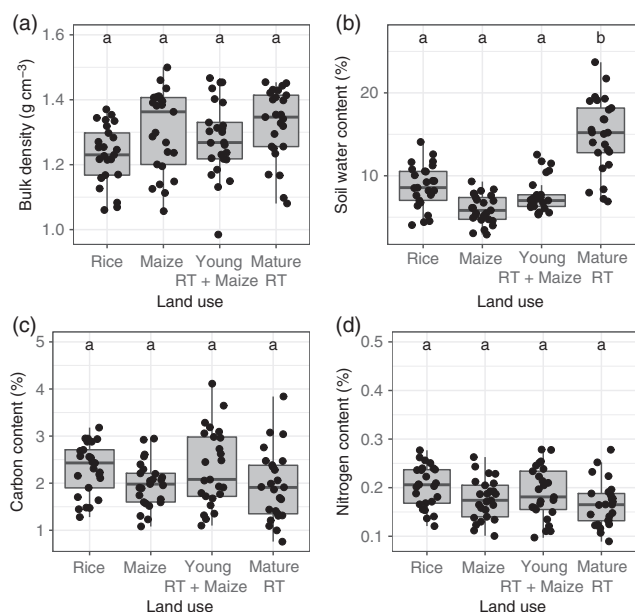


Figure 3 Variations of soil properties with land uses. Soil bulk density (a), soil water (b), carbon (c) and nitrogen (d) contents per square metre in each land use at the end of the dry season, that is 4–5 months after harvesting. Each dot represents one sampling plot. Different letters indicate significant differences at a 5% confidence level.

Table 3 Geomorphological data of the different sampled plots. Field identifiers correspond to crop (M: maize, ULR: upland rice, YR: young RT with maize, OR: mature RT) and field number. Series represent Muak lek serie (MI), Tha Li serie (TI), Wang Saphung serie (Ws), and parentheses indicate series assumed from spatial extrapolation. Position indicates the position along hillside: 0% at the river, 100% at the top. Slope is the slope of the field.

Field	Slope (%)	Position (%)	Hillside		Serie
			length (m)	Exposition	
ULR1	40.3	72	223	N	WS
ULR2	37.6	75	130	NE	TI
ULR3	53.0	30	210	N	(TI)
ULR4	40.5	76	270	NE	MI
ULR5	26.9	39	164	S	TI
M1	27.5	74	70	S	MI
M2	54.0	84	253	E	WS
M3	39.3	27	378	SE	TI
M4	50.3	59	239	NE	MI
M5	34.1	21	157	SE	TI
YR1	43.4	87	185	NE	WS
YR2	39.6	87	292	SW	WS
YR3	37.6	12	291	SE	TI
YR4	32.7	21	149	SE	TI
YR5	50.6	83	240	NE	(MI)
OR1	22.0	78	162	NW	WS
OR2	38.5	53	104	N	WS
OR3	42.7	65	145	NW	(TI)
OR4	44.6	41	209	NW	(MI)
OR5	43.7	33	165	NW	TI

$P < 0.01$, cf. Figure 3b). Carbon and nitrogen contents were respectively $2.1 \pm 0.67\%$ and $0.18 \pm 0.04\%$, and C/N ratio was 11.6 ± 1.5 for all land uses ($P > 0.5$, Figure 3c, d).

Bulk density did not vary with soil water content, but decreased with carbon content ($P < 10^{-5}$, Pearson coefficient = -0.58 , $P < 10^{-3}$).

Weed richness, abundance and composition

Forty-three herbaceous weed species were found, among which 39 were identified at least to the genus level (Table S1). They belonged to 17 families, with Asteraceae (8 species) and Poaceae (11) the most common families. Two species dominated: *Ageratum conyzoides* was present in 91 plots out of 100 and represented 30% of all herbaceous individuals; *Erigeron sumatrensis* was present in 90 plots and represented 51% of all individuals. They were the main species (both in terms of frequency and average abundance) in all land uses except mature RT plantations, where a fern (*Lygodium flexuosum*) was as frequent as (and often more abundant than) *Ageratum conyzoides*. The secondary species varied among land uses (Figure S2). Only two Leguminous species were identified (*Mimosa diplotricha* and *Desmodium gangeticum*). Upland rice fields tended to have a higher species richness (median 15 species per 100 m²) than other land uses (median 8, $P = 0.052$, Figure 4a).

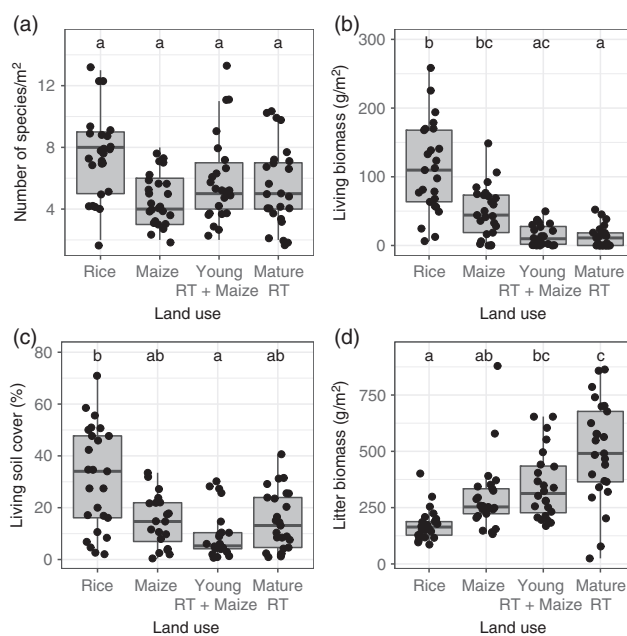


Figure 4 Variations of weed richness and abundance with land uses. Number of species per m² (a), living weed biomass (b), proportion of soil covered with living plants after litter removal (c) and litter biomass (d) in each land use at the end of the dry season, that is 4–5 months after harvesting. Each dot represents one sampling plot. Different letters indicate significant differences at a 5% confidence level.

