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ÉCOLE DOCTORALE 129 "SCIENCES DE L'ENVIRONNEMENT"
Institut d'Écologie et des Sciences de l'Environnement de Paris

Adventices et érosion du sol dans un agroécosystème montagneux du Nord de la Thaïlande : une étude multidisciplinaire



Thèse de doctorat en Écologie

par **Margot NEYRET**

*dirigée par **Christian VALENTIN***

*et coencadrée par **Henri ROBAIN** et **Anneke DE ROUW***

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*À ma soeur et à mes frères : Mariette, Simon, et Émile
Et à ma cousine Alice*

*À ma grand-mère, Madeleine Neyret, et à p'tit Paul
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¹ "Allô Henri ? le terrain ne se passe pas *du tout* comme prévu..."

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LIST OF ABBREVIATIONS

Abbreviation	Meaning
ACC	Annual crop catchment
AIC	Akaike information criteria
API	Antecedent precipitation index
BEST	Beerkan Estimation of Soil Transfer Parameters
cv	Coefficient of variation
Df	Degree of freedom
KE	Kinetic energy
EI ₃₀	Rainfall erosivity
ERT	Electrical resistivity tomography
FAO	Food and Agriculture Organization of the United Nations
GLASOD	Global Assessment of Human-induced Soil Degradation
I ₃₀	Rainfall intensity
LDD	Land Development Department
M	Maize field
NDVI	Normalized difference vegetation index
PCA	Principal components analysis
RDA	Redundancy analysis
REDD+	Reduce emissions from deforestation and forest degradation program
RI	Relative Importance index
RT	Rubber tree
RTC	Rubber tree catchment
ULR	Upland rice field
UNCCD	United Nations Convention to Combat Desertification
YR	Young rubber tree plantations
θ	Soil humidity
γ_{bulk}	Soil bulk density
γ_{fine}	Soil bulk density (fine elements only)
C%	Proportion of coarse elements
W_h	Sample wet weight
W_d	Sample dry weight
W_{dc}	Dry weight of coarse elements
V_t	Sample volume
V_c	Volume of coarse elements

RÉSUMÉ

INTRODUCTION

Conservation du sol dans un contexte d'intensification agricole

La conservation du sol a été reconnue comme l'un des objectifs de développement durable par les Nations Unies en 2012. Elle est en effet à la clé de nombreux défis sociaux et environnementaux, tels que la sécurité alimentaire, les changements climatiques, ou la protection de la biodiversité (KOCH et al. 2013). Quoique les sols puissent être dégradés par des processus naturels, l'homme accentue fortement ces dégradations, notamment du fait de l'intensification agricole. Celle-ci peut être définie à la fois comme la transition depuis un système agricole dépendant essentiellement de ressources locales vers l'utilisation massive d'apports extérieurs (e.g. herbicides, engrais); et par le changement d'une agriculture vivrière vers un système commercial (MATSON et al. 1997). Cette intensification s'accompagne souvent d'un raccourcissement des séquences culturales et de l'utilisation quasi-exclusive de variétés commerciales à haut rendement. La mécanisation a aussi rendu possible, dans de nombreux environnements, l'augmentation de la taille des champs et des fermes, conduisant à une disparition des éléments semi-naturels du paysage (BAESSLER et KLOTZ 2006). Bien que l'intensification agricole a permis des avancées considérables en matière de sécurité alimentaire, ses impacts environnementaux en termes de pollution, de dégradation de la biodiversité et des sols sont désormais largement reconnus (TILMAN 2001).

Les adventices dans l'agroécosystème

Les adventices sont l'ensemble des plantes non cultivées d'un agroécosystème. Elles sont en général perçues comme des nuisibles qu'il faut contrôler pour assurer des rendements agricoles élevés (OERKE 2006). Aujourd'hui, ce contrôle est principalement réalisé par l'application d'herbicides. Pendant les dernières décennies, l'augmentation de leur usage, ainsi que la simplification des rotations culturales et l'utilisation croissante d'engrais chimiques, ont fortement modifié les communautés adventices, avec de manière générale une diminution de leur richesse et une prolifération des espèces les plus compétitives, du moins en milieu tempéré (BAESSLER et KLOTZ 2006; STORKEY et NEVE 2018). Or, de nombreuses études ont montré que les adventices assuraient de nombreux services écosystémiques : principale source de biodiversité végétale en milieu agricole, elles sont à la base des réseaux trophiques et représentent la ressource principale des insectes, oiseaux, et mammifères dans les milieux agricoles (MARSHALL et al. 2003; PETIT et al. 2011). D'autre part, les plantes jouent un rôle majeur dans la protection du sol et l'atténuation des processus d'érosion : les feuilles diminuent l'érosion par "splash" en réduisant l'énergie

cinétique des gouttes de pluie; les tiges augmentent la rugosité du sol et ralentissent le ruissellement de l'eau; tandis que leurs racines améliorent l'infiltrabilité du sol tout en augmentant sa cohésion (SEYBOLD et al. 1999; DURÁN ZUAZO et PLEGUEZUELO 2008). Bien que peu nombreuses, les quelques études s'intéressant à quantifier l'effet des adventices sur l'érosion du sol ont montré une diminution importante des processus de ruissellement et de détachement du sol lorsque le couvert adventice est important (PODWOJEWSKI et al. 2008; LIU et al. 2016) et que sa richesse spécifique augmente (CHEN et al. 2004).

Dans ce contexte, il semble important de conserver la diversité des adventices et les services écosystémiques qui leur sont associés, en atténuant les dégradations causées par l'intensification agricole. Une des solutions pour répondre à ce problème consiste à maintenir une diversité temporelle et spatiale de l'agroécosystème. Par exemple, il a été montré que la complexité spatiale du paysage agricole (e.g. la présence d'éléments semi-naturels et de cultures variées), tout comme les séquences culturales diversifiées, étaient favorables à la diversité des adventices (TSCHARNTKE et al. 2005).

Changements d'usage du sol et intensification agricole en Asie du Sud-Est

Les régions montagneuses d'Asie du Sud-Est forment un "hotspot" de biodiversité (SODHI et al. 2004), mais sont particulièrement vulnérables à la dégradation du sol du fait de conditions climatiques défavorables (e.g. érosivité importante des précipitations, PANAGOS et al. (2017)) et de rapides changements d'usage des sols. La déforestation et le développement agricole rapide, en lien avec la pression démographique, y ont causé de fortes dégradations de la biodiversité et du sol (SODHI et al. 2004; VALENTIN et al. 2008). À la fin du XXe siècle, les gouvernements ont donc encouragé l'expansion de cultures pérennes, comme l'hévéa, afin d'augmenter le couvert arboré en zone montagneuse tout en augmentant les revenus des petits exploitants agricoles. *Hévéa brasiliensis* est un arbre originaire des zones équatoriales d'Amérique du Sud, cultivé pour son latex, à la base du caoutchouc naturel; ainsi que son bois en fin de cycle d'exploitation. Il était attendu que son expansion permettrait de restaurer les zones montagneuses dégradées. Cependant, la durabilité socio-économique et environnementale de ces plantations est fortement controversée (FOX et al. 2014; AHRENDTS et al. 2015): en particulier, l'afforestation provoquerait une augmentation des processus d'érosion (LACOMBE et al. 2016). Cependant, la plupart des études abordant ce sujet comparent les plantations d'hévéa à des forêts ou à d'autres plantations d'arbres, ce qui ne correspond pas à la situation principale observée au nord de la Thaïlande, où ces plantations sont plantées sur des terres agricoles (BLAGODATSKY et al. 2016). D'autre part, il semble que l'impact de ces plantations sur les processus d'érosion est fortement dépendant de l'existence d'un sous-bois, dont la présence diminue fortement l'érosion - par exemple dans les hévéas de "jungle" (BEUKEMA et al. 2007; GUILLAUME et al. 2015).

Dans ce manuscrit, j'étudie l'effet des changements d'usage du sol sur les communautés adventices et l'érosion du sol dans une région montagneuse du nord de la Thaïlande. En particulier, je cherche à déterminer quelles sont les interactions entre les adventices et le sol, et si une gestion moins intensive des adventices permettrait d'assurer une meilleure protection du sol. Ainsi, dans le premier chapitre de résultats (Chapitre 3), je m'intéresse aux relations à petite échelle entre les propriétés

physico-chimiques du sol et les caractéristiques des communautés d'adventices, et à la façon dont ces relations sont impactées par le type d'usage du sol. Les chapitres 4 et 5 concernent principalement les processus affectant les communautés végétales : dans le chapitre 4, j'étudie l'effet de la variabilité temporelle des cultures sur la richesse et la diversité des adventices. Dans le chapitre 5, je quantifie les effets relatifs des facteurs environnementaux locaux, de l'usage des sols, du contexte paysager et de composantes spatiales sur ces communautés. Enfin, dans le dernier chapitre, j'étudie l'effet de l'usage des sols (plantations d'hévéa vs. cultures annuelles) sur le ruissellement et le détachement du sol ; et dans les plantations d'hévéa, j'examine l'effet du couvert de sol par les adventices sur l'atténuation de ces processus érosifs.

SITE D'ÉTUDE ET ACQUISITION DES DONNÉES

Site d'étude

Mon site d'étude est situé à Huai Lang, province de Chiang Rai, au nord de la Thaïlande. Les champs étudiés étaient disséminés dans deux petits bassins versants, l'un principalement occupé par des cultures annuelles, et l'autre par des plantations d'hévéa. La région, située à des altitudes variant entre 400 et 900 m d'altitude, est caractérisée par des précipitations annuelles moyennes d'environ 1 600 mm et une température annuelle moyenne de 24.8 °C. Les sols sont classés dans la catégorie des Haplustalfs.

La grande majorité de la région est occupée par des exploitations familiales. Les vallées sont principalement occupées par des rizières, dans lesquelles du riz est planté en début de saison humide, suivi par du maïs ; les terrains plus en pente (sur lesquels est centrée cette étude) sont surtout cultivés avec du riz pluvial (principale culture vivrière), du maïs, ou des plantations d'arbres (plantations d'hévéa ou, en minorité, de teck ou vergers). Le modèle agricole est assez intensif, avec une utilisation poussée d'engrais et d'herbicides dans la plupart des champs. Le travail du sol est en revanche très restreint et non mécanisé en raison des fortes pentes (en général > 30%).

Suivi des champs d'étude

Les 20 champs étudiés ont été choisis en mars 2016 et étaient équitablement répartis entre quatre types d'usages des sols représentatifs de la transition des cultures annuelles vivrières (riz pluvial) aux cultures annuelles de rente (maïs) puis aux plantations pérennes (jeunes plantations d'hévéa avec culture annuelle en inter-rang, plantations matures). Les mêmes sites ont ensuite été suivis deux fois par an, à la fin de la saison sèche et à la fin de la saison pluvieuse, jusqu'en mars 2018. À l'exception des plantations d'hévéas matures, nous y avons donc observé différentes successions culturales, avec par exemple l'apparition de friches ou la disparition des cultures d'inter-rang dans les jeunes plantations.

Dans chaque site, nous avons défini une zone de 100 m² (fixe d'une saison à l'autre) dans laquelle nous avons placé aléatoirement cinq parcelles de 1 m² (variables d'une année à l'autre). Dans chacune de ces parcelles, nous avons réalisé des inventaires botaniques complets, mesuré la biomasse végétale, mesuré in situ

l'humidité volumique du premier décimètre du sol et prélevé un cylindre de 100 cm³ de sol. Cet échantillon de sol a ensuite été analysé pour en mesurer la densité apparente, les concentrations en carbone et azote, la proportion d'éléments grossiers et, pour une saison d'échantillonnage, la texture. Nous avons également réalisé, en mars 2016 et mars 2017, des tests Beerkan dans le but de caractériser l'infiltrabilité du sol. Ces descriptions à petite échelle ont été complétées par des profils de sol (profondeur de 1 m) et des analyses de tomographie de résistivité électrique. Le couvert végétal a été mesuré sur la base de photos prises à la verticale de chaque parcelle. Toutes ces données ont ensuite été agrégées pour chaque champ et chaque saison d'observation. Une description des pratiques agricoles a été réalisée à partir d'observations de terrain et d'entretiens avec les propriétaires des différents champs. J'ai également réalisé à partir de digitalisation manuelle et d'analyses d'images satellites Sentinel-2 une description précise du paysage. Le paysage est ici défini par la proportion et configuration de différents types d'usage des sols et par la variabilité de la végétation dans une zone de 200 m de rayon centrée sur chaque champ étudié.

Suivi des plots d'érosion

Nous avons également utilisé des "plots" d'érosion pour mesurer les processus de ruissellement et de détachement du sol sous différentes conditions. Un plot d'érosion est un cadre métallique de 1 m², enfoncé dans le sol. Un seau en aval du plot permet, après chaque évènement pluvieux et tout au long de la saison pluvieuse, de mesurer le volume de pluie qui a ruisselé à la surface du sol ainsi que la concentration de particules de sol détachées durant l'évènement pluvieux. Une station météo localisée près des deux bassins versants permet de mesurer la hauteur et l'intensité des précipitations.

La première expérience menée en 2015-2016 avait pour but de comparer le ruissellement et le détachement du sol sous cultures annuelles et sous plantations d'hévéa. Trois plots ont été installés en 2015 dans chacun des contextes suivants : un champ de maïs, une jeune plantation d'hévéa avec une culture annuelle (riz ou maïs) en inter-rang, et une plantation d'hévéa matures, soit entre les rangs d'arbres, soit dans les rangs d'arbres. Ce protocole a été répété en 2016 dans de nouveaux champs avec des usages du sol identiques.

Pour la seconde expérience, menée en 2017 et 2018, nous nous sommes plus particulièrement intéressés aux plantations matures d'hévéa. L'objectif était de mesurer l'effet du couvert herbacé sur le ruissellement. Nous avons installé six plots dans deux plantations et sous deux traitements (avec et sans application d'herbicides, soit 12 plots en tout). Des photos hebdomadaires et standardisées de chaque plot ont été prises chaque semaine entre mars 2017 et décembre 2018, puis analysées afin de mesurer l'évolution du couvert végétal au cours du temps.

IMPACT DE L'USAGE DES SOLS SUR LES INTERACTIONS SOL-ADVENTICES

Dans ce chapitre, j'étudie l'effet du type d'usage du sol sur les interactions entre les propriétés des communautés adventices (biomasse, densité, richesse spécifique)

et les caractéristiques du sol (humidité, densité, concentration en carbone et azote, infiltrabilité). Ce premier chapitre de résultats s'appuie sur une étude déjà publiée (NEYRET et al. 2018).

En ce qui concerne les caractéristiques des communautés d'adventices, je montre que le type de culture annuelle a un effet important sur la richesse spécifique des herbacées : les champs de riz comportent en moyenne plus d'espèces que les autres. La biomasse végétale et la densité de plantes sont plus faibles dans les plantations d'hévéa matures que dans les plantations de jeunes hévéa ou dans les champs sans arbres. En moyenne, les richesses spécifiques observées sont semblables à celles rapportées dans d'autres contextes agricoles en Thaïlande, bien que la richesse spécifique observée sous hévéa matures en particulier soit beaucoup plus faible que celle décrite ailleurs (SHRESTHA et al. 2010). Les biomasses observées, en revanche, sont beaucoup plus élevées dans notre site d'étude, probablement du fait de différences de pratiques et de période d'échantillonnage (SHRESTHA et al. 2010). La densité d'adventices, tout comme leur biomasse, augmente avec la richesse spécifique. Concernant les caractéristiques du sol, les densités de sol observées sous plantations d'hévéa (1.22 g cm^{-3}) sont légèrement supérieures ou similaires à celles décrites dans d'autres plantations (de BLÉCOURT et al. 2013; GUILLAUME et al. 2016). Les sols sous plantations matures d'hévéa sont plus humides que dans les cultures, mais le type d'usage du sol n'a pas d'impact significatif sur les autres caractéristiques du sol. L'humidité du sol est corrélée à la densité d'adventices dans les champs de riz, mais anti-corrélée avec la densité dans les champs sans culture annuelle en saison sèche. D'autres interactions entre les propriétés physico-chimiques du sol et les adventices sont apparues, telles qu'une corrélation entre les taux de carbone et d'azote et la biomasse végétale. Ceci montre une augmentation du taux de matière organique du sol, et donc de sa cohésion et de sa résistance à l'érosion, lorsque le couvert adventice est élevé. Cependant ces relations ne sont pas significatives lorsque la corrélation spatiale entre les observations était prise en compte.

LA DIVERSITÉ DES ADVENTICES AUGMENTE AVEC LE NOMBRE DE CHANGEMENTS D'USAGE DES SOLS

Dans les agroécosystèmes tempérés, l'intensification agricole a fortement affecté la diversité, la composition et l'abondance des communautés d'adventices, en favorisant les espèces les plus semblables aux cultures (SQUIRE et al. 2000; FRIED et al. 2015). Ces modifications menacent le maintien des multiples services écosystémiques assurés par les adventices. Diverses études ont montré que la diversification des séquences culturales permet d'améliorer le contrôle des adventices tout en favorisant leur biodiversité (LIEBMAN et DYCK 1993; ULBER et al. 2009); cependant, ces études dans les agroécosystèmes tempérés s'attachent principalement à décrire l'effet de différents types de rotations, plutôt que la diversité temporelle des cultures en elle-même. Dans ce chapitre, je quantifie l'effet de la diversité temporelle de l'usage des sols pendant les trois années précédant l'échantillonnage, calculée soit comme le nombre de cultures observées dans un champ, soit le nombre de changements de culture. À ma connaissance, cette étude est la première à tester

l'effet de la diversité temporelle sur les adventices (herbacées et buissons ou arbres) en Asie du Sud-Est et à partir d'observations.

Les séquences culturelles observées à Huai Lang sont très variables, et dépendent à la fois de facteurs de gestion (par exemple liés à l'infestation par les adventices) et socio-économiques (e.g. prix du maïs, nécessité de planter du riz pour consommation familiale). Le riz n'est jamais cultivé plus de deux ans de suite tandis que certains champs présentent une culture quasi continue de maïs. Je montre qu'en saison sèche, la richesse spécifique et la diversité des herbacées augmentent avec le nombre de changements de cultures. Ceci coïncide avec une diminution de la dominance des espèces les plus abondantes, qui représentent une moindre part de la communauté dans les champs temporellement diversifiés. Ces effets sont aussi observés, quoique plus faiblement, lorsque la diversité temporelle est calculée comme le nombre de cultures. En revanche, ni le nombre de cultures ni le nombre de changements d'usages du sol n'ont d'effet sur la richesse et la diversité des buissons et arbres, ni sur la biomasse végétale ou la densité de plantes. Enfin, le nombre de cultures (mais non le nombre de changements) a un effet significatif, quoique faible, sur la composition des communautés, avec quelques espèces fortement associées avec les champs les plus divers temporellement sur la période donnée.

Ces résultats montrent qu'une fréquence élevée de perturbations, ainsi qu'une variabilité temporelle importante des conditions de germination et de croissance (e.g. date de semis, ombre fournie par la culture, etc.) augmentent la diversité spécifique des adventices (GABA et al. 2013; COLBACH et al. p. d.). En revanche, ces facteurs ne modifient pas leur abondance. Ceci peut s'expliquer par le fait que la biomasse et la densité végétale dépendent principalement des espèces ultra-dominantes et très bien adaptées à une culture donnée.