Living biomass indicates productivity of the ecosystem and potential weed competitiveness for the coming crop. It was higher where the previous crop was upland rice ($110 \pm 65 \text{ g/m}^2$) than in other crops ($25 \pm 30 \text{ g/m}^2$, $P < 0.02$, Figure 4b). Soil cover by living weeds measures the degree of soil protection from rainfall. It was higher in upland rice fields ($31 \pm 20\%$) than in other land uses ($13 \pm 10\%$, $P < 0.009$, Figure 4c). Finally, litter biomass complements living weeds by accounting for the soil protection by mulch. It was high in mature RT plantations ($500 \pm 222 \text{ g/m}^2$), low in upland rice fields ($173 \pm 69 \text{ g/m}^2$) and intermediate in maize and young RT plantations (Figure 4d). Living biomass increased with living soil cover ($P < 10^{-3}$, $R^2 = 55\%$ for fixed effects only, $R^2 = 86\%$ for fixed and random effects). Living soil cover also increased with weed density, although less variance was explained by the model ($P < 10^{-3}$, $R^2 = 31\%$ for fixed effects only, $R^2 = 77\%$ for fixed and random effects).

The first two axes of the PCA represented 15% of the total inertia, while land uses significantly affected weed species composition and accounted for 9.7% of the total inertia ($P = 1.10^{-3}$, Figure 5a). The first axis separated mature RT plantations from other land uses, while the second axis separated upland rice and mature RT plantations on the one side, and maize and young RT plantations on the other. Figure 5b shows the coordinates of the 19 species which participated the most to the creation of

axes. The first axis was negatively correlated with the abundance of *Lygodium flexuosum* (mostly present in mature RT plantations) and positively correlated to the abundances of *Erigeron sumatrensis*. A cluster of species, many of which were C_4 plants (*Eleusine*, *Digitaria*, *Cynodon*) was associated mostly with upland rice fields. *Euphorbia hirta* and *Acmella paniculata* appeared to be mostly associated with maize fields and young RT plantations.

Interactions between weeds and soil properties

Results for weed–soil interactions are summarized in Tables 4 and 5, which also specifies other close-to-significant interactions. Pearson correlation coefficients can be found in Table 6 for all land uses taken together, and Table S2 for separate analyses.

Soil bulk density and carbon content did not vary significantly with weed assemblages characteristics (Figure 6a–d and m–p).

All land uses taken together, soil water content increased with living soil cover, litter biomass and slightly with living biomass (respectively, $P < 0.05$, $P < 0.05$, $P < 0.1$. Pearson coefficient ($=0.47$) was significant only for litter biomass). Besides, when considering land uses separately, in mature RT plantations, soil water content decreased with species richness and increased with litter

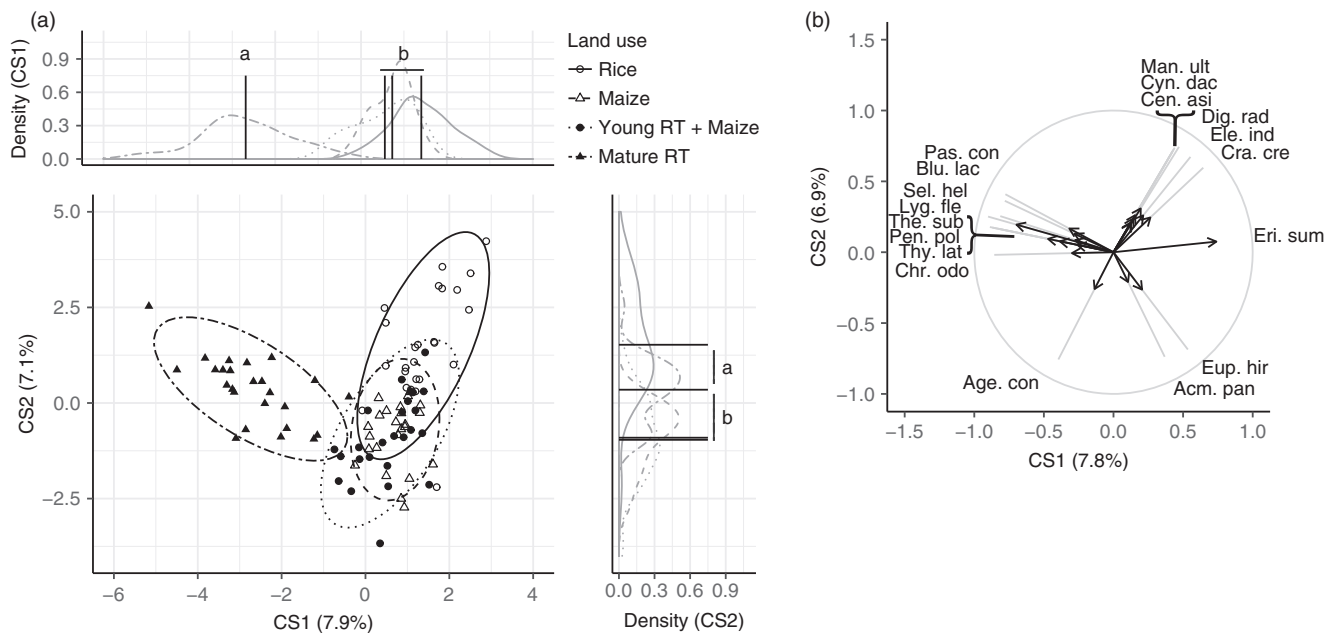


Figure 5 Variation of weed assemblages with land uses. (a) Position of the different land uses on the first two axes of the BCA (third axis not shown). Density curves indicate the smoothed kernel density of coordinates of each crop along axes, with the density on the y -axis (equivalent to smoothed histograms). Vertical and horizontal lines on density plots indicate barycentre coordinates of the density. The different letters indicate significant differences of the coordinates on the axis considered with crop (linear mixed models with a field random effect): on axis CS1, maize, rice and young RT are similar to each other and different from mature RT. On axis CS2 rice is different from maize and young RT. (b) Coordinates of the 19 most influential species in the BCA. Complete species names can be found in Table S1. Species labels have been moved to enhance visibility, and only the dark arrows are considered for interpretation.