EFFETS RELATIFS DU PAYSAGE, DU SOL, DE L'USAGE DU SOL ET DE COMPOSANTES SPATIALES SUR LES COMMUNAUTÉS ADVENTICES

La composition d'une communauté végétale dans un milieu donné dépend à la fois de facteurs environnementaux tels que le climat, mais aussi de facteurs locaux biotiques ou abiotiques (HYVÖNEN et al. 2011). D'autre part, si l'on considère un écosystème dans sa globalité, une communauté n'est pas isolée mais en relation avec d'autres communautés, via la dispersion d'espèces d'une communauté à l'autre : elles forment des méta-communautés (LEIBOLD et al. 2004). Dans un contexte agricole, les communautés d'adventices dépendent non seulement du type de sol ou de l'usage du sol (CARDINA et al. 2002; FRIED et al. 2008) mais également du paysage alentour, c'est-à-dire de la composition et de la configuration des différents habitats voisins (GABRIEL et al. 2005), qui conditionnent la dispersion des espèces et donc la structure des méta-communautés. En milieu agricole tempéré, il a été montré que la complexité du paysage était en général favorable à la diversité végétale (GABRIEL et al. 2005; GABA et al. 2010). Dans ce chapitre, je quantifie les impacts relatifs du paysage, du sol, de l'usage du sol et de composantes spatiales (décrites comme une combinaison des coordonnées spatiales) sur la richesse et la composition des

communautés d'adventices à Huai Lang, où le paysage est beaucoup plus fragmenté et hétérogène que dans les agroécosystèmes habituellement étudiés.

À partir d'analyses de partition de variance, je montre que le sol a un effet assez restreint sur les communautés adventices. Le paysage, en revanche, est l'un des principaux facteurs déterminant la composition et la richesse des communautés herbacées et ligneuses, ainsi que la biomasse végétale. En particulier, l'hétérogénéité du paysage (quantifiée par exemple par la taille du champ étudié ou par la variabilité de la végétation dans une zone circulaire de 200 m de rayon autour du champ) a un effet positif sur la richesse spécifique des espèces herbacées et sur leur biomasse. Cependant, cet effet n'est pas indépendant mais plutôt joint avec celui d'autres variables explicatives, en l'occurrence avec l'effet du type d'usage du sol et des composantes spatiales, respectivement. Je montre enfin que les mécanismes de tri d'espèce et d'effet de masse sont les principaux processus de métacommunauté caractérisant les communautés d'adventices étudiées.

Ces résultats sont cohérents avec le concept de mosaïque proposé par DUELLI (1997), qui propose que la diversité végétale augmente avec la variabilité des habitats dans les agroécosystèmes. En particulier, il semble que certains habitats semi-naturels agissent comme des réserves d'espèces (FRIED et al. 2009), permettant le maintien d'espèces peu adaptées aux pratiques agricoles dans le paysage.

IMPACT DE L'AFFORESTATION PAR L'HÉVEA SUR LE RUISSELLEMENT ET LE DÉTACHEMENT DU SOL

L'Asie du Sud-Est est particulièrement vulnérable à la dégradation du sol, en raison de changements rapides d'usage des sols et de conditions climatiques adverses, en particulier en termes d'érosivité des pluies (BORRELLI et al. 2017; PANAGOS et al. 2017). L'expansion des plantations d'hévéa dans les régions montagneuses a été encouragée afin d'augmenter les revenus des petits exploitants et de reforester des environnements dégradés. Son effet réel sur l'érosion du sol est fortement contesté. La plupart des études, à ce jour, comparent les plantations d'hévéa à des forêts ou à d'autres plantations d'arbres, mais peu d'études existent qui estiment l'impact du remplacement des cultures annuelles par des plantations d'hévéa sur l'érosion du sol. Dans ce chapitre, je présente les résultats de deux études menées à Huai Lang à partir de plots d'érosion de 1 m².

La première étude présentée dans ce chapitre avait pour objet d'estimer les effets de différentes variables météorologiques (énergie cinétique, cumul de pluie), des caractéristiques de surface, et du type d'usage du sol sur le ruissellement et le détachement de sol. Mes résultats indiquent que les plantations d'hévéa adultes produisent entre 10 et 30 fois plus de ruissellement que les champs de maïs ou les jeunes plantations d'hévéa avec culture en inter-rang. Ceci s'accompagne de taux de détachement du sol très élevés, probablement liés à une dégradation intense de la surface du sol. Ces résultats sont explicables par la proportion élevée de sol nu en fin de saison pluvieuse sous les plantations d'hévéa adultes.

Au vue de ces résultats, j'ai donc testé lors de la seconde expérience l'effet du couvert végétal sur le ruissellement sous plantations d'hévéa adultes. Bien que le traitement par herbicides n'ait que partiellement réussi en raison de difficultés de terrain, mes résultats montrent que l'exclusion d'herbicides pourrait permettre de

limiter le ruissellement d'environ 20 % à 30 %. En outre, à cumul de pluie donné, le coefficient de ruissellement diminue progressivement lorsque le couvert végétal augmente.

Ces résultats sont cohérents avec de précédentes études, qui montrent que l'afforestation par des plantations d'arbres (de teck notamment) peut fortement augmenter les risques d'érosion en Asie du Sud-Est (RIBOLZI et al. 2017; PATIN et al. 2018). Ce chapitre souligne l'importance de faire évoluer les pratiques de gestion des plantations d'hévéa pour favoriser la protection du sol en zone montagneuse.

CONCLUSION

Cette étude multidisciplinaire a mis en évidence des relations originales entre les adventices, les pratiques agricoles et le sol. L'agroécosystème observé à Huai Lang est en transition entre plusieurs modèles agricoles - depuis le système "traditionnel" basé sur le riz pluvial, vers des systèmes plus "modernes" de cultures annuelles ou pérennes de rente. Réaliser des observations en champs réels a parfois complexifié l'interprétation des résultats, principalement à cause du manque de données fournies par les agriculteurs concernant leurs pratiques agricoles. Cela m'a toutefois permis de bien caractériser les communautés d'adventices rencontrées par les agriculteurs dans l'agro-écosystème étudié, ainsi que leurs interactions avec le sol.

Malgré les différences pédo-climatiques, agraires, biotiques, et les différentes structures de paysage observées à Huai Lang par rapport à certains agroécosystèmes tempérés plus étudiés, mes résultats montrent que des mécanismes similaires déterminent les communautés adventices. La variabilité temporelle et spatiale des usages des sols y a un effet fort sur les communautés, et semble favoriser leur diversité. L'évolution des pratiques agricoles vers une utilisation plus faible d'intrants est peu probable sur le court-terme : en effet, le manque de main-d'œuvre rend impossible le désherbage uniquement manuel des cultures annuelles. Cependant, mes résultats suggèrent que privilégier d'autres éléments du système, par exemple en maintenant des rotations diversifiées et le caractère très fragmenté du paysage, pourrait favoriser un maintien de la diversité des adventices - et donc de leurs services écosystémiques.

Les plantations d'hévéa ont non seulement un effet direct sur la composition des communautés adventices et l'érosion du sol, mais leur expansion risque également de conduire à l'homogénéisation spatiale (plantations de grande taille, homogènes) et temporelle (plantation pérennes) du paysage. Bien que les pratiques de désherbage, notamment, soient encore très variables d'une plantation à l'autre - probablement du fait de l'introduction récente des hévéas dans la région - une stabilisation de ces pratiques vers celles qui visent à supprimer le couvert du sol pourrait conduire à de sévères dégradations du sol et de la biodiversité. Cependant, cette instabilité dans les pratiques de gestion pourrait aussi être une opportunité pour les faire évoluer de manière positive pour l'environnement, en particulier en favorisant le couvert végétal naturel. Il n'existe en effet pas d'indication de compétition entre les hévéas matures et un couvert herbacé. La mise en place de ces pratiques nécessiterait des études à la fois écologiques et socio-économiques en

coopération avec les agriculteurs locaux pour pouvoir comprendre les différentes contraintes qui conditionnent la gestion des plantations d'hévéa.

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INTRODUCTION

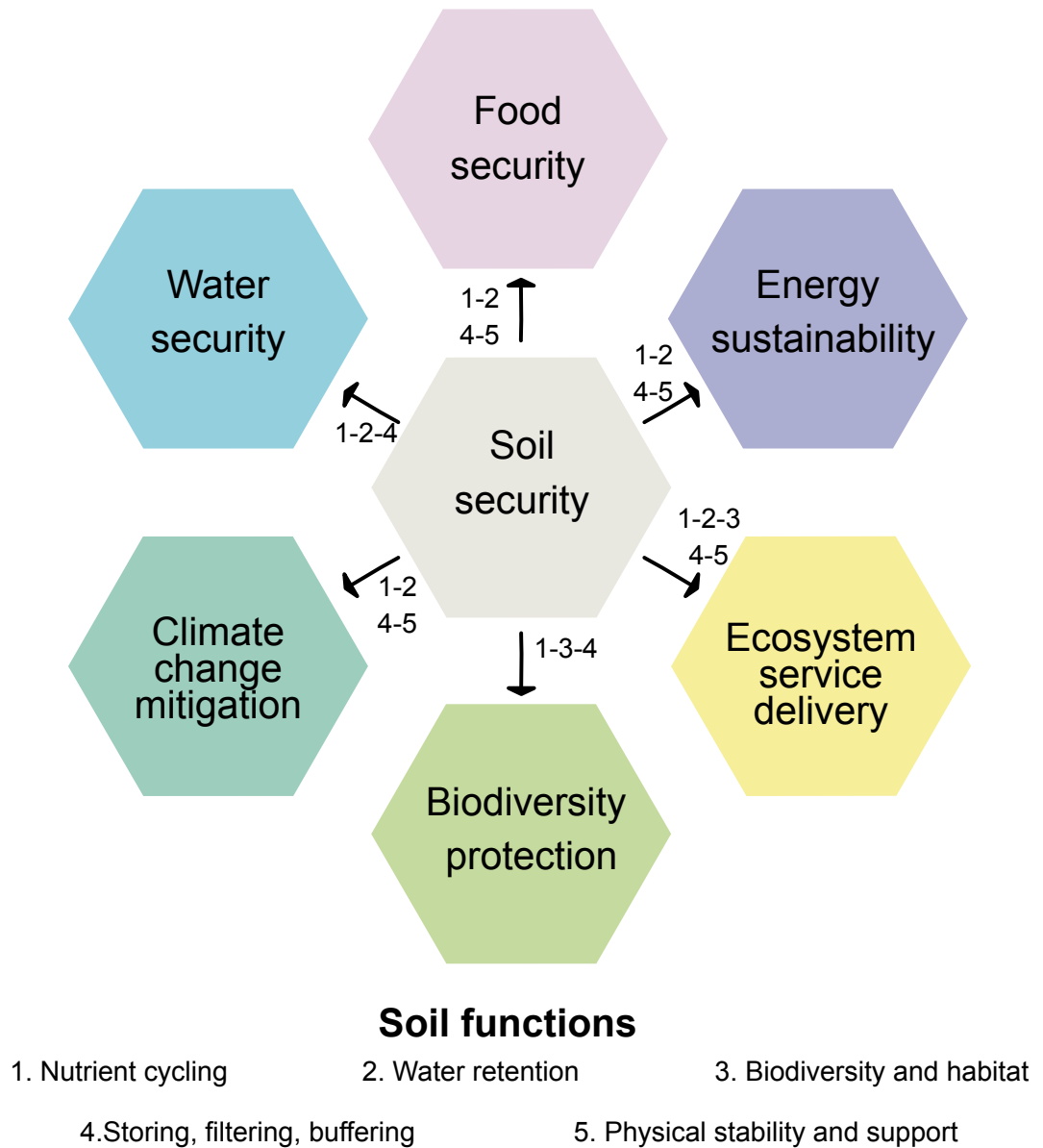
The objective of this Ph.D. was to investigate the effects of land use change in mountainous northern Thailand on non-cultivated plant diversity and soil conservation, as well as the interactions between weeds and soil erosion. In the first part of this chapter, I describe the context of agricultural intensification and its impact on soil security. I then show that weed communities, strongly affected by this intensification, could provide various ecosystem services and mitigate environmental degradation. I finally characterise more particularly the agrarian transition ongoing in Southeast Asia, with the specific environmental concerns raised by the expansion of rubber tree plantations.

1.1 SOIL SECURITY IN THE CONTEXT OF AGRICULTURAL INTENSIFICATION

In 2012, the UN Rio+20 conference on sustainable development acknowledged the importance of soil conservation and sustainable land management, stressing its key contribution to "economic growth, biodiversity, sustainable agriculture and food security, eradicating poverty, women's empowerment, addressing climate change and improving water availability" (United Nations 2012). Following this recognition, the Sustainable Development Goals pledged to "protect, restore and promote sustainable use of terrestrial ecosystems [...] and halt and reverse land degradation and halt biodiversity loss" (Sustainable Development Goal 15). Land degradation impacts directly several other Sustainable Development Goals regarding food production, health, climate change mitigation and the protection of biodiversity (Vlek et al. 2017). Ensuring soil security by maintaining its functionality and resilience capacities is thus a major element of the global challenges of sustainable development: food and water security, climate change mitigation, ecosystem service provision, biodiversity protection, and energy sustainability (Fig. 1.1, Koch et al. (2013) and McBratney et al. (2014)).

The global "soil crisis" (Koch et al. 2013) encompasses diverse forms of soil degradation. Some, such as erosion, acidification, salinisation or compaction, are natural processes that are accelerated by inappropriate land use or land clearing. Others are purely anthropogenic and include soil pollution and "soil sealing", i.e. the expansion of paved urban areas over high-quality agricultural soils (Koch et al. 2013). **Here I focus on the threats to soil security specifically related to land use change and land use intensification.**

Figure 1.1: Major societal challenges affected by soil security (adapted from Koch et al. (2013)). Each of these challenges depends on the provision of different soil functions. For instance, food security relies on the possibility to grow food in sufficient quantity and quantity (i.e. depending on nutrient cycling, water retention, and soil physical support) and on the mitigation of contamination (which depends on the filtering and buffering functions of the soil).



In both temperate and tropical areas, agricultural intensification can be described as two concomitant processes resulting in an increase of yield or income per unit of land surface. Firstly, intensification is based on the transition from the use of local resources (e.g. manure, own seeds) to the dependence on external inputs, such as fertilisers, herbicides, commercial seeds or irrigation (Matson et al. 1997). This, in turn, allows the transition from subsistence systems, in which farmers produce for their own consumption, to market-based systems in which the farmers' objective is to build an income by selling their product. In order to fulfil this objective, the transition to cash crops is usually accompanied by a focus on high-yield varieties and a shortening of crop rotations (Matson et al. 1997). In areas where the terrain and financial investments allowed it, the mechanisation allowed an increase of the size of fields and farms, progressively leading to a loss of semi-natural habitats (field borders, hedges) and a homogenisation of agricultural landscapes (Baessler and Klotz 2006). Together with the rapidly expanding cultivated areas, agricultural intensification led to a massive rise in crop yields and food production over the past 70 years, although this growth is now much slower and, for many crops, a recession of the yields appeared in the recent years (FAO 2019). In developing countries, this intensification started approximately in the 1960s as the "Green Revolution" and provided considerable advances in terms of food security. **In this manuscript, I specifically focus on a modern agricultural system of Southeast Asia which largely relies on modern crop varieties and high external inputs, but is mostly constituted of smallholders and still includes remnants of subsistence farming with traditional varieties.**

However, the negative environmental impacts of agricultural intensification have now been largely recognised (Tilman 2001). These impacts stem at various levels, from the field scale (increased erosion, lower soil fertility, and reduced biodiversity) to the regional (water pollution and eutrophication of rivers and lakes) and global scales (Matson et al. 1997). In terms of soil security, agricultural intensification often decreases soil organic matter content and fertility, promotes soil structure degradation and erosion (de Rouw and Rajot 2004). The diversity of farmland birds and arthropods has been strongly impacted (Benton et al. 2003; Devictor and Jiguet 2007). For instance, Donald et al. (2001) showed that cereal yield alone, which almost tripled between 1960 and 2000 and is closely correlated with fertilizer use, could be used as an indicator to predict over 30% of the decline of European bird populations. Similar trends have been observed for weed biodiversity.

1.2 WEEDS IN THE AGROECOSYSTEM

1.2.1 *Weeds as crop pests*

Weeds represent all the non-cultivated (or unintentional) plants found in an agricultural field. They are one of the major factors of yield loss worldwide: Oerke (2006) for instance estimated that weeds represented the highest potential yield loss among major crops (on average 34% in wheat, maize, rice, potatoes and cotton), before pathogens or animal pests. By competing with crops for nutrients, light and water, weeds directly decrease yield quantity. They might also have indirect effects by decreasing yield quality (e.g. when weed seeds contaminate a harvest,

Le Bourgeois and Marnotte (2002)) or by hosting crop pathogens. Weed control historically involved labour-intensive manual or mechanical weeding practices. The introduction of herbicides in the early 1900s, and their development in the following decades, drastically changed agricultural production systems (Oerke 2006), notably through the reduction in labour time spent on weeding. In areas where demographic pressure caused the shortening of fallow periods, or where tillage caused intense soil degradation, herbicides were perceived as an effective alternative for weed management (Saito et al. 2006; de Rouw et al. 2013; Odhiambo et al. 2015). Herbicides are now seen as essential in maintaining current crop yields.

However, recent studies have challenged the necessity of maintaining the current levels of herbicides. For instance, Gaba et al. (2016) found no relationship between herbicide application rates and crop yield in winter wheat fields. In a meta-analysis, Hossard et al. (2016) showed that low-input systems, using lower fertiliser and herbicide input, had only slightly lower yields than conventional systems. Such findings, altogether with the growing recognition of, on the one hand, the severe effects of agricultural intensification on weeds and, on the other hand, the importance of weed diversity and weed ecosystem services to the functioning of agroecosystems, question the existing dichotomy between weed control and biodiversity conservation (Storkey and Neve 2018). In the following paragraphs, I describe the severe effects on weed communities caused by agricultural intensification, before developing on the importance of weed diversity and ecosystem services.

1.2.2 *The effect of agricultural intensification on weeds*

Most studies focusing on the response of weeds to land use changes have been conducted in Europe, where the intensification and homogenisation of agricultural landscapes led to a drastic decrease in plant diversity (Matson et al. 1997; Foley et al. 2004; Andreasen and Stryhn 2008; Kleijn et al. 2009). In some cases, a local increase of weed diversity was found due to the local occurrence of very rare species, but this was usually associated with a decline of the regional species pool (Baessler and Klotz 2006; Scursioni et al. 2014). This decline in weed species diversity has been attributed to simpler rotations, loss of semi-natural habitats and increased fertiliser and herbicides use (Pyšek and Lepš 1991; Storkey et al. 2012; Storkey and Neve 2018). Storkey et al. (2012) showed that in Europe, species that were specialist to a single crop were particularly vulnerable, while generalist species, in some cases herbicide-resistant and particularly competitive to crops, thrived (Baessler and Klotz 2006; Edesi et al. 2012). Yet, besides the conservation value of biodiversity for its own sake, maintaining weed diversity is important in order to ensure the maintenance of ecosystem functioning.

1.2.3 *Weed diversity and ecosystem services*

Diverse plant communities are indicative of the wider sustainability and resistance to stress of the cropping system (Chen et al. 2004; Storkey and Neve 2018). Besides, diversity promotes the complementary occupation of the ecological niche and better use of the resource pool (Tschardt et al. 2005), which is thought to decrease the competitiveness of weed communities towards the crop (Storkey and Neve 2018). According to the insurance hypothesis, even when species have similar traits or

functions, this redundancy is expected to provide a higher capacity for ecosystem resilience and recovery after a disturbance (Loreau et al. 2003; Tscharrntke et al. 2005).

1.2.3.A Weeds support biodiversity at higher trophic levels

In many agroecosystems, weeds represent the main source of plant biodiversity. They are the primary producers at the basis of the agroecosystemic food web. They promote biodiversity at higher levels by providing food and habitats to earthworms, ants, pollinators, farmland birds, and mammals (Marshall et al. 2003; Franke et al. 2009; Petit et al. 2011). Diverse plant communities provide food sources during extended periods (Edesi et al. 2012) and promote large and rich populations of pollinators necessary to the cultivation of arthropod-pollinated crops (Bàrberi et al. 2010). Weeds also play a role in the regulation of crop pests. They may have a negative impact on the agroecosystems when they benefit harmful insects or disease vectors (Franke et al. 2009), but they can also provide alternative food sources for pest predators, or act as "pest traps" and prevent pests from completing their life cycles (Bàrberi et al. 2010). Petit et al. (2011) highlighted that while weeds have strong interactions to multiple other organisms, these relations are often species-specific. Thus, the actual functions delivered by a given weed community will be highly dependent on its composition and diversity.

1.2.3.B Weeds support soil conservation

Plants enhance both the resistance and resilience of soils (Seybold et al. 1999). Soil resistance is defined as its capacity to maintain its functions, e.g. sustaining biological diversity, regulating water flow, detoxifying and storing nutrients. Soil resilience is its ability to recover its functional and structural integrity after a degradation. After a degradation, plants enhance both the speed and extent of the recovery: litter accumulation allows the restoration of surface conditions favourable to infiltration and promotes soil biological activity, which is essential to most of the recovery mechanisms including nutrients cycling, detoxification, and structure stabilisation (Seybold et al. 1999).

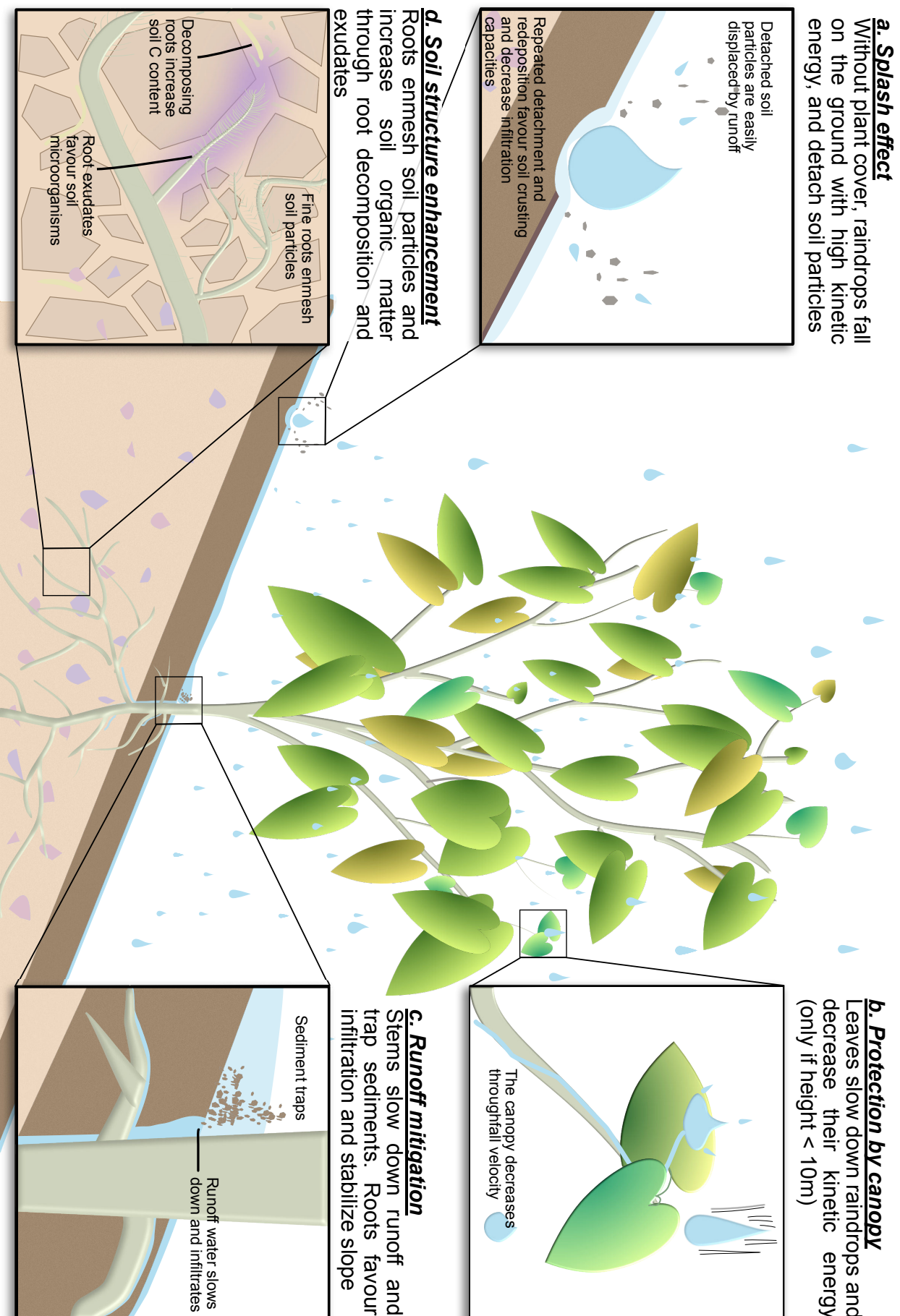
One of the most common forms of soil degradation, and the focus of this study, is soil erosion due to water. Water erosion can be separated into three different steps.

SPLASH EROSION. The kinetic energy of falling raindrops and slaking causes soil aggregates to break down into smaller, more easily transportable particles (Fig. 1.2a.).

SHEET EROSION. The detached particles are carried downslope by water that flows over the soil surface. These water sheets can also further detach soil particles when they flow overland sufficiently rapidly. Together with splash erosion, this process also causes soil crusting that further impedes water infiltration.

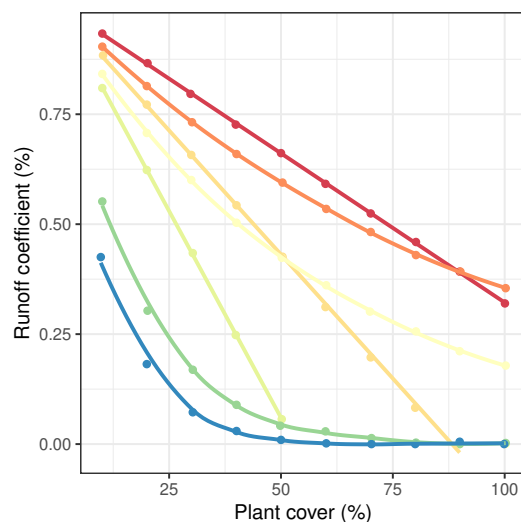
RILL OR GULLY EROSION. Where the slope is steep or long, runoff tends to concentrate and leads to the creation of small, temporary streams of water (rills) that can then converge into deeper, more permanent and highly erosive gullies.

Figure 1.2: Soil erosion mitigation by plant cover.



Plants significantly mitigate these different processes through their aerial and root systems (Fig. 1.2). If close to the ground, the plant canopy decreases the kinetic energy of raindrops and reduces the intensity of splash erosion, responsible for the detachment of soil particles (Fig. 1.2a, b.). At the inter-rill level, plant aerial parts increase soil surface roughness, slow down overland flow and trap sediments (Fig. 1.2c., Chau and Chu (2017)). Roots also have a decisive impact on soil structure. They favour the formation and stability of soil aggregates by direct enmeshment of soil particles. They participate to soil organic matter pool through litter and plant roots turnover, root exudates, rhizodeposition, and by supporting active macro- and microfaunal communities, overall increasing soil stability (Fig. 1.2d., Durán Zuazo and Pleguezuelo (2008) and Fattet et al. (2011)). Plant roots also increase soil shear strength (Gyssels et al. 2005) and stabilise slopes (Stokes et al. 2008; Stokes et al. 2009). This results in very significant mitigation of soil erosion: Durán Zuazo and Pleguezuelo (2008) estimated that in most environments, the relationship between runoff coefficient and soil cover can be described as a negative exponential curve, and more rarely as a linear decrease (Fig. 1.3).

Figure 1.3: The relationship between soil cover and runoff coefficient follows a linear or negative-exponential curve (adapted from Durán Zuazo and Pleguezuelo (2008)). Each colour line reports results from one study reviewed by Durán Zuazo and Pleguezuelo (2008).



Not all plants species, however, provide the same level of soil protection. Perennial herbaceous species, on the one hand, provide year-round soil cover, improve soil structure and organic matter, and overall reduce water runoff and soil detachment at small scale; woody crops, on the other hand, physically stabilise slopes and protect the soil through raindrops interception and litter accumulation (Durán Zuazo and Pleguezuelo 2008). Some traits, such as the leaf area index, root area ratio, root density, proportion of fine roots, and canopy density were found to be highly correlated with the erosion-reducing potential of plants (Burylo et al. 2012a; Burylo et al. 2012b; Chau and Chu 2017). As a result, diverse weed communities are likely to enhance erosion mitigation: diverse root growth forms, for instance, have been shown to increase soil protection (Beierkuhnlein & Jentsch, 2005 in Shrestha et al. (2010)).

Few studies investigated the role of weeds, specifically, on erosion mitigation in agricultural contexts. Among them, Liu et al. (2016) showed that herbicide application under rubber tree plantations increased soil detachment by a factor 8. Podwojewski et al. (2008) also found a negative correlation between weed cover and annual soil detachment and runoff at the 1 m² scale in northern Vietnam, while Chen et al. (2004) showed that soil erosion in orchards decreased with increasing richness of naturally occurring plants. **In the second chapter of this manuscript, I investigate the relationships between weed communities and soil physicochemical characteristics. I also quantify the effect of weed cover on soil erosion in the second part of the fifth chapter.**

1.2.4 *Spatial and temporal land use diversity to promote weeds diversity*

One of the solutions proposed to counter the negative effects of agricultural intensification on biodiversity and to support weed ecosystem services is the spatial and temporal diversification of agricultural areas. A diversified farming system is defined as a "system of agricultural production that, through a range of practices, incorporates agrobiodiversity across multiple spatial and/or temporal scales" (Kremen and Miles 2012). These systems involve practices at different scales, from the plot level (e.g. intercropping) to the field (e.g. crop rotations) and landscape scales (e.g. riparian corridors, natural areas). Before being replaced by highly simplified monocultures, they were very common in farming systems worldwide (Tscharntke et al. 2005; Kremen and Miles 2012). The farming system I studied during this project cannot be directly classified as a diversified farming system, because this term is usually constrained to systems in which the diversification is intentional, which is not certain here. However, the framework of these diversified farming systems provides a basis to understand and interpret the effects of temporal or spatial variability in the studied agroecosystem.

Complex landscapes favour plant diversity, both locally and regionally (Baessler and Klotz 2006; Kremen and Miles 2012; Liebman and Schulte 2015; Petit et al. 2016). For instance, Gaba et al. (2010) showed that weed diversity decreased with field size and increased with the number of fields within 200 m. Indeed, complex landscapes present higher densities of field borders that provide habitats to species that are sensitive to agricultural practices (Fried et al. 2009) and act as seed reservoirs for the adjacent fields. Crop temporal diversification also supports the maintenance of diverse plant communities: crop rotations, as opposed to continuous monocultures, are known to improve soil health and fertility. Various studies have proposed to implement more diverse crop rotations to favour weed communities diversity while decreasing their ability to compete with the crop (Liebman and Dyck 1993; Doucet et al. 1999; Squire et al. 2000; Ulber et al. 2009). This is because different land uses provide different growing conditions for weeds, and might promote more diverse soil resource pools (Smith et al. 2010).

To my knowledge, the literature reports very few studies about crop rotations effects on weed diversity in Southeast Asian agricultural systems (but see Jiang et al. (2016)), or about the effect of landscape characteristics on weeds in these relatively heterogeneous habitats. **In Chapters 4 and 5 of this manuscript, I investigate the effects of land use temporal diversification on the one hand, and landscape**

composition and configuration, on the other, on weed communities composition and diversity.

1.3 AGRICULTURAL INTENSIFICATION AND LAND USE CHANGE IN SOUTHEAST ASIA

1.3.1 *Southeast Asia, a hotspot of environmental degradation*

Southeast Asia is doubly exposed to land degradation, due to extreme meteorological conditions and to rapid changes of land use. Oldeman et al. (1991) classified all Southeast Asia as having medium to high land degradation rates due to water erosion. Indeed, as in many tropical areas, soil conservation in Southeast Asia is particularly imperilled by adverse meteorological conditions: for example, the Global Rainfall Erosivity Database classifies the area as one of the regions with the highest rainfall erosivity ($> 7400 \text{ MJ ha}^{-1} \text{ yr}^{-1}$, Panagos et al. (2017)). In 2002, the GLASOD estimated that 18% of Asian lands had been degraded by humans (ISRIC 2012). More recently, Borrelli et al. (2017) found that soil erosion rates in most of Southeast Asia were increasing quickly ($>5\%$ each year) due to very high rates of land use change. Indeed, in recent decades, economic development in mountainous Southeast 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 Southeast Asia they have occurred at an unprecedented scale, threatening biodiversity and environmental resources (Rerkasem et al. 2009; Fox et al. 2014).

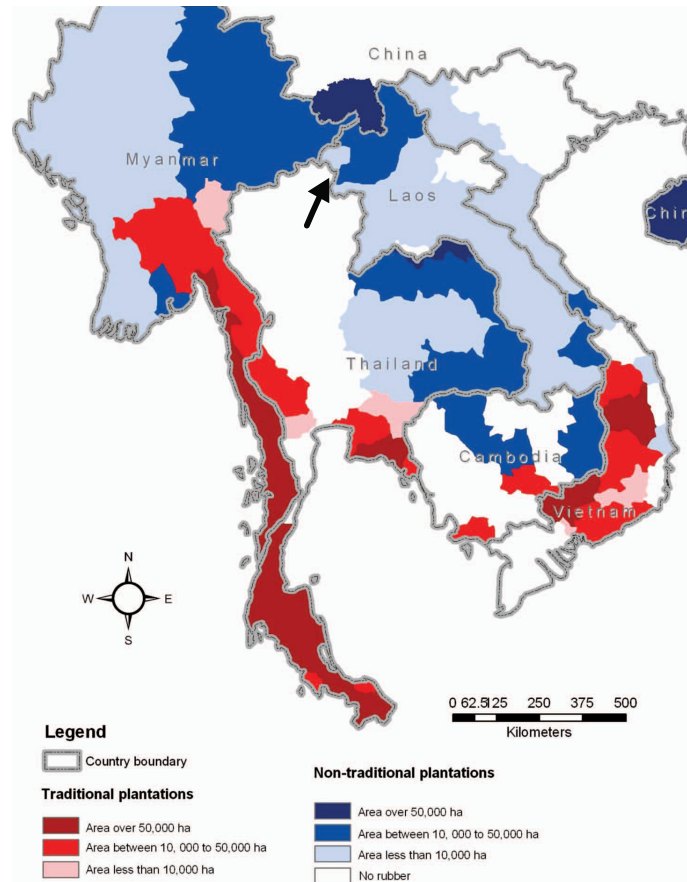
1.3.2 *Land use changes in uplands of northern Thailand: socio-economic context*

The mountainous region of Southeast Asia, defined as the land above 300 m, covers approximately one half of the combined surfaces of Myanmar, Thailand, Laos, Vietnam, and Yunnan province (China). Historically occupied by species-rich evergreen/deciduous forests (Gardner et al. 2000), it is considered to be a hotspot of biodiversity (Sodhi et al. 2004). The flat valleys in this areas have long been cultivated as paddies. However, a rapid demographic and economic growth led to progressive deforestation and to the expansion of subsistence crops into the hillslopes, rapidly followed in the 1970s by market-oriented agriculture based on continuous monocultures of commercial crops (Fox and Vogler 2005). The expansion of agriculture into previously forested areas led to intense environmental degradation (Wangpakapattanawong et al. 2016). It had strong impacts on insect, bird, mammal and plant biodiversity (Sodhi et al. 2004; Wilcove et al. 2013) but also on soil conservation, with increased surface runoff, erosion (Valentin et al. 2008; Mohammad and Adam 2010) and soil organic carbon losses (Häring et al. 2014). Maize and cassava cultivation systems were found to be particularly prone to soil erosion (Valentin et al. 2008).

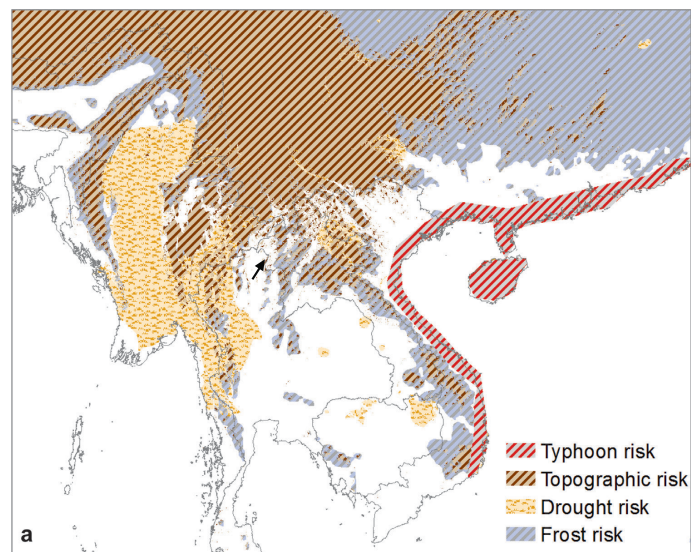
Thus, more recently, governments and international organisations and programmes such as UNCCD and REDD+ encouraged the replacement of annual cash crops by perennial cash crops, such as teak or rubber trees, in order to increase

Figure 1.4: Rubber tree expansion in Southeast Asia. a. Traditional and non-traditional rubber growing areas in Southeast Asia (Fox and Castella 2013) and b. associated risks (Ahrends et al. 2015). Note that my study site (black arrow) is in a particularly marginal area that was considered in none of these two studies.

(a) Extracted from Fox and Castella (2013).



(b) Extracted from Ahrends et al. (2015).



farmers' income and to expand tree cover in the uplands. It was expected that the replanting of trees in degraded areas would increase carbon stocks and restore favourable soil conditions and water resources.

1.3.3 *Rubber tree expansion in Southeast Asia*

The Para rubber tree *Hevea brasiliensis* is a deciduous, monoecious tree reaching a height of 30 m to 40 m in the wild and of approximately 15 m in cultivation (Boer and Ella 2000). After an establishment phase of about two months during which it is relatively vulnerable to competition by weeds, the young saplings go through a phase of rapid vegetative growth for approximately 4 to 5 years before they start flowering. Intercropping maize or rice under young trees during the first four years after planting (i.e. before the shade from the canopy prevents it) is common among smallholders, as it provides income during the immature phase of the trees without affecting their growth. Intercropping with legumes (*Mucuna sp.*, *Pueraria sp.*) is most common in large plantations to improve soil fertility (Gelder 1950; Boer and Ella 2000).

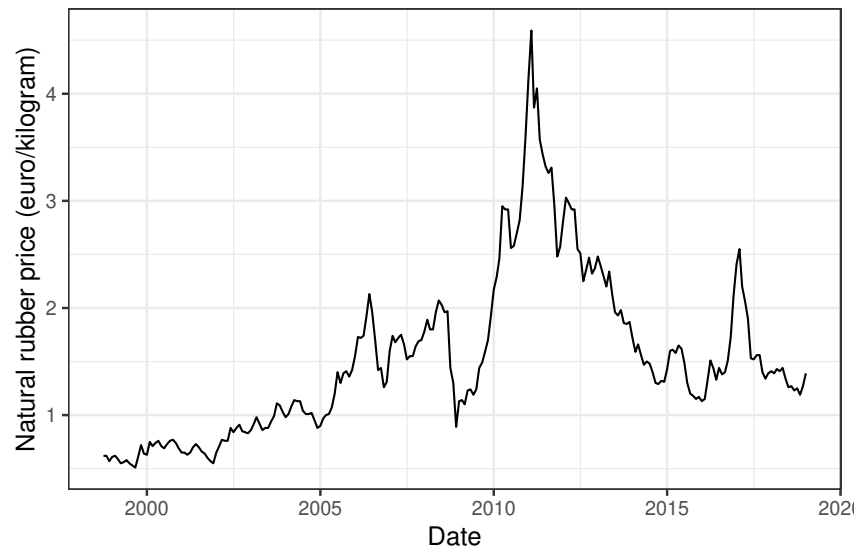
Rubber tree was first introduced in Southeast Asia from South America in 1876. It was traditionally grown in the equatorial zone between latitudes of 10 °N and 10 °S, such as in Malaysia or Indonesia. Extensive research allowed the expansion of rubber tree plantations into marginal areas with cooler climate and a distinct dry season (up to 27 °N latitude and up to 1 100 m above sea level, Fox and Castella (2013)). The traditional planting areas have been progressively replaced by oil palm plantations (which are strictly limited to humid-tropical areas) and rubber tree cultivation has extended into continental Southeast Asia, usually as monocultures (Fox and Castella 2013). Today, Southeast Asia provides 97 % of the global natural rubber production, with Thailand producing the largest amount, i.e. 31 % of the total production. Rubber tree is now being planted beyond its natural range (Fig. 1.4a), which severely threatens the sustainability of the plantations due to risks of frost, drought or typhoons (Fig. 1.4b, Ahrends et al. (2015)).