Table 4 Results of the regressions (mixed models) for weed-soil interactions. First model: (i) Simple mixed model to determine the effect of the quantitative, weeds-related variable (X: living or litter biomass (g/m^2), species richness (m^2) or living soil cover (%)) on a soil property (Y: soil bulk density (g/cm^3), soil water content (%), carbon and nitrogen content (%)) after removal of land-use (LU) effects : $Y' \sim X$ (model A), with $Y' \sim X$ the residuals from the linear model $Y \sim \text{LU}$. * Indicates coefficients different from 0 at 5%, • differences at 10%, and different letters indicate coefficients different from each other ($P < 0.05$).

Response variable	Explanatory variable (e.v.)	Estimation of e.v. effect	R^2 m (%)	R^2 c (%)
Bulk density	Living biomass	5.1×10^{-5}	0	40
	Species richness	-4.5×10^{-3}	1.1	41
	Litter biomass	2.7×10^{-6}	0	39
	Living soil cover	1.4×10^{-5}	0	38
Water content	Living biomass	1.1×10^{-2} •	4.1	74
	Species richness	-6.3×10^{-2}	0.3	73
	Litter biomass	3.5×10^{-3} *	5.4	75
	Living soil cover	3.9×10^{-2} *	4.2	74
C	Living biomass	1.5×10^{-3}	1.5	53
	Species richness	-4.7×10^{-2}	3.5	50
	Litter biomass	2.7×10^{-4}	0.6	52
	Living soil cover	3.9×10^{-5}	0	49
N	Living biomass	1.8×10^{-4} •	4.5	61
	Species richness	-2.9×10^{-3}	2.8	54
	Litter biomass	2.2×10^{-5}	0.1	57
	Living soil cover	3.5×10^{-4}	1.3	57

biomass (Figure 6e, f, $P < 0.05$, correlation n.s.). In rice fields, it increased with living soil cover and living biomass (Figure 6g, h, $P < 0.05$, correlation highly significant of 0.74 and 0.78, respectively). Nitrogen content decreased with species richness in mature RT rubber tree plantations (Figure 6i, Pearson coefficient = -0.45 , $P < 0.05$). It tended to increase with living biomass when considering all land uses ($P < 0.1$, Table 4). It did not vary with the proportion of legumes (*Mimosa diplotricha*, *Desmodium gangeticum*) in the community ($P > 0.3$).

Discussion

We adopted a synchronic approach to address this transition from annual crops to perennial plantations: we sampled at one specific time different fields representative of the steps of the transition. While the use of chronosequences, as the one we investigated, may yield less precise results compared to diachronic approaches (i.e. long-term sampling to follow the transition in one or more fields), they can inform us about major trends and are an effective compromise when long-term studies are not feasible (Costa Junior *et al.*, 2013). We

sampled fields at the end of the dry season, with no intervention occurring in the fields since harvesting or the end of tapping operations (October–November). Thus, we observed the residual effects of previous crop on soil, weeds and mulch characteristics.

Weed biomass, frequency and richness

Both *Ageratum conyzoides* and *Erigeron sumatrensis* have been described as major weeds in various staple crops due to allelopathy for *Ageratum* and resistance to some herbicides for *Erigeron* (Itoh *et al.*, 1992). They were the most important species in terms of abundance and frequency for most fields, although secondary species varied widely. Nam-Matra (2017) reported some of the same species as serious weeds in Thailand, especially in upland rice fields (e.g. *Ageratum conyzoides*, *Acmella paniculata*, *Bidens pilosa*, *Mimosa diplotricha*, *Mitracarpus hirtus*, *Eleusine indica*). Consistently with our results, they found that Asteraceae and Poaceae were the dominant families.

In terms of biomass and species richness, our results differ from what has been previously described in other areas of Thailand. A comparison of 11 land use types in eastern Thailand showed that herbaceous specific diversity varied from nine species in paddy rice to 22 for mature RT plantations (Gnanavelrajah & Shrestha, 2007; Shrestha *et al.*, 2010). Average living biomasses (from 0.3 to 0.5 kg/m^2) in our study were much higher than those recorded under similar crops in eastern Thailand (0.18 kg/m^2 in mature RT plantations, 0.08 kg/m^2 for herbaceous species under paddy rice in Shrestha *et al.* (2010)). This might be related to differences in sampling time (in the crop v. 3 months after harvest), to climate or soil differences, or to different strategies of weed management. Such abundance, despite the rather intensive weeding, suggests a very ample weed seedbank, as usually builds up under annual cropping (de Rouw *et al.*, 2013).

Enhancing species diversity in either weeds or crops is thought to increase functional group diversity, that is the diversity of ecological functions in the ecosystem, leading to increased resource use and total biomass (Schmid *et al.*, 2002). This was not the case in this study. The communities were in general overdominated by *Ageratum* and *Erigeron*, and less abundant species had probably little influence on total biomass, which might explain this result. However, we did not directly investigate functional diversity: as subordinate species often play a major role in ecosystem functioning (Mariotte *et al.*, 2016), the variations in species richness and secondary species, even in such unbalanced communities, maybe resulted in changes other than biomass production that we did not measure.

We also investigated variations in plant communities. The relatively low amount of variance explained by the first axes of the BCA had two main causes. Firstly, the abundance matrix was a sparse matrix (with many zeros), resulting in

Table 5 Results of the regressions (mixed models) for weed-soil interactions. Second model: interaction mixed model to determine the interaction of X (living or litter biomass (g/m^2), species richness (m^{-2}) or living soil cover (%)) with land-use (LU) on a soil property (Y: soil bulk density (g/cm^3), water content (%), carbon and nitrogen content (%)); $Y \sim \text{XxLU}$. * indicates coefficients different from 0 at 5%, • differences at 10%, and different letters indicate coefficients different from each other ($P < 0.05$)

Response variable	Explanatory variable (e.v.)	Estimation of land-use -e.v. effect					Estimation of land-use -e.v. effect					R^2 m (%)	R^2 c (%)
		Rice	Maize	Young RT + maize	Mature RT	Rice	Maize	Young RT + maize	Mature RT				
Bulk Density	Living biomass	1.23	1.31	1.22	1.33	6.78×10^{-5}	4.17×10^{-4}	-1.80×10^{-3}	1.12×10^{-4}	10	47		
	Species richness	1.25	1.29	1.28	1.33	-1.18×10^{-2}	-1.53×10^{-2}	-9.43×10^{-3}	1.38×10^{-2}	14	51		
	Litter biomass	1.21	1.31	1.28	1.33	-9.08×10^{-5}	1.74×10^{-4}	-1.73×10^{-4}	-3.33×10^{-5}	11	51		
	Living soil cover	1.22	1.34	1.25	1.32	6.47×10^{-4}	3.55×10^{-4}	-2.58×10^{-3}	-2.48×10^{-4}	15	51		
Water content	Living biomass	7.26 ^a	5.96 ^a	7.61 ^a	14.81 ^b	2.28×10^{-2} *	3.87×10^{-4}	-1.00×10^{-3}	-2.42×10^{-3}	58	89		
	Species richness	8.29 ^a	5.58 ^a	7.65 ^a	14.62 ^b	0.28 ^a	-0.31 ^{a•b}	0.18 ^a	-0.82 ^b	59	91		
	Litter biomass	9.47 ^{ab}	6.01 ^b	7.56 ^b	13.93 ^b	4.71×10^{-3}	1.41×10^{-3}	3.84×10^{-3}	5.63×10^{-3} *	57	90		
	Living soil cover	7.66 ^a	6.26 ^a	7.46 ^a	14.87 ^b	7.91×10^{-2} *	6.86×10^{-2}	-2.52×10^{-2}	-1.02×10^{-2} •	56	89		
C	Living biomass	2.13	1.98	2.56	2.20	2.77×10^{-3}	-7.02×10^{-4}	6.25×10^{-3}	7.22×10^{-3}	8.6	60		
	Species richness	2.41	1.83	2.32	1.91	-6.54×10^{-2}	-1.22×10^{-1}	2.74×10^{-2}	-1.07×10^{-1}	13	59		
	Litter biomass	2.33	1.97	2.33	1.88	1.43×10^{-4}	-3.52×10^{-4}	1.12×10^{-3}	4.22×10^{-4}	7.8	61		
	Living soil cover	2.32	1.96	2.35	1.97	-8.89×10^{-4}	-1.80×10^{-3}	-1.91×10^{-3}	9.64×10^{-3}	7.2	57		
N	Living biomass	0.19	0.18	0.21	0.19	2.72×10^{-4} •	6.03×10^{-5}	4.64×10^{-4}	7.72×10^{-4}	15	64		
	Species richness	0.21	0.16	0.19	0.16	-3.05×10^{-3}	-1.02×10^{-2}	-2.76×10^{-3}	-8.04×10^{-3} *	9.3	66		
	Litter biomass	0.20	0.18	0.19	0.16	-8.57×10^{-5}	-2.87×10^{-5}	-6.85×10^{-5}	5.05×10^{-5}	9.1	65		
	Living soil cover	0.20	0.18	0.19	0.17	3.13×10^{-4}	-1.64×10^{-3}	5.80×10^{-5}	1.30×10^{-3}	12	64		

Table 6 Pearson correlation coefficients for plants- and soil- related variables, all land uses considered. Significativity: *: 5% – **: 1% – ***: 0.1%.

	Plant density	Living biomass	Living cover	Litter biomass	Species richness	C content	N content	Soil bulk density
Living biomass	0.59***							
Living soil cover	0.68***	0.82***						
Litter biomass	-0.18	-0.36***	-0.15					
Species richness	0.48***	0.39***	0.52***	-0.07				
C content	-0.13	0.08	-0.07	-0.16	-0.11			
N content	-0.06	0.20	0.05	-0.17	-0.11	0.91***		
Soil bulk density	-0.02	-0.25*	-0.18	0.28**	-0.15	-0.58***	-0.59***	
Water content	-0.01	-0.10	0.14	0.47***	0.04	-0.14	-0.10	0.15

lower explained variance (Legendre & Gallagher, 2001). Secondly, this result shows that variability in species composition is high; land use is not the only parameter determining plant communities, and other parameters (landscape characteristics, historical factors, stochasticity in plants' reproduction and migration) are likely to affect communities' composition. For instance, landscape scale management and landscape heterogeneity have been shown to impact weeds richness (Gaba *et al.*, 2010; Petit *et al.*, 2016); disturbances are known to have long-lasting effect on weed communities, in particular through seedbank (Renne & Tracy, 2007; Plaza *et al.*, 2015). We showed that mature RT plantations had very specific weed assemblages compared to other land uses and were for instance characterized by ferns (*Lygodium flexuosum*, *Selaginella helferi*). This was likely due to higher soil water content and lower light availability than for annual crops. Many plantations have undergone thorough weeding in the first years. Thus, although some are now herbicide-free, these past weeding practices might concur with low light availability to decrease weed biomass and richness. Among open-field crops, variations between upland rice fields on the one hand, and maize and young rubber with maize on the other, were probably due to more intensive weed management in maize during the growth period. Yet, the association of C₄ weeds with upland rice fields shown in Figure 5 suggests a potential threat to upland rice cultivation, as C₄ weeds can be extremely competitive and difficult to control (de Rouw *et al.*, 2010).