Besides, most rubber tree growers are smallholders who switched to rubber tree cultivation at the expense of food crops (Fox and Castella 2013; Ahrends et al. 2015): in Thailand, 95 % of the rubber is produced by smallholders, and these proportions reach about 80% and 85% in Indonesia and Malaysia, respectively. They are particularly vulnerable to the high volatility of natural rubber price, which responds to short-term imbalances of supply and demand in industrial countries (Boer and Ella 2000). The price for natural rubber is currently 70 % lower than at its peak in 2011, which severely endangers the socio-economic sustainability of this system (Fig. 1.5, Index mundi (2019)).

1.3.4 *Rubber tree plantations and the environment*

While one of the justifications for the expansion of perennial monocultures was environmental restoration and afforestation, its actual impact on the environment is far from consensual. Here I summarise previous findings on the effects of rubber tree plantations and other tree plantations on hydrological regimes, biodiversity and soil conservation.

Figure 1.5: Monthly natural rubber price from 1989 to 2019. Prices are for Singapore Commodity Exchange, No. 3 Rubber Smoked Sheets (RSS3) (Index mundi 2019).



The large-scale expansion of rubber tree plantations disturbs hydrological regimes and modifies local microclimates (Fox et al. 2014; Ahrends et al. 2015). Guardiola-Claramonte et al. (2010), considering vegetation dynamics and rubber tree evaporative demand, showed that rubber trees acted as "water pumps" and generated higher water losses than natural forest vegetation. This led to a decrease in basin water discharge or storage, especially during the refoliation period that happens in February, at the driest period of the year in northern Thailand. Moreover, the conversion of secondary forests to rubber tree plantations also has large impacts on biodiversity (He and Martin 2015). Rubber tree plantations strongly decrease insect (Li et al. 2013), bird (Aratrakorn et al. 2006; Beukema et al. 2007), bat (Phommexay et al. 2011) and plant diversity (Beukema et al. 2007) compared to natural forests. They also strongly affect soil biodiversity (Brauman et al. 2014; Thoumazeau et al. 2019).

One of the main impacts of tree plantations is their effect on soil degradation. Early studies found that clean-weeded rubber tree plantations caused very high amounts of soil degradation on flat terrains (Swart 1921). Various studies found that in mountainous areas, tree plantations increased overland flow and sediment loss (Ribolzi et al. 2017) and overall exacerbated soil degradation (Podwojewski et al. 2008; Valentin et al. 2008; Paiboonvorachat and Oyana 2011). The replacement of annual crops by teak plantations in Laos led to a sharp increase of sediment yield and overland flow (Ribolzi et al. 2017; Patin et al. 2018) and to an increase of streamflow, while natural forest regrowth had opposite effects (Lacombe et al. 2016). Soil carbon stocks have been shown to decrease following the conversion of forests to rubber tree plantations (Li et al. 2012; Blagodatsky et al. 2016), with some studies estimating average carbon losses as high as $37.4 \pm 4.7 \text{ Mg ha}^{-1}$ (de Blécourt et al. 2013), although this might be alleviated in mountainous areas by the construction of terraces (de Blécourt et al. 2014). Most of these studies compared the effects of rubber tree plantations to forests or other tree plantations; but in northern Thailand rubber tree plantations mostly replace annual crops, in which

case their effect might be completely different. For instance, Blagodatsky et al. (2016) found that in Southeast Asia, the conversion from intensive annual crops to rubber tree plantations led to short-term carbon sequestration and generally to enhanced soil quality, especially when considering old rubber tree plantations (Thoumazeau et al. 2019). To my knowledge, the literature reports few studies about the effect on soil erosion of afforestation by rubber trees in previously arable lands. **In the sixth chapter of this manuscript (part 1), I compare runoff and soil detachment processes in rubber tree plantations compared to annual crops.**

It should also be noted that the severity of the impacts of rubber tree plantations on biodiversity and soil degradation strongly varies from one study to the other (Lan et al. 2017). For instance, Kerfahi et al. (2016) found a variation in the composition, but not richness, of soil microorganisms communities, in rubber tree plantations compared to forests. Guillaume et al. (2015) found no significant soil erosion in rubber tree agroforests of Indonesia, and Peerawat et al. (2018) found higher microbial and megafaunal richness in old rubber tree plantations than under cassava cultivation. This is at least partly due to the wide diversity of plantation management, from rubber agroforests ("jungle rubber") to multilayered rubber tree plantations intercropped with more or less diverse shrubs and to rubber tree monocultures. While monocultures are often clean-weeded (Gnanavelrajah and Shrestha 2007; Guillaume et al. 2016), management practices allowing understory regeneration positively affect species biodiversity (Aratrakorn et al. 2006; Lan et al. 2017) and are likely to support soil conservation. For instance, rubber agroforests have much higher diversity than monocultures (Beukema et al. 2007; Wilcove et al. 2013).

It thus appears that the presence of understory is a key factor in determining the environmental impact of rubber tree plantations. **I will test this hypothesis in the second part of Chapter 6, in which I quantify the effect of weed cover on runoff in rubber tree plantations.**

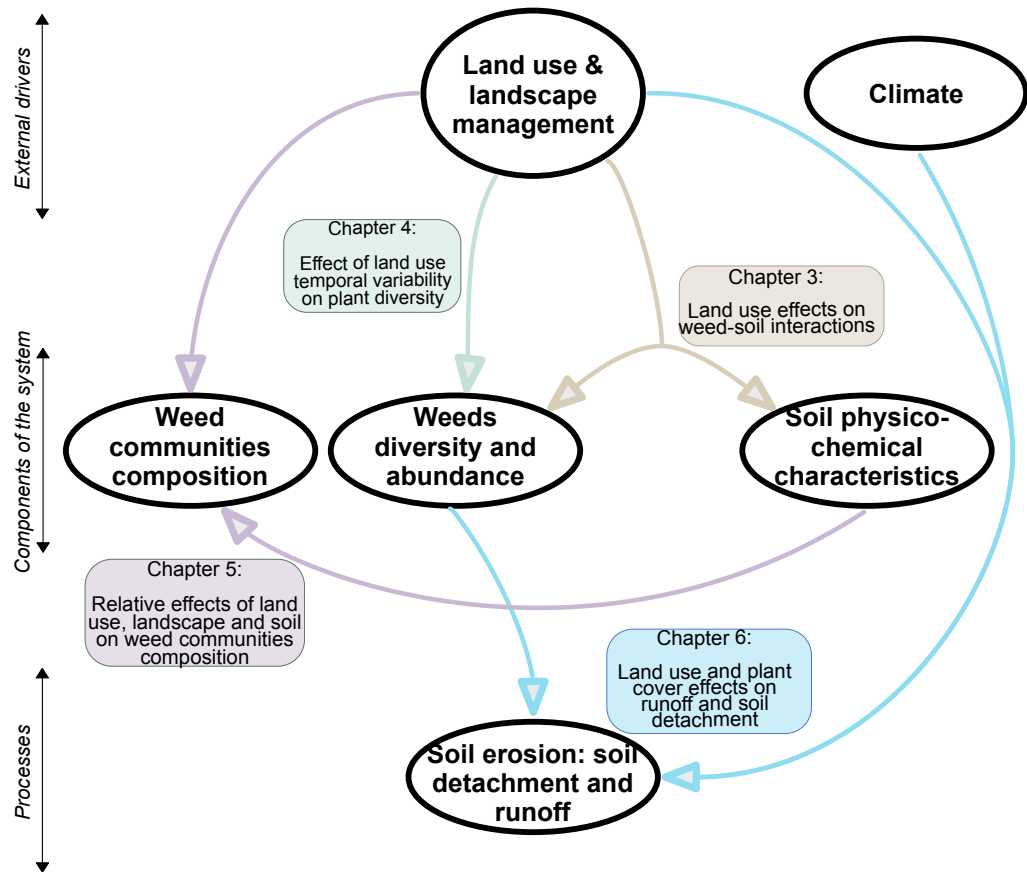
1.4 AIMS OF THE PROJECT AND STRUCTURE OF THIS MANUSCRIPT

In this project, I investigated the inter-relations between the transition of land uses and associated farming practices, weed communities, and soil conservation in an agricultural context of mountainous northern Thailand (Fig. 1.6). This manuscript is based on work that has been conducted since March 2016. Following this introductory chapter, I will first introduce my study site and the protocol used for data collection. The results are organized among Chapters 3 to 6, studying different aspects of the interactions between the components of the agro-ecosystem.

1.4.1 Chapter 3. Plant-soil interactions

This first study addresses the interactions between soil physicochemical properties and weed communities characteristics at small scale. It is based on a previously published study using only data from March 2016 (Neyret et al. 2018), but extends the analysis to the complete dataset. In this study I address the following questions:

Figure 1.6: Structure of this manuscript.



- How does land use affect weed communities composition, abundance and diversity?
- How does land use affect soil physicochemical characteristics?
- How does land use impact the interactions between soil and plant communities characteristics?

1.4.2 Chapter 4. Impact of land use temporal variability on weed communities

In this second study I investigate how the past temporal variability of the land use, quantified either as the number of crop types or the number of land use shifts, affects the richness and composition of plant communities. I answer the following questions:

- How does the temporal diversity of crops modify weed communities diversity?
- How does it affect their abundance?
- Do herbaceous and shrub/tree species respond similarly to land use temporal variability?

1.4.3 Chapter 5. Relative effect of soil, landscape, land use and spatial components on weed communities

In this chapter I investigate how landscape, soil and spatial components, in addition to land use, affect weed communities.

- What are the main local and landscape factors affecting weed communities?
- What is the relative effect of landscape, land use, soil and spatial components on the determination of weed communities?
- What is the dominant process structuring meta-communities in the studied agro-ecosystem?

1.4.4 Chapter 6. The effect of rubber tree plantations on soil erosion

In this last part, I rely on an article submitted to *Catena*, in which I compare runoff and soil detachment under annual crops and rubber tree plantations. I also present preliminary results on the effects of understory management in rubber tree plantations on runoff. I answer the following questions:

- What is the effect of the transition from annual crops to rubber tree plantations on soil erosion?
- How do meteorological conditions affect runoff and detachment in these different land uses?
- Can weed cover mitigate runoff, and to what extent?

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STUDY SITE AND DATA ACQUISITION

In this chapter, I describe the study site as well as the general methodology used during this PhD project. Details regarding chapter-specific material and analyses can be found in the corresponding chapters 3-6.

2.1 STUDY SITE

This study was conducted in Huai Lang, Wiang Kaen district, Northern Thailand (20°00' N, 100°27' E, Fig. 2.2, 2.1). All observation plots were located in two small catchments, one (78.3 ha) mostly under annual crops, the other (29.9 ha) largely under rubber tree plantations. Huai Lang is located in a mountainous area, with elevation ranging from 400 m to 900 m AMSL (above mean sea level). The original vegetation was evergreen/deciduous low land forest (Gardner et al. 2000). No original forest remains and the area is now largely cultivated. Flatlands are mostly occupied by rice paddies, bounded plots where rice is cultivated in the wet season only. Hillslopes are a more constrained environment, where farmers grow rainfed rice (also called dry, hill, or upland rice), maize and trees (rubber, teak or fruit trees).

Between 2015 and 2018, the area was characterised by 1600 ± 200 mm of annual rainfall, mostly concentrated during the rainy season (April-October). The rainy season is usually bimodal, with a first rainfall peak in May and another in August, although annual variations exist (e.g. bimodality less visible in 2016, Fig. 2.3). Mean annual temperature was 24.2 °C with low inter-annual variability of 0.4 °C but a high amplitude between maximum and minimum daily values, 43.5 °C and 4.8 °C respectively. The total annual potential evapotranspiration was approximately 900 mm with a gentle inter-annual variability of 30 mm.

General soil mapping (1/25000) showed that the region is dominated by steep slopes, as 31.7% of the study area has a slope angle above 35%. A detailed soil mapping showed that soils are Haplustalfs (Alfisols) and belong to three soil series (Tha li, Wang Saphung, and Muak Lek) which I describe in Table 2.4 and are mostly differentiated on depth and slope criteria (based on Jumpa (2012)).

Smallholder fields covered most of the area. Table 2.1 summarises the various practices reported by the owners of the fields selected for this study in 2016, for the preceding cropping season (see part 2.2.4 for details). On the hillslopes, maize

Figure 2.1: Topographical map of continental Southeast Asia, showing the distribution of mountainous areas (over 300 m AMSL). The black arrow shows the location of the study site.

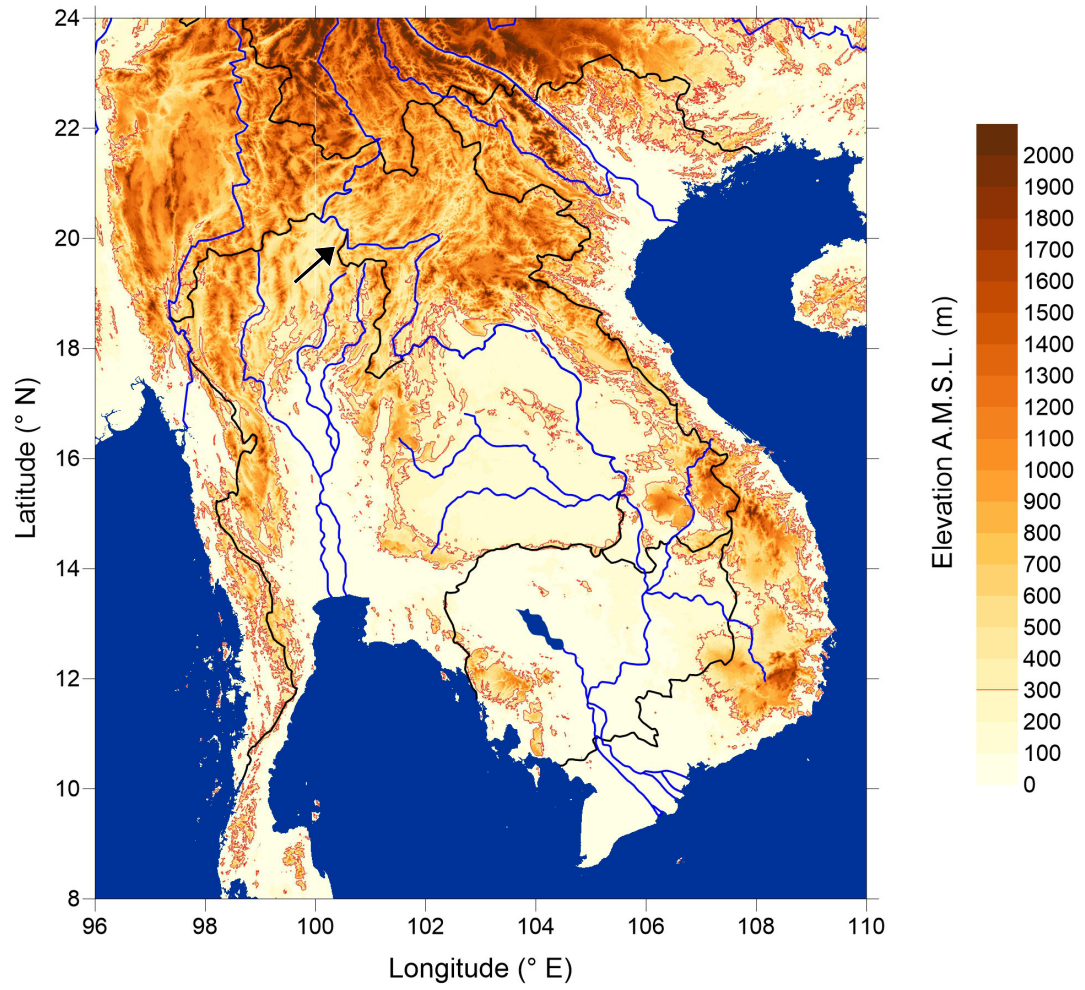


Figure 2.2: Mountainous landscapes in Huai Lang.

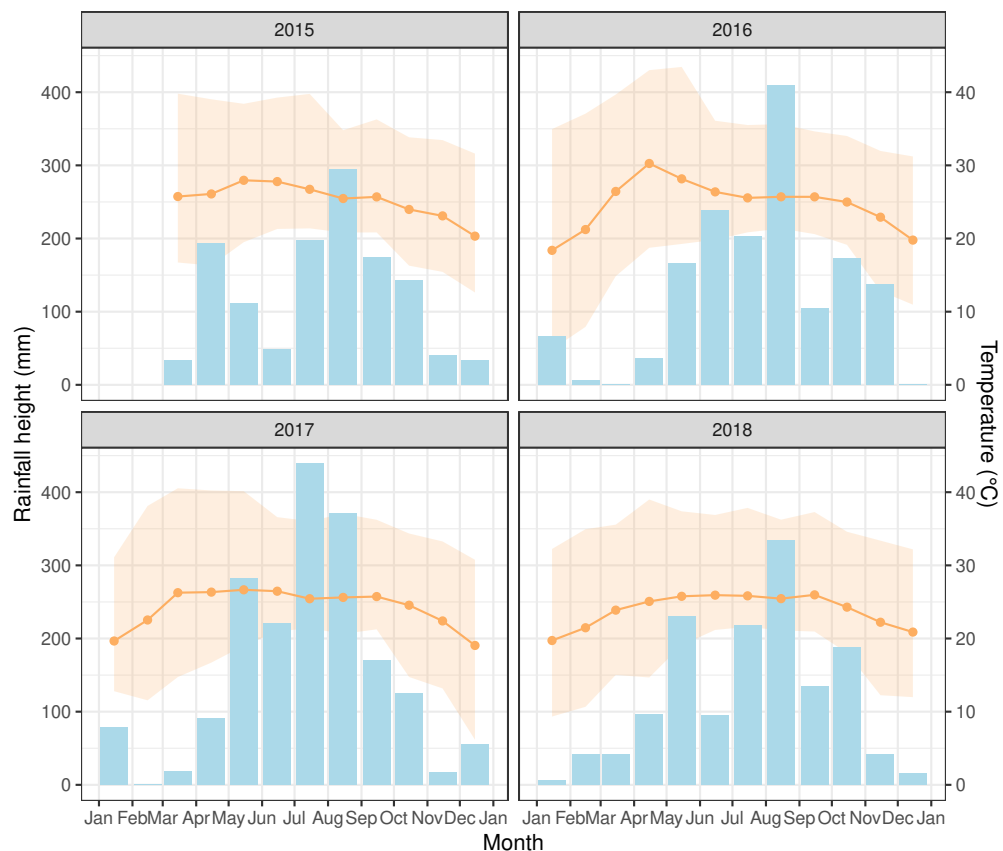
- (a) Hillslopes are dominated by tree plantations and upland rice or maize fields.



- (b) Flatland at the end of the rainy season, after paddy rice harvest.