Soil physical properties and erosion

We did not find variations of soil density with land use. The bulk density in our sampled plantations (1.3 ± 0.1 g/cm³) was higher than reported in RT monoculture in lowland Acrisols of Sumatra (Indonesia) (0.93–0.98 g/cm³, Guillaume *et al.* (2016)) and similar to bulk density in mountainous RT plantations planted on Ferralsols and Cambisols in Yunnan (China) (1.1–1.3 g/cm³, de Blécourt *et al.* (2013)).

The interactions between plant abundance and soil water content are ruled by complex processes. High soil water

content favours plant growth but plants can have antagonist effects on soil water content. Plants tend to increase soil porosity, which favours water infiltration, and to protect soil from evaporation (Chen *et al.*, 2004), overall increasing soil water content, but plants also uptake water reserves and transpire. We showed that in upland rice fields, soil water content was low but increased with weed abundance. This suggests either that in these conditions, water availability is a limiting factor for plant growth or that weeds limit evaporation more efficiently than they increase transpiration. In such conditions, allowing weeds to grow might thus increase water availability for crops. In mature RT plantations, high relative air humidity under the canopy decreases the atmospheric evaporative demand in respect to open-field situations. There, soil water content was high and decreased with species richness.

The impact of soil water content on soil erosion can be contrasted, depending on soil sorptivity and the slaking down of dry aggregates. When soil water content is high, soil sorptivity is low, which might increase runoff. On the opposite, dry aggregates are more likely to slake down when rehumected (Le Bissonnais, 1996). In both open fields and mature RT plantations, weed cover is thus likely to decrease erosion: in humid plantations, soil cover can decrease runoff; in dry open fields, weed cover tends to decrease crust formation and thus runoff and erosion (Patin *et al.*, 2012).

Organic C content is known to increase aggregation, porosity and aggregates' stability, as confirmed by our finding that bulk density decreases with carbon content. However, contrarily to previous studies (Guillaume *et al.*, 2016), we did not find any variation of C or N content, or C:N ratio with land use, maybe because the mature RT plantations sampled in this study were relatively young (around 12 yr old, compared to 17 on average in Guillaume *et al.* (2016)) and only the first to be planted in the study area. Abundant soil cover by weeds has been shown to favour higher organic C and N contents (Abraham & Joseph, 2016). Considering our study's timescale, it is more likely that in our case the increase in N content with soil

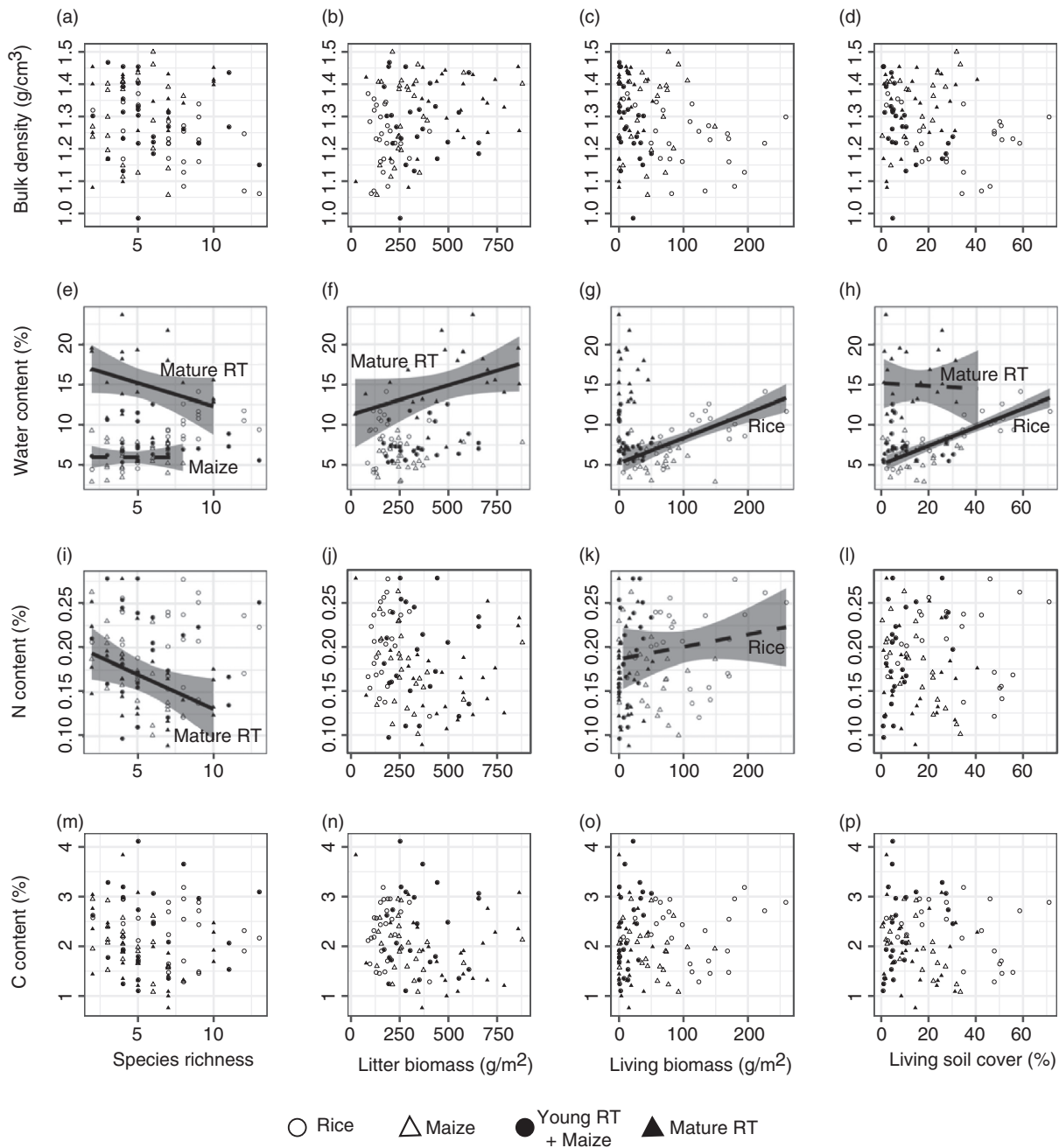


Figure 6 Interactions of weed richness and abundance with soil properties. Solid and dashed lines indicate, respectively, trends significant at 5% and 10%.

cover results from erosion mitigation rather than actual nutrient storage in the soil. Indeed, C and N content observed at a given time are a residual from quantities removed by erosion processes, by plants and transformed by microflora over the previous years. Thus, soils that have undergone low erosion rates and retain high organic matter content might now favour abundant weed assemblages, as suggested by the correlation between N content and living biomass. These relations could also be related to variations

in fertilization levels, which we chose not to investigate due to the uncertainty of the amounts of fertilizer used (collected from farmers' reports and not checked on-field). A longer term study on fields' history might be necessary in investigating weed interactions with C and N content.

Some authors have pointed out the herbicide-related simplification of plant biodiversity leading to increased soil erosion (Buhler *et al.*, 1997). Weed diversity might also have indirect effects on soil protection. For instance, diverse plant

assemblages favour diverse and active micro- or macrofaunal communities that might increase soil structure and stability or even surface roughness (Jouquet *et al.*, 2008). It is thus surprising that we did not detect major changes in soil properties with species richness, with the exception of soil water content: this shows that the dominance of *A. conyzoides* and *E. sumatrensis* in the communities was too strong to detect any effect of changes in subordinate species that could have impacted the interactions between plant communities and soil properties. Investigating the annual variations of species richness at seasons less constrained environmentally might allow better understanding of the impact of plant richness in such conditions.

Management and erosion control

We showed that rains were very erosive at the onset of the rainy season. Despite low water availability during the dry season, soil cover by weeds at the end of the dry season was high, which may constitute an important asset to protect soil from the high erosivity. Yet, field preparation in most fields (weeding by cutting or herbicides and in some cases burning) often occurs in April or at the beginning of May, causing soil baring and increasing its susceptibility to erosion just when rainfall erosivity is the highest. However, altering the weeding and planting schedule might be difficult for farmers, who have to manage meteorological conditions, crop growth and weed competition. On the contrary, as an abundant cover does not compete with mature rubber trees and is unlikely to decrease rubber yield in mature RT (Abraham & Joseph, 2016), its acceptance might be easier for rubber than for upland rice or maize farmers. Thus, less intense weed management under mature RT plantations is a pressing need to decrease erosion.

Conclusions

We found variations in both weed abundance (biomass, soil cover) and assemblage composition with land use. Soil water content was the highest in mature RT plantations and varied differently with weed abundance depending on the land use, which suggests that different types of weed assemblage might have different impacts on soil properties. However, further fine-scale soil characterization as well as a better comprehension of field history and management practices are needed to understand better soil–weed interactions. Besides, erosion processes take place on various timescales: continuous monitoring of soil erosion and weed cover is needed i. on an annual basis to appreciate the seasonal variation of these processes and ii. over a few years to investigate the effect of land use history and crop rotations. Finally, interdisciplinary research addressing the farmers' decision-making processes and the potential yield–soil

protection compromise will be essential for tackling current threats to sustainability.

Acknowledgements

This study was realized during a research project of Sorbonne University and Institut de Recherche pour le Développement; and was supported by the ANR HévÉAdapt project, grant ANR-14-CE03-0012-04, of the French Agence Nationale de la Recherche. Fieldwork was realized with the cooperation of the Huai Lang Royal Project Center and the Land Development Department of Thailand. Analytical data were obtained on the ALYSES facility (IRD-SU) that was supported by grants from Région Ile-de-France.

Data availability

Data and code used in this paper are published online (<https://doi.org/10.5281/zenodo.1257310>) and are available at https://github.com/mneyret/Neyret_etal_SUM_2018.