Figure 2.3: Monthly rainfall (blue, left axis) and temperature data (orange, right axis) in Huai Lang weather station from 2015 to 2018. Orange dots show monthly average temperatures, and the light orange area shows monthly minimal and maximal temperatures.



and upland rice were grown in monoculture, or as intercrop under young tree plantations. Farmers prepared their fields between April and June and, with a few exceptions, they burnt crop residues before seeding. In a given field, crop sequences usually involved alternating maize (1 to 3 years) and rice (1 to 2 years). Upland rice was planted at the beginning of the rainy season (late May-June) whereas the planting period of maize was more flexible. Indeed, being a short-cycle crop, maize could be sown later in the rainy season (up to July) and benefited from the long growing season associated with the bimodality of the climate. Maize and rice were harvested during October and November, respectively. The steep slopes did not permit ploughing and the soil was mostly left undisturbed, except for occasional manual surface hoeing. The upland rice varieties found in the study area were landraces (i.e. locally adapted, traditional varieties), typically tall, long-cycle varieties with dense and drooping leaves (thus providing dense shadow) and cultivated for subsistence or the local market. In contrast, the maize varieties were modern, short-cycle improved varieties cultivated as a cash-crop for animal feed. Rice was planted in hills with an average density of 130 000 hill ha⁻¹, which was common for landraces in the area. Maize was sown in densities of 31 000 hill ha⁻¹, with two plants per hill, which was in the low range of typical sowing densities (20 000 hill ha⁻¹ to 80 000 hill ha⁻¹).

All the rubber tree plantations in the area belong to a first rubber tree cycle, contrarily to other areas in Center and Southern Thailand where rubber tree plantations are currently in their third or fourth cycle (Thoumazeau et al. 2019). Young rubber trees (2-3 years old in 2016) had an average girth at 130 cm height of 15 cm (\pm standard deviation 4 cm), while mature (8-15 years old) rubber tree girth was 55 ± 10 cm. Mature rubber trees were tapped during the rainy season.

Mechanic weed control was usually restricted to hand-cutting the tallest weeds and ligneous species and herbicides were the chief mean of weed control. Glyphosate was the most common herbicide, used in 79 % of the fields (Table 2.1). Farmers sprayed up to 3 different herbicides per field (also including atrazine, gramoxone, metsulfuron-methyl and chlorimuron-ethyl), up to three times a year. They chemically fertilised rubber tree plantations twice or three times a year (except one plantation which was not fertilised) and other fields once (or more rarely twice) a year. The modern maize varieties were herbicide-resistant, which allowed farmers to use herbicides after maize germination.

2.2 DATA ACQUISITION

2.2.1 Context: *Heveadapt* project

Hévéadapt is an ANR-funded project based on a collaboration between the Institute of Research for Development (IRD, France), the Center of International Cooperation for Research in Agronomy (CIRAD, France) and multiple Thai institutions: the Land Development Department, the Agriculture Department, the Rubber Research Institute of Thailand, Kasetsart University, Prince of Songhla University, and Khon Kaen University. It aims at investigating how smallholders adapt to global changes, in this case in the light of the expansion of rubber tree plantations in marginal areas of SE Asia. The two small catchments - one under annual crops mostly (ACC), the other under rubber tree plantations (RTC) - were chosen in 2015 to investigate the effect of rubber tree plantations on soil erosion. They have been equipped with hydrological stations where discharge and suspended sediment loads are monitored since March and June 2015 (in RTC and ACC, respectively), before the start of this PhD project. The monitoring of the streams is complemented with erosion plots where runoff and soil detachment are recorded after each rainy event: I will detail the precise experimental design in Chapter 6. We also recorded meteorological data in a local weather station which I further describe in part 2.2.6.

2.2.2 Weed and soil monitoring

We chose the study fields in March 2016. We selected five fields from each of four land use types, representative of the transition from traditional agriculture to tree plantations (upland rice, maize, young rubber tree with maize, mature RT) in and around the two catchments, with the objective of distributing the land uses around the landscape as uniformly as possible to avoid any spatial bias (Fig. 2.4). We then sampled the fields twice a year, in October 2016, March 2017, November 2017 and March 2018. I provide a description of plot characteristics in Table 2.2.

Table 2.1: Summary of farming practices reported by field owners for the crop preceding sampling. Gly = Glyphosate (L ha⁻¹), Gra = Gramoxone (L ha⁻¹), Met = Metsulfuron-methyl (g ha⁻¹), All = Allmix (Metsulfuron-methyl + Chlorimuron-ethyl, g ha⁻¹), At = Atrazine (kg ha⁻¹). All fertilizer amounts are given in kg ha⁻¹.

Field	Crop	Planting	Harvest	Crop density (m ⁻²)	Average distance between rows x trees (m) ^a	Fire	Type	Herbicide Date	Total amount	Type	Fertilizer Date	Total amount
ULR1	Rice	Late May	Oct	11.6±3.0		Y	Gra	May	15.6	46-00	Aug	95
ULR2	Rice	Late May	Oct	13.6±4.0		Y	Gly	May	7.5	46-00	June, Aug	125
							Met	May, August	90			
ULR3	Rice	June	Nov	12.8±3.0		Y	Gly	May, June	25	21-00	July	125
ULR4	Rice	Late June	Late Nov	15.8±2.7		Y	Gly	July	15	46-00	Aug	65
							All	August	45			
ULR5	Rice	July	Nov	12.8±2.3		Y	Gly	July	0.7	46-00	June	125
M1	Maize			3.4±0.9		N	Gly	April	10	46-00	May	130
							Gra	May	3.6			
M2	Maize	May	Sept-Oct	3.4±1.3		Y	Gly	Late May	1.8	46-00	July	13
							At	Late May	0.4	15-15-15	Late July	95
							Gra	Late July	2.7			
M3	Maize	May	Sept	2.8±1.9		N	Gly	April, May	12.5	46-00	July	95
							At	April, May, July	3.5	15-15-15	July	95
							Gra	July	3.8			
M4	Maize	May	Aug	4.8±1.5		Y	Gly	July	10	46-00	July	125
							At	July	0.9			
M5	Maize	July	Sept	1 ±1.2		N	Gly	June, August	1.7	46-00	August	95
YR1	RT + Maize			2.4±0.5	6.4 ± 0.7 / 2.9 ± 0.3	N	Gly	Avril	2.1	46-00	June	85
YR2	RT + Maize			1.2±1.3	7.1 ± 0.5 / 3.8 ± 1.0	N	Gly	Avril	2.1	46-00	June	85
YR3	RT + Maize	July	Sept	3 ±0.7	7.1 ± 0.3 / 3.7 ± 0.5	N	Gly	June, July	1.7	46-00	July	60
YR4	RT + Maize			2.6±2.1	6.4 ± 0.5 / 3.5 ± 0.2	N	Gly	June	18.8	46-00	July	80
							At	Late June	2.8			
							Gra	Late June	15.6			
YR5	RT + Maize	July	Sept	1.6±1.3	6.2 ± 0.5 / 3.0 ± 0.2	N	Gly	June	25	46-00	June	125
OR1	RT				4.7 ± 0.9 / 4.1 ± 0.5	N	Gra	Late June	2.5			
OR2	RT				7.7 ± 0.6 / 3.1 ± 0.1	N	Gra	May, Oct	5.2	46-00	May, July, Sept	1 250 ^b
OR3	RT				7.6 ± 1.3 / 4.6 ± 0.4	N				15-15-15	May, August	85
OR4	RT				7.3 ± 0.9 / 3.5 ± 0.4	N				15-15-15	June, October	80
OR5	RT				6.4 ± 0.3 / 3.1 ± 0.1	N	Gly	June, Aug, Sept	7.5	15-15-15		

^a Irregular planting patterns can be explained by steep slopes that make the following of contour lines more difficult.
^b The owner reported that he used 1kg of fertilizer per tree, 3 times a year.

Figure 2.4: Location of study sites and distribution of soil series in the Huai Lang catchments. Left: ACC catchment. Right: RTC catchment. Land uses indicated by the different shapes correspond to the first sampling period in March 2016. Further description of soil series can be found in Table 2.4. Dashed areas correspond to interpolations from known soil series data.

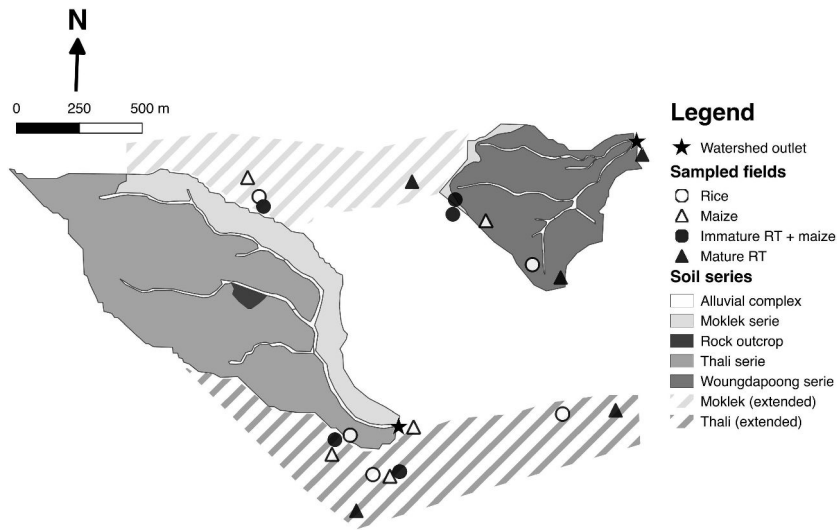


Table 2.2: Geomorphological data of the different sampled plots in 2016 (M: maize, ULR: upland rice, YR: young rubber tree with maize, OR: mature rubber tree) and field number. Soil series represent Muak Lek serie (MI), Tha Li series (TI), Wang Saphung serie (Ws) (based on Jumpa (2012)) and parentheses indicate series assumed from spatial extrapolation. Position indicates the position along hillside: 0% at the river, 100% at the top. Slope is the general slope of the field.

Field	Slope (%)	Position (%)	Hillside length (m)	Exposition	Serie
ULR ₁	40.3	72	223	N	WS
ULR ₂	37.6	75	130	NE	TI
ULR ₃	53.0	30	210	N	(TI)
ULR ₄	40.5	76	270	NE	MI
ULR ₅	26.9	39	164	S	TI
M ₁	27.5	74	70	S	MI
M ₂	54.0	84	253	E	WS
M ₃	39.3	27	378	SE	TI
M ₄	50.3	59	239	NE	MI
M ₅	34.1	21	157	SE	TI
YR ₁	43.4	87	185	NE	WS
YR ₂	39.6	87	292	SW	WS
YR ₃	37.6	12	291	SE	TI
YR ₄	32.7	21	149	SE	TI
YR ₅	50.6	83	240	NE	(MI)
OR ₁	22.0	78	162	NW	WS
OR ₂	38.5	53	104	N	WS
OR ₃	42.7	65	145	NW	(TI)
OR ₄	44.6	41	209	NW	(MI)
OR ₅	43.7	33	165	NW	TI

Figure 2.5: Different land uses found in the study plots.

- (a) Initial land uses in the chronosequence (from top left to bottom right): upland rice, maize, young rubber tree plantation with maize intercrop and mature rubber tree plantation.



- (b) Additional land uses (from top left to bottom right): young rubber tree plantation with rice intercrop, young rubber tree plantation with no intercrop, longan fields, fallow.



I define the land use of a field as the last land use preceding sampling: for instance, it was the crop grown in the rainy season 2016 for both November 2016 (rainy season sampling) and March 2017 (dry season sampling). The land uses of the different fields changed each year, and we decided to follow the same sites from year to year instead of keeping a balanced design. As a result, we obtained a much larger number of land uses than what was initially expected (Fig. 2.5). Because the number of individual land uses was high, I summarised the land use as two variables. The annual land use variable described the annual land use in the field (i.e. either upland rice, maize, or no annual crop). The second variable described the presence of rubber trees in the field, with either no rubber tree, young rubber tree (2-5 years) or mature rubber tree (older than 8 years). Some fields had small saplings (longan trees or rubber trees, < 0.5 m in height), planted during the study period. Their density was low (approx. 200 tree ha⁻¹) and we considered that they had little influence on the surrounding vegetation, so I did not take them into account when classifying land uses. Table 2.3 shows the crop sequences in each field from 2015 to 2018.

In each field we defined a 100 m² square (henceforth "field"), whose location remained identical from year to year; the positioning was realised using both local references (trees, terraces) and GPS coordinates (GPSMAP 62S Garmin). In each field, and for each new sampling period, we randomly chose five 1 m² squares (henceforth "plots"). If a plot comprised a rubber tree or overlapped with an area sampled during the previous sampling period it was slightly moved. Sampling in each plot followed nine steps. I describe the precise methodology for each step in part 2.3.

1. Describe the field topography and position (cf. 2.3.1);
2. Take picture for total soil cover (cf. 2.3.5);
3. When in rice or maize fields, measure crop density;
4. Remove and store in separate paper bags crop residues (e.g. depending on the crop, rice or maize leaf and straw, rubber tree leaves) and dry (brown or yellow) weeds for biomass measurement (cf. 2.3.2);
5. Take picture for living soil cover (cf. part 2.3.5);
6. Count and identify (cf. 2.2.3) all living plants in the plot, store in paper bags for biomass measurement (cf. 2.3.2);
7. Take 8 to 17 pictures for photogrammetry analyses (cf. 2.3.3);
8. Take 13 humidity measurements using a TDR probe (on alternate rows of a 20 cm*20 cm grid) and sample a 100 cm³ soil cylinder (cf. 2.2.3);
9. Only in March 2016 and 2017, conduct a Beerkan infiltration test (cf. 2.3.4.a).

Unless stated otherwise, I then averaged the five values from the five plots within each field.

Table 2.3: Crop sequences between 2013 and 2018. Mature rubber tree plantations are not presented, as their land use did not change. M: maize, ULR: upland rice, YR: young rubber tree with fallow, YR + ULR: young rubber tree with rice intercrop, YR + M: young rubber tree with maize intercrop. (*lon*) and (*yr*): longan and rubber tree saplings, not taken into account for land use classification. Shaded boxes: unknown.

	2013	2014	2015	2016	2017	2018
ULR1		Maize	Rice	Rice	Fallow	Rice
ULR2	Maize	Maize	Rice	Maize	Maize (+ <i>lon</i>)	Maize (+ <i>lon</i>)
ULR3		Rice	Rice	Maize	Rice	Fallow
ULR4	Maize	Maize	Rice	Maize	Rice	Maize
ULR5		Rice	Rice	Fallow (+ <i>lon</i>)	Fallow (+ <i>lon</i>)	Fallow (+ <i>lon</i>)
M1		Maize	Maize (+ <i>lon</i>)	Maize (+ <i>lon</i>)	Rice (+ <i>lon</i>)	Maize (+ <i>lon</i>)
M2	Maize	Maize	Maize	Maize	Fallow (+ <i>yr</i>)	Fallow (+ <i>yr</i>)
M3	Maize	Maize	Maize	Maize	Rice	Fallow
M4	Maize	Maize	Maize	Maize	Rice	Maize
M5	Rice	Maize	Maize	Maize	Fallow	Maize
YR1	Young rubber tree + maize	Young rubber tree + maize	Young rubber tree + maize	Young rubber tree + Rice	Young rubber tree + fallow	Young rubber tree+ fallow
YR2	Young rubber tree + maize	Young rubber tree + maize	Young rubber tree + maize	Young rubber tree + Rice	Young rubber tree+ fallow	Young rubber tree+ fallow
YR3	Young rubber tree + maize	Young rubber tree + maize	Young rubber tree + maize	Young rubber tree+ fallow	Young rubber tree+ fallow	Young rubber tree+ fallow
YR4	Young rubber tree + maize	Young rubber tree + maize	Young rubber tree + maize	Young rubber tree+ fallow	Young rubber tree+ fallow	Young rubber tree+ fallow
YR5	Rice	Young rubber tree + Rice	Young rubber tree + maize	Young rubber tree+ fallow	Young rubber tree+ fallow	Young rubber tree+ fallow

2.2.3 *Plant communities*

Bounsamay SOULILEUTH and Anneke DE ROUW, both with long experience of southeast Asian flora, provided plant identification. I collected and prepared herbarium specimen of all species for reference (Fig. 2.6). The specimens are currently kept at the LDD office in Bangkok. We counted in total a bit more than 239 000 individuals from 65 plant families. Species names, codes, and abundances are summarised in Appendix S2.1: I use accepted species names as per the PlantList database (<http://www.theplantlist.org/>) and species codes based on the EPPO database (<https://gd.eppo.int/>). Species absent from the EPPO database were given custom codes, not existing in the database and respecting the genus code.

In this whole manuscript, I will distinguish different characteristics of weed communities. Their **abundance** will be described based on their density (individuals m^{-2}) and biomass (g m^{-2}). The **richness** and **diversity** of a community correspond respectively to the number of species observed in a community and their evenness, described by Shannon index. Finally, the **composition** of a community is multidimensional, as it corresponds to the identity of the species found in a community and their respective abundance.

In addition to species abundance-based analyses, I initially planned to conduct plant trait analyses. Indeed, plant traits can inform us about community functioning: for instance, they can help to identify filtering processes, that would exclude some species from a given land use. Identifying weed traits related to better soil resistance to erosion (e.g. Burylo et al. (2012), Ghestem et al. (2014), Seitz et al. (2016) and Chau and Chu (2017)) would also have been a significant advance in determining which weed communities to favour for erosion control. However, on-field measurements of plant traits were not carried out and many of the tropical species identified on the fields were absent from, or poorly described in, most surveyed databases. The description of the databases investigated as well as the preliminary results obtained are presented in Appendix S1.1.

2.2.4 *Description of farming practices*

Information about farming practices was obtained from a combination of direct observations in the field and formal and informal interviews with farmers. This was complemented with published documents and expert knowledge on farming practices in Thailand and Southeast Asia.

We conducted interviews with owners of all fields in March 2016, except one who refused to give an interview (15 owners in total). In these interviews, I aimed at determining the type, dose, and date of application of herbicides and fertilisers; the planting and harvesting dates; as well as the time spent on hand weeding and the use of fire (Table 2.1). I also tried to rank the perceived severity of weed infestation and soil erosion among farmers. However, the farmers were difficult to reach; some of them lived quite far from Huai Lang. They often seemed reluctant to answer our questions. They sometimes did not understand our questions or their purpose: although a native Thai speaker translated all the exchanges, some farmers spoke local dialects and the communication was difficult. Besides, their answers were sometimes inconsistent or contradictory to field observations. This could be explained by the fact that field owners were not always those who actually worked

Figure 2.6: Identification of plant samples.

(a) *Angiopteris evecta* sample.



(b) *Broussonetia papyrifera* sample.



(c) A few Poaceae samples.



in the field, as they often hired workers; and to a willingness to give expected, rather than factually correct, answers. As a result, the reliability of this data is uncertain. Colleagues from the LDD conducted similar interviews for the following years but were able to contact only 8 owners and obtained data for the 2016 farming season only. It was sometimes inconsistent with ours, and we could not determine whether it was due to annual variability in farmers' practices or inaccuracy of one or the other dataset.

As the chief mean of weed control proved to be herbicides, we looked for an additional data source on farming practices and proceeded to directly measure herbicides in the field. Glyphosate was the most common herbicide, and I thus adapted an immunoassay method, initially designed to measure glyphosate concentration in liquids, to measure glyphosate in our soil samples. The underlying hypothesis was that the quantity of residual glyphosate in the soil would be an indicator of the intensity of herbicide application, based on glyphosate concentration decay curves. I conducted preliminary tests, soil samplings (two per field, i.e. approximately 40) and glyphosate extraction (5 per samples, i.e. approximately 200 extractions) but due to technical problems I was unable to complete the last step, which consisted in actually measuring glyphosate concentration in the extracts. The detailed approach of the problem, along with the protocol and results of preliminary tests are described in Appendix [S1.2](#).

2.2.5 Soil characterisation

Previous work by the Land Development Department classified the soil within the catchment as Alfisols belonging to three soil series, which description can be found in Table [2.4](#) (adapted from Jumpa (2012)). Additional soil description was achieved by augering down to 1 m. We described two profiles in each field, one at the top and one at the bottom (Fig. [2.7](#)). We determined the hue, value and chroma (Munsell Color System) as well as the texture class of each horizon. Some profiles were shorter than 1 m due to the auger being jammed by coarse elements. A complete description of soil profiles is available in Appendix [S2.3](#).