References

- Abraham, J. & Joseph, P. 2016. A new weed management approach to improve soil health in a tropical plantation crop, rubber (*Hevea brasiliensis*). *Experimental Agriculture*, **52**, 36–50.
- Ahrends, A., Hollingsworth, P.M., Ziegler, A.D., Fox, J.M., Chen, H., Su, Y. & Xu, J. 2015. Current trends of rubber plantation expansion may threaten biodiversity and livelihoods. *Global Environmental Change*, **34**, 48–58.
- Bartoń, K. (2016). *Mumin: multi-model inference*. R package version 1.15.6.
- Beukema, H., Danielsen, F., Vincent, G., Hardiwinoto, S. & van Andel, J. 2007. Plant and bird diversity in rubber agroforests in the lowlands of Sumatra, Indonesia. *Agroforestry Systems*, **70**, 217–242.
- de Blécourt, M., Brumme, R., Xu, J., Corre, M.D. & Veldkamp, E. 2013. Soil carbon stocks decrease following conversion of secondary forests to rubber (*Hevea brasiliensis*) plantations. *PLoS ONE*, **8**, e69357.
- Buhler, D.D., Hartzler, R.G. & Forcella, F. 1997. Implications of weed seedbank dynamics to weed management. *Weed Science*, **45**, 329–336.
- Chen, X., Yang, Y.-S. & Tang, J.-J. 2004. Species-diversified plant cover enhances orchard ecosystem resistance to climatic stress and soil erosion in subtropical hillside. *Journal of Zhejiang University Science*, **5**, 1191–1198.
- Costa Junior, C., Corbeels, M., Bernoux, M., Piccolo, M., Siqueira Neto, M., Feigl, B. ... Lal, R. 2013. Assessing soil carbon storage rates under no-tillage: comparing the synchronic and diachronic approaches. *Soil and Tillage Research*, **134**, 207–212.
- Descroix, L., Nouvelot, J. & Vauclin, M. 2002. Evaluation of antecedent precipitation index to model runoff yield.pdf. *Journal of Hydrology*, **263**, 114–130.
- Dray, S., Dufour, A. & Chessel, D. 2007. The ade4 package-II: two-table and K-table methods. *R News*, **7**, 47–52.

- Durán Zuazo, V. & Pleguezuelo, C. 2008. Soil-erosion and runoff prevention by plant covers, A review. *Agronomy for Sustainable Development*, **28**, 65–86.
- Fox, J.M. & Castella, J.-C. 2013. Expansion of rubber (*Hevea brasiliensis*) in Mainland South East Asia: what are the prospects for smallholders? *Journal of Peasant Studies*, **40**, 155–170.
- Fox, J.M. & Vogler, J.B. 2005. Land-use and land-cover change in montane mainland Southeast Asia. *Environmental Management*, **36**, 394–403.
- Fox, J.M., Castella, J.-C., Ziegler, A.D. & Westley, S.B. 2014. Rubber plantations expand in mountainous Southeast Asia: what are the consequences for the environment? *AsiaPacific Issues*, **114**, 1–8.
- Gaba, S., Chauvel, B., Dessaint, F., Bretagnolle, V. & Petit, S. 2010. Weed species richness in winter wheat increases with landscape heterogeneity. *Agriculture, Ecosystems & Environment*, **138**, 318–323.
- Gnanavelrajah, N. & Shrestha, R. P. (2007). Assessing Plant Diversity in Cultivated Landscape: A case of Khlong Yai Sub-watershed, Thailand. Second GMSARN International Conference. Pattaya, Thailand.
- Guillaume, T., Holtkamp, A.M., Damris, M., Brümmer, B. & Kuzyakov, Y. 2016. Soil degradation in oil palm and rubber plantations under land resource scarcity. *Agriculture, Ecosystems & Environment*, **232**, 110–118.
- Itoh, K., Azmi, M. & Ahmad, A. (1992). Paraquat resistance in *Solanum nigrum*, *Crassocephalum crepidioides*, *Amaranthus lividus* and *Conyza sumatrensis* in Malaysia. In: Proceedings of the 1st International Weed Control Congress (Vol. 2, pp. 224–228).
- Janeau, J.-L., Mauchamp, A. & Tarin, G. 1999. The soil surface characteristics of vegetation stripes in Northern Mexico and their influences on the system hydrodynamics. *Catena*, **37**, 165–173.
- Janeau, J.-L., Bricquet, J.P., Planchon, O. & Valentin, C. 2003. Soil crusting and infiltration on steep slopes in northern Thailand. *European Journal of Soil Science*, **54**, 543–553.
- Jordan, N. & Vatovec, C. 2004. Agroecological Benefits from Weeds. In: *Weed biology and management* (ed. Inderjit), pp. 137–158. Springer Netherlands, Dordrecht.
- Jouquet, P., Podwojewski, P., Bottinelli, N., Mathieu, J., Ricoy, M., Orange, D. ... Valentin, C. 2008. Above-ground earthworm casts affect water runoff and soil erosion in Northern Vietnam. *Catena*, **74**, 13–21.
- Jumpa, K. 2012. *LDD internal report*. Land Development Department, Thailand.
- Le Bissonnais, Y. 1996. Aggregate stability and assessment of crustability and erodibility: 1. Theory and methodology. *European Journal of Soil Science*, **47**, 425–437.
- Legendre, P. & Gallagher, E. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129**, 271–280.
- Liu, W., Luo, Q., Li, J., Wang, P., Lu, H., Liu, W. & Li, H. 2015. The effects of conversion of tropical rainforest to rubber plantation on splash erosion in Xishuangbanna, SW China. *Hydrology Research*, **46**, 168–174.
- Mariotte, P., Le Bayon, R.-C., Eisenhauer, N., Guenat, C. & Buttler, A. 2016. Subordinate plant species moderate drought effects on earthworm communities in grasslands. *Soil Biology and Biochemistry*, **96**, 119–127.
- Nakagawa, S. & Schielzeth, H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133–142.
- Nam-Matra, R. 2017. Diversity of weed and agricultural management. In: *Biodiversity conservation in Southeast Asia: challenges in a changing environment* (eds S. Morand, C. Lajaunie & R. Satrawaha), pp. 119–146. Routledge, London.
- Paiboonvorachart, C. & Oyana, T.J. 2011. Land-cover changes and potential impacts on soil erosion in the Nan watershed, Thailand. *International Journal of Remote Sensing*, **32**, 6587–6609.
- Patin, J., Mouche, E., Ribolzi, O., Chaplot, V., Sengtahevanghoun, O., Latsachak, K. ... Valentin, C. 2012. Analysis of runoff production at the plot scale during a long-term survey of a small agricultural catchment in Lao PDR. *Journal of Hydrology*, **426–427**, 79–92.
- Petit, S., Gaba, S., Grison, A.-L., Meiss, H., Simmoneau, B., Munier-Jolain, N. & Bretagnolle, V. 2016. Landscape scale management affects weed richness but not weed abundance in winter wheat fields. *Agriculture, Ecosystems & Environment*, **223**, 41–47.
- Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D., & R Core Team 2017. nlme: linear and nonlinear mixed effects models. R package version 3.1-131.
- Plaza, E.H., Navarrete, L. & González-Andújar, J.L. 2015. Intensity of soil disturbance shapes response trait diversity of weed communities: the long-term effects of different tillage systems. *Agriculture, Ecosystems & Environment*, **207**, 101–108.
- Podwojewski, P., Orange, D., Jouquet, P., Valentin, C., Nguyen, V.T., Janeau, J.-L. & Tran, D.T. 2008. Land-use impacts on surface runoff and soil detachment within agricultural sloping lands in Northern Vietnam. *Catena*, **74**, 109–118.
- R Core Team 2017. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Renard, K.G., Foster, G.R., Weesies, G.A., McCool, D.K. & Yoder, D.C. (1997). Predicting soil erosion by water: a guide to conservation planning with the revised universal soil loss equation (RUSLE). USDA Agricultural Handbook Volume 703, USDA, Washington, DC.
- Renne, I.J. & Tracy, B.F. 2007. Disturbance persistence in managed grasslands: shifts in aboveground community structure and the weed seed bank. *Plant Ecology*, **190**, 71–80.
- Rerkasem, K., Lawrence, D., Padoch, C., Schmidt-Vogt, D., Ziegler, A.D. & Bruun, T.B. 2009. Consequences of Swidden transitions for crop and fallow biodiversity in Southeast Asia. *Human Ecology*, **37**, 347–360.
- Revelle, W. (2017). Psych: procedures for psychological, psychometric, and personality research. R package version 1.7.5. Northwestern University. Evanston, Illinois.
- Ribolzi, O., Evrard, O., Huon, S., de Rouw, A., Silvera, N., Latsachack, K. O. ... Valentin, C. 2017. From shifting cultivation to teak plantation: effect on overland flow and sediment yield in a montane tropical catchment. *Scientific Reports*, **7**, 3987.
- Riwthong, S., Schreinemachers, P., Grovermann, C. & Berger, T. 2015. Land use intensification, commercialization and changes in pest management of smallholder upland agriculture in Thailand. *Environmental Science & Policy*, **45**, 11–19.

- de Rouw, A., Huon, S., Soullieuth, B., Jouquet, P., Pierret, A., Ribolzi, O. ... Chantharath, B. 2010. Possibilities of carbon and nitrogen sequestration under conventional tillage and no-till cover crop farming (Mekong valley, Laos). *Agriculture, Ecosystems & Environment*, **136**, 148–161.
- de Rouw, A., Casagrande, M., Phaynaxay, K., Soullieuth, B. & Saito, K. 2013. Soil seedbanks in slash-and-burn rice fields of northern Laos. *Weed Research*, **54**, 26–37.
- Schindelin, J. (2012). Fiji: an open-source platform for biological-image analysis.
- Schmid, B., Joshi, J. & Schlöpfer, F. 2002. Empirical evidence for biodiversity-ecosystem functioning relationships. In: *Linking biodiversity and ecosystem functioning* (eds A. Kinzig, S. Pacala & D. Tilman), pp. 120–150. Princeton University Press, Princeton, NJ.
- Seitz, S., Goebes, P., Song, Z., Bruehlheide, H., Härdtle, W., Kühn, P. ... Scholten, T. 2016. Tree species and functional traits but not species richness affect interrill erosion processes in young subtropical forests. *SOIL*, **2**, 49–61.
- Shrestha, R. P., Schmidt-Vogt, D. & Gnanavelrajah, N. 2010. Relating plant diversity to biomass and soil erosion in a cultivated landscape of the eastern seaboard region of Thailand. *Applied Geography*, **30**, 606–617.
- Storkey, J., Meyer, S., Still, K.S. & Leuschner, C. 2012. The impact of agricultural intensification and land-use change on the European arable flora. *Proceedings of the Royal Society of London B: Biological Sciences*, **279**, 1421–1429.
- Valentin, C., Agus, F., Alamban, R., Boosaner, A., Bricquet, J., Chaplot, V. ... Vadari, T. 2008. Runoff and sediment losses from 27 upland catchments in Southeast Asia: Impact of rapid land use changes and conservation practices. *Agriculture, Ecosystems & Environment*, **128**, 225–238.
- Wangpakapattanawong, P., Tiansawat, P. & Sharp, A. (2016). Forest restoration at the landscape level in Thailand. In: *Forest landscape restoration for Asia-Pacific forests* (eds Appanah S.), pp. 149–166. FAO/RECOFTC, Bangkok, Thailand.
- Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A. & Smith, G. M. (2009). *Mixed effects modelling for nested data. Statistics for biology and health*. Springer New York, New York, NY.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Meteorological data of Huai Lang meteorological station. Gray areas indicate the rainy season.

Figure S2. Variations of mean plant density per 1 m² for each field for the 8 most abundant species.

Table S1. Description of abundance of identified species.

Table S2. Pearson correlation coefficients separated for each land use.