H. ROBAIN also conducted electrical resistivity tomography (ERT) measurements in all plots with SYSCAL PRO 72 equipment (Iris Instruments). ERT is a geophysical technique aimed at imaging sub-surface structures using electrical resistivity variations (Loke et al. 2013). The measurements were done in March and November 2017 along 106 m profiles with 1.5 m unit spacing between electrodes. ERT allows computing a model of 2D variations of underground electrical resistivity. The average geoelectrical vertical section was then calculated for each plot (eg. Fig. [2.8a](#)). A clustering analysis allowed identifying three main types of vertical geo-electrical profiles (Fig. [2.8b](#)). These three classes provide a categorisation of our study fields, which I will use in Chapter [5](#) as a general descriptor of their soil type and organisation and is more accurate and reliable than the extrapolations derived from the detailed soil map. The soil classes were independent of land use type ($P > 0.1$).

2.2.6 Meteorological monitoring

An automatic weather station (Campbell BWS200) has been installed since March 2015 in the middle of a small flat grassland located at an elevation of 535 m AMSL.

Figure 2.7: Soil profile characterisation in a rubber tree plantation.

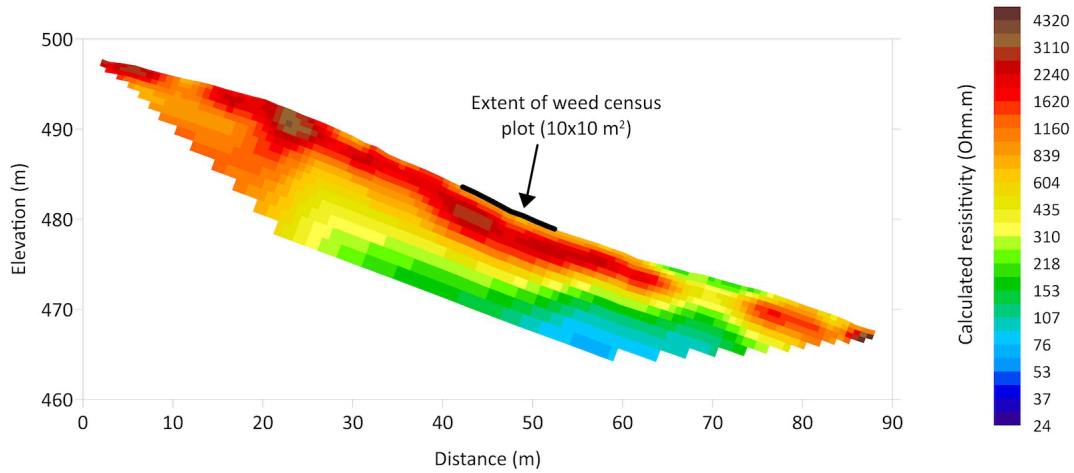


Table 2.4: Characterisation of soil series (adapted from Jumpa (2012)).

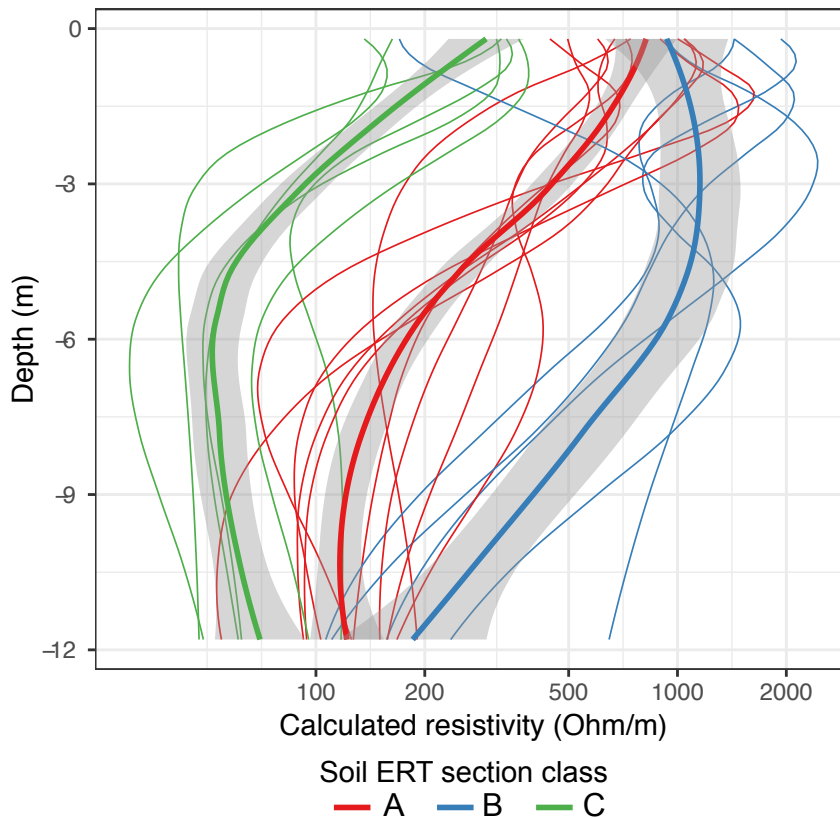
Serie name (abbrev.)	USDA classification	Texture	Soil depth	Soil pH
Muak Lek Serie (Ml)	Ultic Haplustalfs	Clayey-skeletal	shallow	5.5-6
Tha Li serie (Tl)	Ultic Haplustalfs	Clayey-skeletal	medium	5.5-7
Wang Saphung serie (Ws)	Typic Haplustalfs	Fine, clay-loam	deep	5.5-6.5

Figure 2.8: Electrical resistivity tomography measurements in Huai Lang (from H. ROBAIN).

- (a) An example of soil resistivity cross-section from field M3. 2D resistivity model was calculated with RES2DIXV64W software (Loke et al. 2013). Cool colours show low resistivity areas, and warm colours show high resistivity areas.



- (b) Classification of ERT cross-sections. The fine lines represent the average resistivity cross section of each field, clustered into 3 soil classes (represented in different colours). The bold lines represent the average cross section for each class.



Meteorological parameters were measured on a one minute basis: temperature and air relative humidity with CS215 Sensor; wind speed and direction with Wind Sentry Sensor; rainfall with a tipping bucket rain gauge adjusted to tip once for each 0.2 mm of rain (Campbell ARG100); sun plus sky radiation (300 nm to 1100 nm) with a silicon photovoltaic detector (Campbell CS300). Taking into account longitude, latitude and elevation of the station and using wind, temperature, air humidity and solar radiation data, we calculated potential evapotranspiration using Monteith Penmann formula. Data from the weather station was complemented by manual rain gauges installed in open areas near the catchment outlets.

2.2.7 *Landscape characterisation*

The objective of the landscape analysis was to obtain a precise description of the surroundings of each study field, in order to quantify the effect of these surroundings (both in terms of composition and complexity) on local weed communities. This corresponds to Chapter 5 of this manuscript.

In November 2017 and March 2018, we conducted a survey to identify and measure the geographical coordinates of multiple points in the area surrounding our study fields. I then combined this extensive field data with a visual interpretation of remote sensing images (for instance, mature rubber tree plantations were easily identifiable at high resolution due to tree rows) to manually digitise a land use map of the area in using QGIS software (Fig. 2.9a). I initially planned to use the visual interpretation of earlier images to build the land use maps of the previous years. The annual land uses (maize, rice, fallow) were the most likely to change from one year to another, contrarily to rubber plantations that are perennial for instance. However, it was not possible to visually distinguish maize, rice and fallow fields from each other.

I thus tried to use Sentinel 2 multi-spectral images to automatically classify earlier image sets. The objective was to use the detailed, manually digitised land use map and the corresponding Sentinel-2 images (2017) to train a classification algorithm which could then be used to classify Sentinel-2 images from the previous years. We selected Sentinel-2 multi-spectral images (spatial resolution: 10 m) from multiple dates in 2017, which we thought would help to distinguish the various land uses. For instance, forests and mature rubber tree plantations can be difficult to distinguish at low resolution but might be distinguished based on an image taken in February when rubber trees are defoliated. Because of the complexity of the landscape (fragmented mosaic where fields represented only a few pixels; mountainous area forcing to conduct elevation and atmosphere corrections), the classifications obtained initially were not very accurate (65-70% accuracy). Working on the same dataset and using multiple indices, Christophe MAHUZIER was able to obtain good classifications (90% accuracy). However, the application of the trained algorithm to images from previous years is still under development and could not be used for this thesis.

I thus had to work only from the manually digitised map. I retained only six land use classes that I assumed to be unchanging, in a given location, over the three years of the study:

- Streams, rivers and associated vegetation (riparian areas);

- Forests;
- Orchards (longan or mango trees without annual crop)
- Annual fields (upland rice, paddy rice, maize, young fallows);
- Semi-natural elements (roadsides, thickets, marginal areas, old fallows);;
- Mature tree plantations (rubber trees or teak trees).

In order to complement this "static landscape" dataset, I used NDVI data to investigate the spatial heterogeneity of the vegetation in each neighbour area. The Normalized Difference Vegetation Index (NDVI) is a simple indicator characterising the health of green vegetation (Fig. 2.9b). A high coefficient of variation of NDVI indicates large spatial heterogeneity of vegetation, and thus of the variability of the land cover around each point. This was particularly useful in annual fields. Indeed, areas with more than one land use (among rice, maize and fallow) had higher NDVI variance than areas with only one of these land uses (non-parametric test made on all pairwise drawings of two fields among the maize, rice and fallow fields identified during the survey, $P < 10 \cdot 10^{-12}$). In this regard, I selected one Sentinel-2 image dated just before the start of each sampling period and conducted elevation and atmospheric corrections on each image before calculating NDVI.

Finally, I defined "neighbouring areas" as 200 m-radius areas centred on each sampling point. These areas covered approximately 1250 pixels of 10 m by 10 m (the resolution of the Sentinel-2 images). In each neighbouring area, I computed:

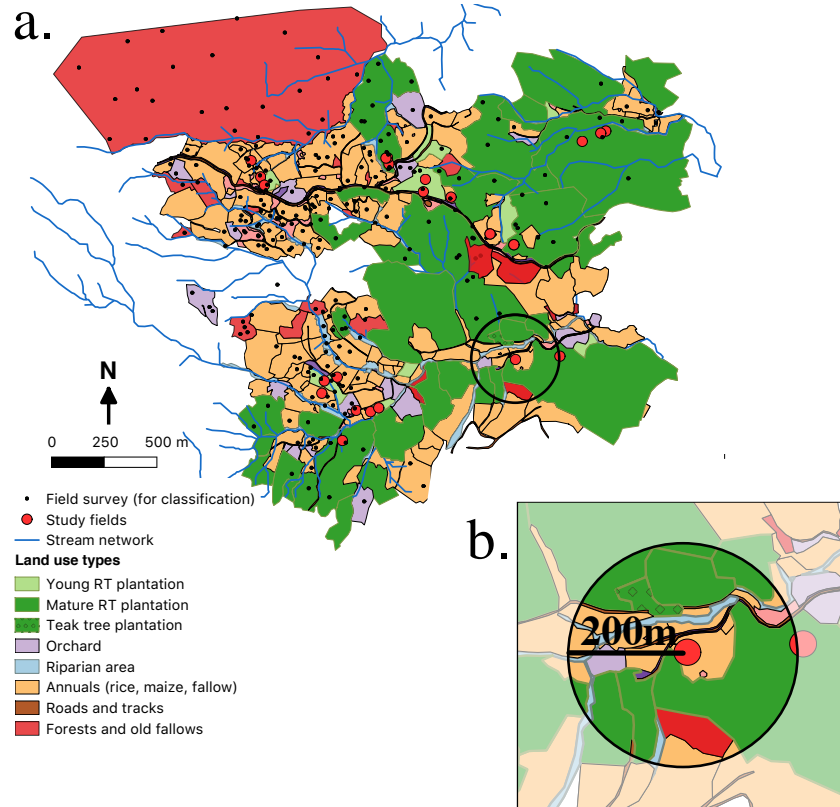
- The relative area of each land use class;
- The edge length and mean patch area of each land use class (R package SPATIALECO);
- The number of land use classes and landscape diversity index (Shannon index, based on each class relative area).

This formed the "static" part of the dataset, which I complemented by calculating for each neighbouring area and each sampling period:

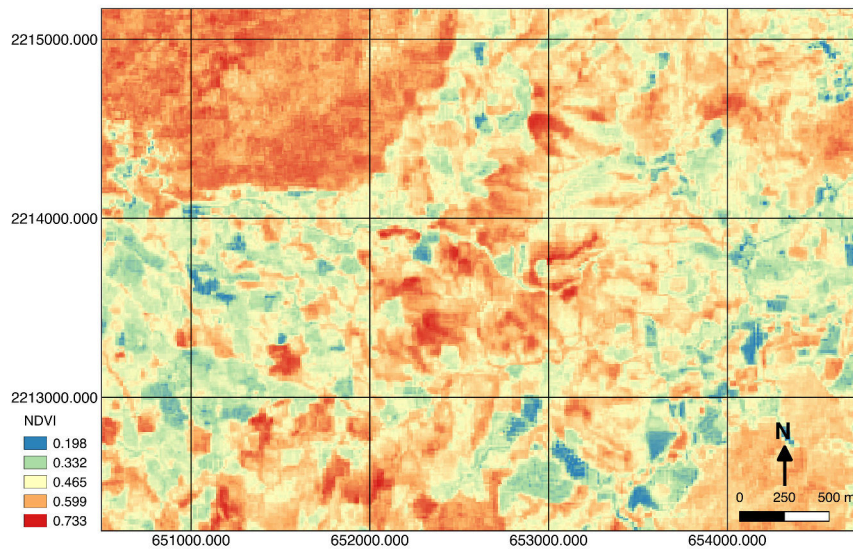
- The mean and coefficient of variation (cv) of NDVI (based on individual pixels NDVI values) of the whole neighbour area, noted $\text{mean}(\text{NDVI}_{all})$ and $\text{cv}(\text{NDVI}_{all})$;
- The mean and cv of NDVI of each land use class, separately (i.e. calculated based on the NDVI values of all pixels belonging to the considered class), noted $\text{mean}(\text{NDVI}_i)$ and $\text{cv}(\text{NDVI}_i)$ with i corresponding to annual fields, seminatural elements, forests, riparian areas, orchards, or young and mature rubber tree plantations.

Figure 2.9: Landscape characterisation of Huai Lang area. The stream network was obtained from topographical maps (Jumpa 2012).

(a) a. Digitised land use map of Huai Lang area. b. Close-up on the 200 m-radius "neighbour area" of one field (circled in a).



(b) Example: NDVI map of Huai Lang (February 2018). Warm colours correspond to areas with healthy vegetation (e.g. forest at the Northwest corresponds to the large forest in Fig. a.a) while cool colours correspond to dryer areas.



2.3 DETAILED METHODOLOGY

2.3.1 *Description of the topography*

During each sampling period, we measured the geographical coordinates of the corners of each field (GPSMAP 62S Garmin). When local references were sparse, this allowed us to correctly replace the sampling area from one sampling period to the next. We then determined the relative position of the corners of each plot and rubber trees (if present) within the field using a theodolite Nikon DTM-520. Based on precise angle measurements and triangulation, this allowed us to precisely measure the distance between the plots, between rubber trees, and to calculate the slope of each plot. Because elevation measurements from the GPS were very inaccurate, especially under rubber tree plantations, we extracted the elevation of the corners of the field from a detailed topographical map.

2.3.2 *Biomass measurements*

All paper bags were first air-dried on the field. At the end of each sampling period, they were taken to a laboratory where they were oven-dried at 50 °C for 48 h, then weighted.

2.3.3 *Photogrammetry*

The velocity and volume of runoff depend on soil infiltrability, but also on the roughness of the soil surface. The roughness is quantified by Manning coefficient and depends on the size, shape and distribution of micro- and macro-relief of a soil surface. It is affected by the presence of vegetation and by soil crusting processes. Photogrammetry is a technique used to recreate 3D models based on multiple pictures of the same object. These models can then be used to measure the Manning coefficient for a given plot. We took a series of 8 to 17 pictures of all 1 m² plots, from different angles (Fig. 2.10). 3D models (precision at the 1 mm scale) can then be computed using AgiSoft PhotoScan Pro software. I did not analyse this dataset during my project. However, it will be used in a future MSc project aiming at quantifying the effects of land use and vegetation on soil micro-topography.

2.3.4 *Soil analyses*

2.3.4.A Field analyses: Beerkan test

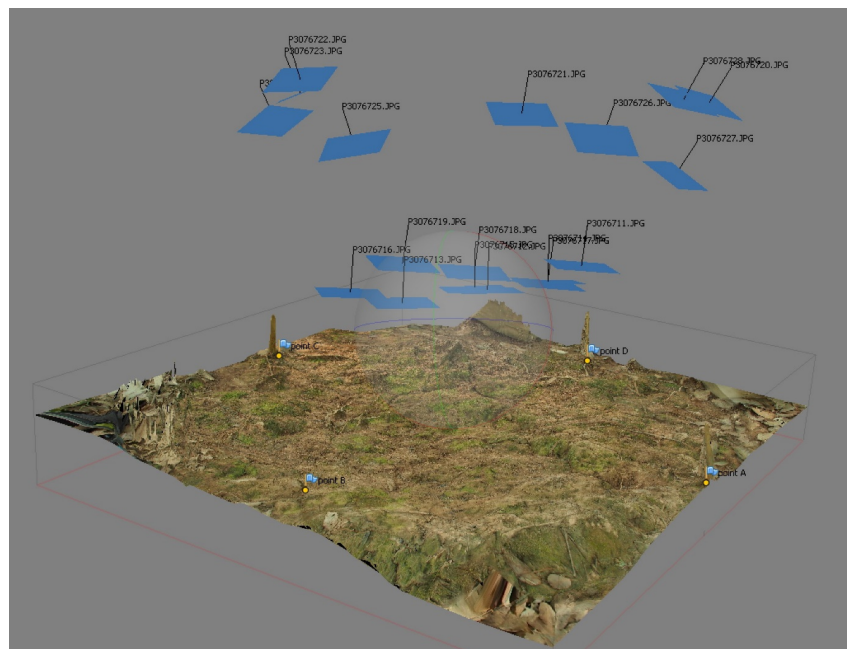
The Beerkan infiltration test aims at measuring soil hydraulic properties. After removing living plants and litter, we flattened an area and removed dust with a brush. We then inserted a 7.6 cm-diameter cylinder vertically in the soil and measured the time needed to infiltrate a unit volume of 60 mL of water. We continued pouring water and timing infiltration time for 30 minutes or until at least 20 volumes were poured. After the test, we sampled a soil cylinder in the test area to measure wet bulk density. We conducted Beerkan tests in all 1 m² plots in March 2016 and March 2017. In March 2016, LDD colleagues measured the texture (% of

Figure 2.10: Example of a photogrammetry analysis (one 1 m² plot in field OR2, March 2017).

- (a) Photo series. Middle: A mosaic of 9 overlapping pictures covering the whole plot area. Around: a picture from each side and corner of the microplot.



- (b) Result of the analysis. Blue rectangles indicate the location and orientation from which the photos were taken.



clay, silt, sand) of soil sampled on the infiltration tests area. We then used this data as well as cumulative infiltration times to estimate hydraulic conductivity based on the BEST model (Haverkamp et al. 1994; Lassabatere et al. 2006).

Although it has been successfully used in mountainous environments (e.g. Eeckman (2017)), Beerkan test is usually used in flat areas, and aims at measuring the permeability and sorptivity of the first centimetres. In our field conditions, we had to flatten the soil surface to correctly conduct the test, partly removing these first centimetres. This might explain the highly variable BEST estimates of hydraulic conductivity parameters found among the five replicates within each field. For both March 2016 and March 2017, I also estimated the volume infiltrated in 10 min as the product of the number of unit volumes infiltrated in 10 min by the unit volume (60 mL), which requires less data transformation than calculating hydraulic conductivity.

2.3.4.B Laboratory analyses

After sampling, we kept soil samples in air-tight plastic bags until returning to the laboratory. There, we weighted the still-wet samples and dried them for one to two weeks at 40 °C, until completely dry. Soil humidity (θ) and bulk density (γ_{bulk}) were calculated as:

$$\theta = \frac{W_h - W_d}{W_d}$$

$$\gamma_{bulk} = \frac{W_d}{V_t}$$

with W_h = wet weight, W_d = dry weight, and V_t the total volume of the cylinder.

We sieved the soil using a 2 mm sieve and measured the weight and volume of coarse materials. We calculated the proportion of coarse materials ($C_{\%}$) and the density of fine elements (γ_{fine}):

$$C_{\%} = \frac{W_{dc}}{W_d}$$

$$\gamma_{fine} = \frac{W_d - W_{dc}}{V_t - V_c}$$

with W_{dc} and V_c the weight and volumes of coarse elements. Although the cylinders used within each sampling season were always the same, we used slightly different cylinders from one sampling period to another. We noticed afterwards that there were slight variations in the volume of the cylinders. In order to remove any effect of these variations on the inter-annual variations of bulk density, we hypothesised that these variations should be close to zero and rescaled the bulk density values so that the average density within each sampling period was equal to the general average.

We then ground an aliquot of the fine elements to 200 μm and measured C and N content using a CHNOS Elemental Analyser Vario EL III (Elementar). We also measured soil pH (H_2O) on samples from March 2017 and March 2018 (i.e. 10 repetitions per field). We mixed 20 g of sieved soil with 50 mL of distilled water and measured pH after two hours. We calculated field pH as the median of the 10 repetitions.

2.3.5 *Soil cover measurements and image analysis*

I conducted soil cover analyses with two purposes:

- Measure soil cover of the sampled 1 m² plots;
- Follow soil cover variations in the erosion microplots installed in rubber tree plantations in 2017 and 2018.

The initial objective was to measure both litter and living plant cover, but I eventually used only living plant cover.

I took high-quality pictures from 150 cm above ground level, on a plane parallel to the ground, of each sampling plot for all sampling periods (approximately 550 images). A field assistant also took standardised weekly pictures of erosion microplots from January 2017 to December 2018 (slightly more than 1200 images in total). I first corrected all images for perspective deformation using GIMP, using the 1 m² frames of the plots as references (Fig. 2.11, step 1). I then segmented the images into different classes (Fig. 2.11, step 2-4, as described below) and calculated the proportion of the area covered by each class (Fig. 2.11, step 5).

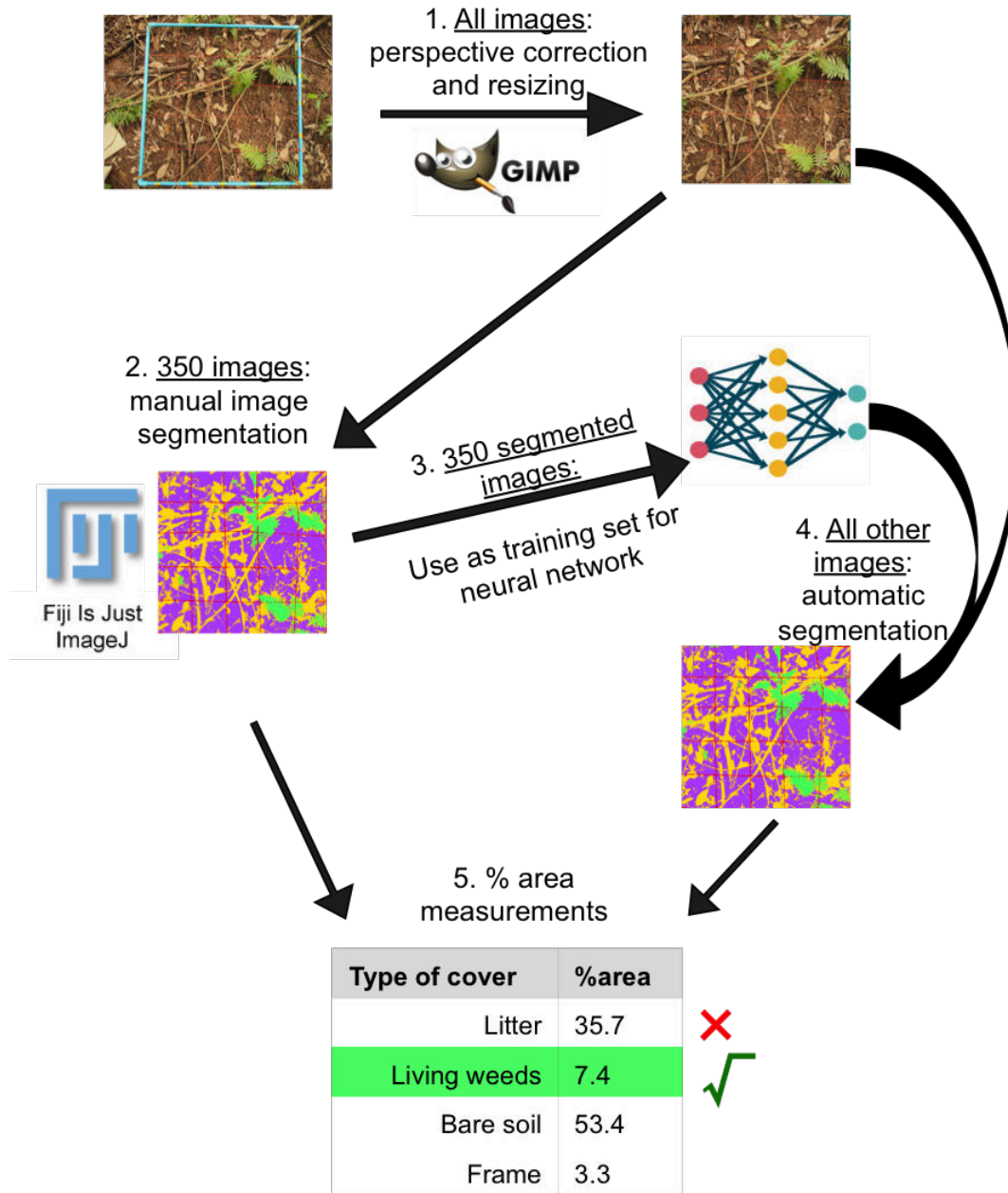
2.3.5.A Semi-manual segmentation using Fiji

I semi-manually segmented the images taken during weed sampling sessions in March 2016, November 2016 and March 2017, and approximately 50 images from the erosion microplots (i.e. approx 350 images in total) using Fiji (Fiji Is Just Image J) plugin Weka Segmentation (Fig. 2.11, step 2). The user manually defines areas of the different classes (living, i.e. green plants; litter; bare soil); these areas are used as training data for a classifier, which segments the whole image. The process is repeated until adequate segmentation is obtained. This method was very precise to detect living plants and moderately successful to differentiate litter from bare soil. It was also relatively time-consuming (5 min to 10 min or more per image), which made it difficult to use it for all the remaining images.

2.3.5.B Automatic segmentation using a neural network

I used these 350 segmented images as a training set for a segmentation neural network developed by Thibault DURAND during his PhD at the Laboratoire d'Informatique de Paris 6 (https://github.com/durandtibo/segmentation_sol, Fig. 2.11, step 3). I then segmented automatically all the images (including the images used in the training, to ensure homogeneity of the segmentation) using the trained network (Fig. 2.11, step 4). It was very efficient to identify living plants, relatively efficient for rice and maize litter but quite ineffective for distinguishing rubber leaves from bare soil in rubber tree plantations, which often had very variable light conditions. I thus decided to measure only the proportion of living plant cover. After obtaining the images segmented by this algorithm I used the colour thresholding tool in Fiji to extract the area corresponding to living plants (Fig. 2.11, step 5).

Figure 2.11: Process of image analysis.



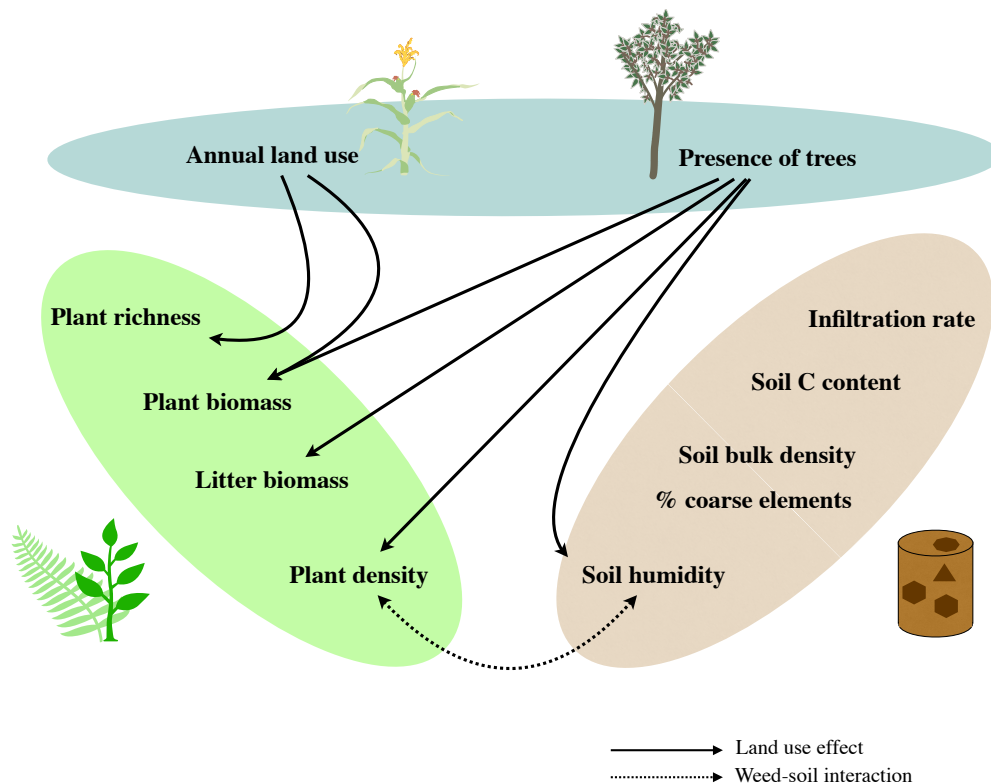
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LAND USE EFFECTS ON WEED-SOIL INTERACTIONS

In this chapter, I investigate the relationships between plant communities properties (biomass, plant density, species richness) and soil characteristics depending on land use. I demonstrate that land use strongly impacts plant biomass, density and richness. Among soil characteristics, soil humidity was the most correlated to land use and plant communities characteristics. This chapter expands on previously published results (Neyret et al. (2018), included as Appendix S3.2).

Figure 3.1: Graphical abstract



Introduction en français

Durant ces dernières décennies, l'expansion récente des plantations d'hévéa dans les zones montagneuses du nord de la Thaïlande a été fortement encouragée (Fox et Castella 2013). Toutefois, ces plantations ont des effets importants sur la conservation des sols: alors que dans les jeunes plantations, le sol est en général protégé par des cultures en inter-rang ou par le sous-bois, les plantations matures sont souvent complètement désherbées. La plupart des études portant sur l'impact des plantations d'hévéa sur le sol et la biodiversité ont comparé les monocultures à des forêts secondaires (Liu et al. 2015) ou à d'autres cultures pérennes comme le teck ou le palmier à huile (Guillaume et al. 2016). Dans les zones en faible pente, les monocultures d'hévéa ont un effet négatif sur la biodiversité et sur les sols par rapport aux forêts (Janeau et al. 2003; Beukema et al. 2007; Podwojewski et al. 2008; Valentin et al. 2008; Paiboonvorachat et Oyana 2011). En revanche, elles seraient légèrement plus favorables à la biodiversité et à la protection du sol que les autres plantations d'arbres (Gnanavelrajah et Shrestha 2007; Guillaume et al. 2016). Cependant, les impacts environnementaux de la transition des cultures annuelles vers les plantations d'hévéa à petite échelle sont encore largement inconnus, en particulier en termes de diversité végétale.

Bien que peu d'études aient spécifiquement étudié l'impact des adventices sur l'érosion du sol, il semble raisonnable de penser que, tout comme les autres plantes, les adventices favorisent la fertilité des sols et le contrôle de l'érosion (Durán Zuazo et Pleguezuelo, 2008). Les plantes proches du sol réduisent l'érosion par "splash" et la vitesse du ruissellement de surface (Seitz et al. 2016). Les racines limitent le ruissellement et le détachement de sol en augmentant la résistance du sol et en favorisant l'infiltration (Janeau et al. 1999); elles améliorent également la stabilité des sols par un maillage direct des agrégats (Durán Zuazo et Pleguezuelo, 2008). Cependant, l'intensification de l'agriculture a fortement modifié les communautés d'adventices, entraînant l'apparition d'espèces résistantes aux herbicides, et la diminution de la diversité des mauvaises herbes et de leurs services écosystémiques (Jordan et Vatovec 2004). Bien que ces études restent peu nombreuses en Asie du Sud-Est, elles ont montré un impact important du type d'usage du sol (Shrestha et al. 2010) et de l'utilisation d'herbicides sur les assemblages d'adventices, pouvant potentiellement affecter le contrôle de l'érosion.

Dans cette première étude, j'étudie l'effet du type d'usage du sol sur les interactions entre les adventices et les caractéristiques physicochimiques du sol à Huai Lang, avant le début et à la fin de la saison de mousson. Par usage du sol, j'entends la culture ou l'assemblage de cultures au cours de l'année précédant l'échantillonnage. Je me suis concentrée sur deux variables d'usage du sol: la présence d'hévéa (pas d'hévéa, jeunes hévéas, hévéas matures) et la culture annuelle associée (pas de culture, riz pluvial, maïs). J'ai mesuré différentes propriétés du sol: i. la teneur en eau du sol; ii. la densité apparente du sol; iii. la teneur en carbone et en azote, ainsi que le rapport C / N; et iv. taux d'infiltration. J'ai utilisé des méthodes statistiques quantitatives pour étudier les relations entre ces caractéristiques et celles du couvert végétal: i. la densité des mauvaises herbes, ii. la biomasse de la litière, iii. la richesse des espèces herbacées, et iv. la biomasse d'adventices vivantes.

The recent expansion of rubber tree plantations in mountainous Northern Thailand has been strongly encouraged due to high financial incentives (Fox and Castella 2013). However, these plantations also have severe effects on soil conservation: while in young plantations the soil is usually protected by intercrop or understory, mature plantations are often clean-weeded. Most studies investigating the impact of rubber tree 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, rubber tree monocultures decrease biodiversity and increase soil degradation compared to forests (Janeau et al. 2003; Beukema et al. 2007; Podwojewski et al. 2008; Valentin et al. 2008; Paiboonvorachat and Oyana 2011), but are similar to or have slightly higher biodiversity and soil conditions than other tree plantations (Gnanavelrajah and Shrestha 2007; Guillaume et al. 2016). 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.

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 and 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 and Pleguezuelo 2008). However, agricultural intensification worldwide has strongly modified weed communities, leading to the appearance of herbicide-resistant weed species and to the decrease of weed diversity and associated benefits (Jordan and Vatovec 2004). Although such studies remain limited in Southeast Asia, they tend to demonstrate a strong impact of land use (Shrestha et al. 2010) and herbicides on weed assemblages, potentially affecting erosion control.

In this first study, I investigate the effects of land use on the interactions between weeds and soil physicochemical characteristics in Huai Lang, before the start and at the end of the monsoon season. By land use, I mean the crop or assemblage of crops and associated farming practices during the year preceding sampling. I focused on two land use variables: the presence of rubber trees (no rubber tree, young rubber trees, mature rubber trees) and associated annual crop (no annual crop, upland rice, maize). I investigated different 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 and nitrogen content, as well as C/N ratio, which respectively impact aggregate stability, plant growth, and organic matter quality; and iv. infiltration rates. I used quantitative statistical methods to investigate the relations between these characteristics and the characteristics of plant cover: i. weed density, ii. litter biomass, iii. herbaceous species richness, and iv. living weed biomass.

3.1 METHODS

3.1.1 Sampling protocol

Data acquisition was conducted from 2016 to 2018 at the end of the rainy (October–November) or dry (March) seasons, in 20 fields and with five repetitions of 1 m² per field, as presented in Chapter 2. Infiltration rates were available for two sampling periods (March 2016 and March 2017). Infiltration data was analysed at the 1 m² level. Species richness was calculated as the total number of herbaceous species found within each field. All other plant and soil data were averaged for each field within each sampling period. Soil cover data was manually measured on the three sampling periods (see part 2.3.5). I complemented this approach with litter biomass (i.e. the sum of dry weeds and crop residues biomass) as an indicator of the level of soil protection provided by dry weeds and crop residues.

3.1.2 Humidity correction

Rainfall variability within and among the sampling periods led to a difficult comparison of soil humidity. For instance, rainfall height was 1 mm during the first sampling period (March 2016) and 18.9 mm during the third (March 2017). I thus normalised soil humidity for previous precipitations using the Antecedent Precipitation Index (API, Descroix et al. (2002)). More specifically, I calculated a corrected soil humidity index as the residuals obtained from the model presented below. I chose this model from a set of models including API , \sqrt{API} , $\log(API + 1)$ and $\log(API)$ as the model with the lowest AIC (Akaike Information Criteria: a measure of the quality of a model, penalised by the number of parameters).

$$\underbrace{\theta}_{\text{observed humidity}} = \underbrace{\alpha \times \log(API + 1)}_{\text{API effect = fitted value}} + \underbrace{\epsilon}_{\text{error = corrected humidity index}}$$

The corrected humidity index was equal to the difference between the observed and fitted values, which corresponds to the model error ϵ .

3.1.3 Data transformation and analysis

Species Accumulation Curves (SAC) represent the number of species found as a function of the cumulative identification effort. They can be used to estimate the total number of species in an environment (represented by the asymptote of the curve); or to estimate the adequacy of the survey in representing the weed communities in the different land uses, which was the objective of their use here (function *specaccum*, package *VEGAN*). To have a convenient representation of site and individuals distance in ordination methods, I Hellinger-transformed the abundance matrices before analysis, as recommended by Legendre and Gallagher (2001). I tested the effect of land use on plant communities composition by conducting redundancy analyses followed by pairwise comparisons (function *multiconstrained*, package *BIODIVERSITYR*).

In order to test the variability of plant and soil characteristics with land use and season, I conducted mixed multivariate ANOVAs (R package `LME4`, function `lmer`) including the two land use variables (trees: no rubber tree, young rubber tree, mature RT; and annual land use: no annual crop, maize, upland rice) and their interaction with the season. Similarly, to investigate plant-soil interactions, I conducted for each soil variable a mixed multivariate ANCOVA including as explanatory variables the season, all plant variables (living plants biomass, litter biomass, richness, and plant density) and their interaction with the land use variables. Plant density and the proportion of coarse elements were log-transformed and biomasses were square-root transformed to ensure normality of the residuals. I did not include interactions between the two land use variables because the design was incomplete (i.e. no maize or rice under mature rubber tree plantations).

For all models I also included a spatial autocorrelation variable, determined with the following steps:

1. I fitted a multivariate regression with all fixed effects included.
2. I calculated the spatial correlogram based on the residuals of this regression and the significance of the correlation for each distance class (function `correlog`).
3. If the correlation was significant only for a distance of 0 m, then the autocorrelation was only within each field, from one sampling period to another. This would be taken into account by random effects in the final model, so I kept no spatial autocorrelation variable.
4. Else, I calculated the autocovariate with the minimal, non-null distance yielding a significant correlation as the neighbourhood radius.
5. I computed a new multivariate ANOVA including all fixed effects, the autocovariate.

Measurements in each field were not independent from one sampling period to another. I thus included field-level random effects in the multivariate ANOVAs in step 5. For infiltration data (for which the data of the 5 repetitions per field were not averaged) I included both field-level and sampling period-level random effects. I then performed an AIC-based model selection. The significance of effects was estimated using ANOVA type III sum of squares when there was at least one significant interaction, ANOVA type II sum of squares otherwise. I estimated marginal effects for each variable or interaction with the `EMMEANS` package (functions `emmeans`, `emtrends`).

I had multiple descriptors of plant communities and soil characteristics. Conducting numerous tests and comparisons increases the risk of false discovery, i.e. the risk of finding a significant variation or difference which is actually due only to chance. In order to lower this risk, I decided to limit the number of variables: I thus removed from the analysis variables with a Pearson correlation coefficient higher than 0.75. Besides, I also applied more stringent conditions on the significance of tests when one type of test was repeated multiple times. More specifically, in parts 3.2.3 and 3.2.4, I conducted 10 multivariate ANOVAs with land use and season as explanatory variables. In part 3.2.5, I run 12 multivariate ANCOVAs. I considered that the control of type-I errors should be conducted within each group of similar models. As a result, I chose as a new significance threshold $P = 0.05/12 = 0.0042$.

This is an approach similar to usual Bonferonni corrections, where each P-value is multiplied by the number of tests (Wright 1992).

3.2 RESULTS

3.2.1 Variations in plant communities composition with land use

As showed in Fig. 3.2, the species accumulation curves reached saturation when considering all land uses, but not when considering separately each land use (especially for land uses for which we had little data, such as fallows). This indicates that although we well-described the communities as a whole, we probably missed some species within individual land uses. As this chapter does not integrate shrub and tree species, their species accumulation curve is not described here but can be found in Fig. S3.1. Poaceae and Euphorbiaceae were the most common families among herbaceous species. The most abundant species were *Ageratum conyzoides*, *Conyza sumatrensis* and *Mitracarpus hirtus*. Both *Ageratum conyzoides* and *Conyza sumatrensis* have been described as major weeds in various staple crops due to allelopathy for *Ageratum* and resistance to some herbicides for *Conyza* (Itoh et al. 1992). Nam-Matra (2017) reported others of the species we identified as serious weeds in Thailand, especially in upland rice fields (e.g. *Ageratum conyzoides*, *Acmella paniculata*, *Bidens pilosa*, *Mimosa diplotricha*, *Mitracarpus hirtus*, *Eleusine indica*). The composition of herbaceous weed communities significantly differed with land use, as both the annual land use and the presence of trees had very significant effects on communities ($P < 0.001$, Fig. 3.3). In particular, the communities in mature rubber trees plantations (with no annual crop) were very different from others, and characterised by the presence of the ferns *Selaginella helferi* and *Thelopterys subelatus* (not shown).

3.2.2 Correlations among soil and plant communities variables

Soil cover data was manually measured on the three first sampling periods (see part 2.3.5) and was highly correlated to plant biomass (Table 3.1). As plant biomass is easier to measure and more precise, I only retained plant biomass in the following analyses. Living plant biomass and plant density were also positively and significantly correlated with species richness (Table 3.1).

Among soil variables, the calculated hydraulic conductivity was strongly correlated with the volume infiltrated in 10 min (Table 3.1). The volume infiltrated in 10 min is a non-transformed variable, not depending on the good adjustment of a model, and I had more data for this variable (March 2016 and 2017) than for hydraulic conductivity (March 2016 only) so I will describe only the results for the volume in the following paragraphs. Soil bulk density decreased significantly with soil carbon and nitrogen content ($P < 10^{-6}$, Table 3.1). As carbon and nitrogen contents were highly correlated, I will only describe results for carbon content in the following analyses.

Figure 3.2: Species accumulation curves for herbaceous species (i.e. number of species found depending on the number of field surveyed), depending of the land use. Bottom right: global species accumulation curve, all land uses considered. The vertical bars indicate the standard deviation of predicted species richness.

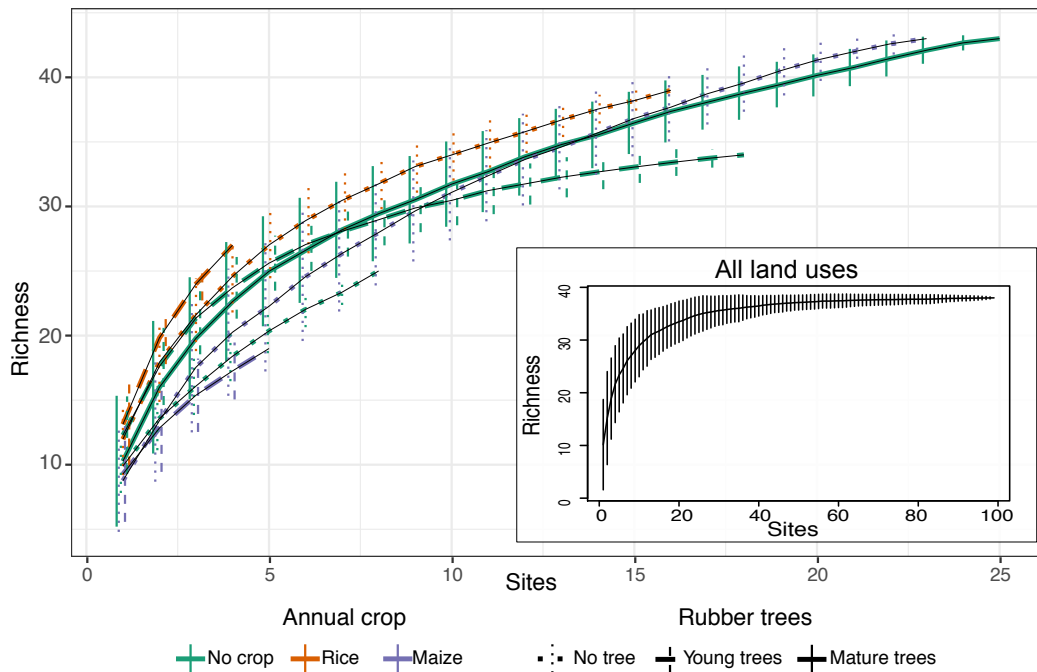
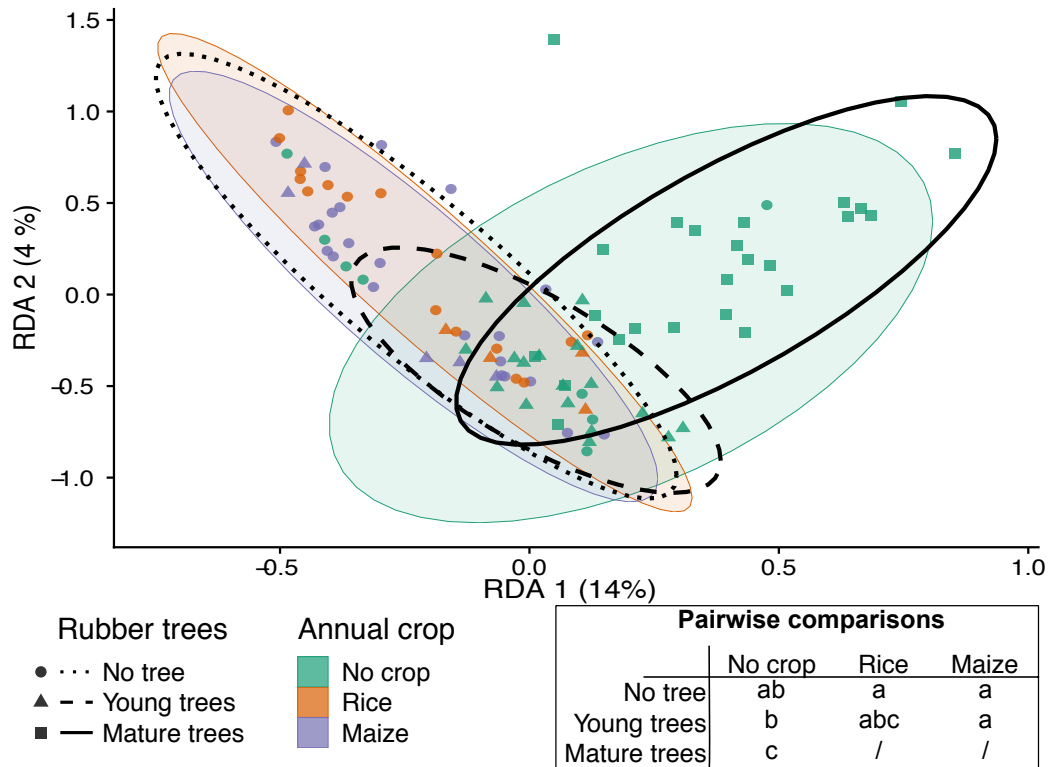


Table 3.1: Pearson correlation coefficients within a. plant and b. soil variables. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

a.	Plant density	Species richness	Litter biomass	Living plant area (%)
Living plants biomass (g m^{-2})	0.30 **	0.25*	-0.18	0.84 ***
Plant density (plant m^{-2})		0.34 *	-0.20 *	0.66 ***
Species richness (n of species)			-0.22 *	0.59 ***
Litter biomass (g m^{-2})				-0.26 *

b.	N content	Soil bulk density	Soil humidity	Vol. inf. 10 min	Hydraulic conductivity ($\mu\text{m s}^{-1}$)
C content (%)	0.94 ***	-0.62 ***	-0.20	-0.15	0.12
N content (%)		-0.60 ***	-0.19	-0.11	0.00
Soil bulk density (g cm^{-3})			-0.02	0.14	-0.45*
Soil humidity (%)				-0.06	0.11
Vol. inf. 10 min (mL)					0.78 ***

Figure 3.3: Variations of plant communities composition with land use. Annual land uses correspond to colours and the presence of trees is represented by different symbols. Each point represents one study field. Full coloured ellipses and black ellipses represent the confidence interval of the communities associated with annual land uses and the presence of trees, respectively. On the bottom right, pairwise comparisons of individual land uses combining the annual crop and the presence of trees; different letters indicate significant differences ($P < 0.05$).

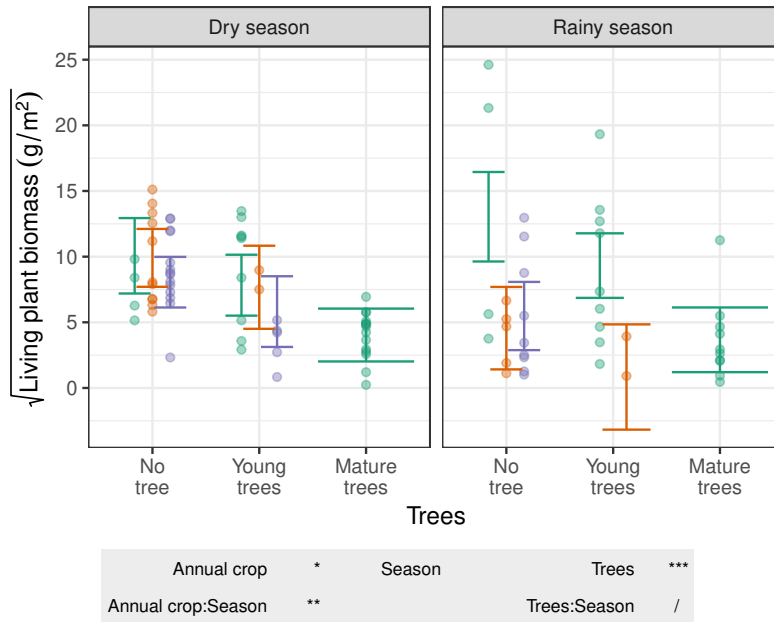


3.2.3 Variations of plant characteristics with land use

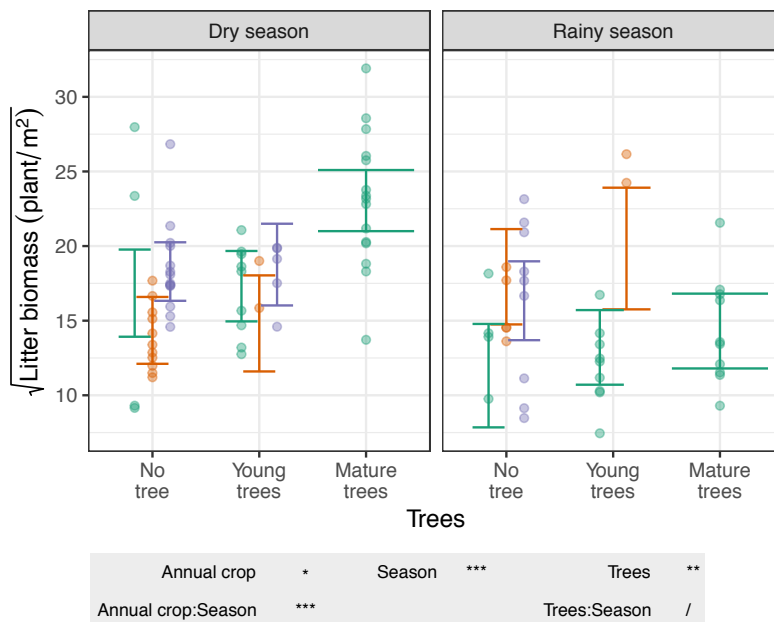
Living plants biomass was on average $67 \pm 57 \text{ g m}^{-2}$ in the dry season, and $73 \pm 132 \text{ g m}^{-2}$ in the rainy season. Mature rubber tree plantations had significantly lower biomass ($24 \pm 26 \text{ g m}^{-2}$) than young rubber tree plantations ($77 \pm 87 \text{ g m}^{-2}$) or fields with no rubber tree ($90 \pm 111 \text{ g m}^{-2}$, $P = 9 \cdot 10^{-5}$, Fig. 3.4a). Fields with no crop tended to have higher biomass than fields with maize or rice in the rainy season, but this was not significant when correcting for multiple testing (interaction: $P = 6 \cdot 10^{-3} > 4.2 \cdot 10^{-3}$). Litter biomass was on average $355 \pm 176 \text{ g m}^{-2}$ in the dry season and $236 \pm 146 \text{ g m}^{-2}$ in the rainy season. In the dry season, it was significantly lower in rice fields than in maize fields and intermediate in fields with no annual crop, but higher under mature rubber tree plantations than young rubber tree plantations or fields without rubber trees. In the rainy season, it was lower in fields with no annual crop than in rice, and intermediate in maize (interaction between annual crop and season: $P = 10^{-7}$, Fig. 3.4b.). Plant density was on average $242 \pm 260 \text{ plant m}^{-2}$ in the dry season and $772 \pm 1322 \text{ plant m}^{-2}$ in the rainy season. Log-transformed plant density was significantly lower in the dry season than in the rainy season ($P < 10^{-3}$). It tended to be lower in mature rubber tree plantations than in young rubber tree plantations, and intermediate in fields with no trees (but

Figure 3.4: Variations of a. living plants biomass and b. litter biomass with land use and season. Annual land uses correspond to colours and the presence of trees is represented as the x-axis. Each point represents the average value of the considered variable in one field within one sampling period. Tables under each plot present the simplified results for each multivariate ANOVA. *: P < 0.05; **: P < 0.01; ***: P < 0.001; n.s.: P > 0.05; /: removed from the model during stepwise model selection.

(a) Living plants biomass.



(b) Litter biomass.

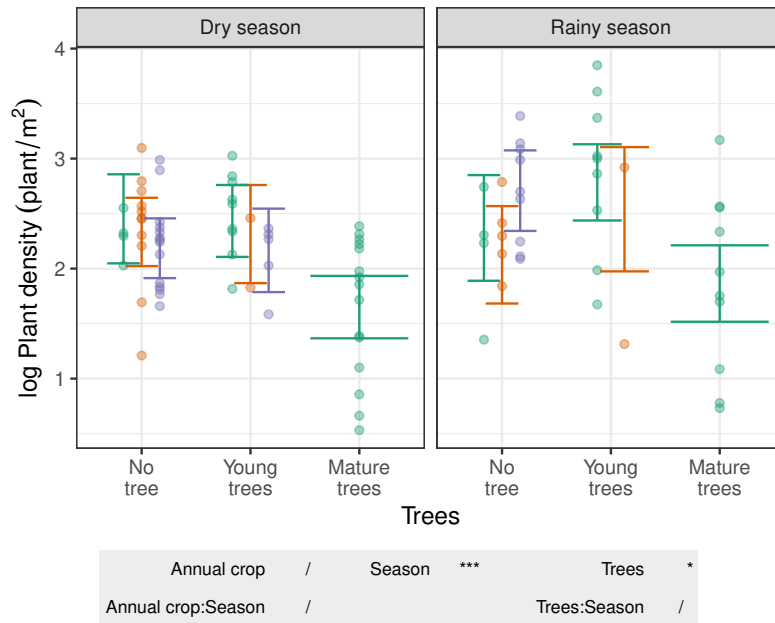


Annual crop

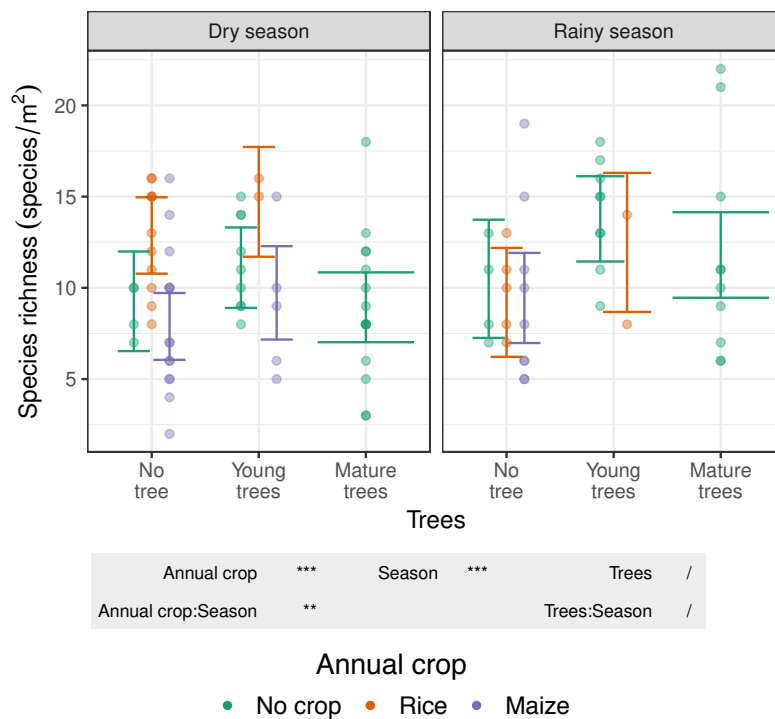
- No crop
- Rice
- Maize

Figure 3.5: Variations of a. plant density and b. species richness with land use and season. Annual land uses correspond to colours and the presence of trees is represented as the x-axis. Each point represents the average value of the considered variable in one field within one sampling period. Tables under each plot present the simplified results for each multivariate ANOVA. *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$; n.s.: $P > 0.05$; /: removed from model during stepwise model selection.

(a) Plant density.



(b) Plant richness.



$P = 2.3 \cdot 10^{-2} > 4.2 \cdot 10^{-3}$, Fig. 3.5a). Herbaceous plant richness was on average 10 ± 4 species m^{-2} in the dry season and 12 ± 5 species m^{-2} in the rainy season. In the dry season, it was higher in rice fields than in maize fields and intermediate in fields with no annual crop (interaction between annual crop and season: $P = 5 \cdot 10^{-4}$, Fig. 3.5b.).

3.2.4 Variations of soil properties with land use

Soil humidity was on average $16 \pm 9\%$ in the dry season and $25 \pm 8\%$ in the rainy season. I observed an increase in soil humidity in the March sampling with time, which could be due to an earlier beginning of the rainy season. The humidity correction allowed to correct for the precipitation heterogeneity among sampling periods. Soil humidity varied significantly with the sampling period ($P < 10^{-6}$), even when including only dry season sampling ($P < 10^{-6}$, Fig. 3.6a.). On the contrary, corrected humidity index still varied between the dry and rainy season ($P < 10^{-5}$) but not among dry season sampling periods ($P = 0.11$, Fig. 3.6b.).

Corrected humidity index was significantly higher in mature rubber tree plantations than in young rubber tree plantations or fields without trees ($P < 3 \cdot 10^{-15}$) and was significantly higher in the rainy season compared to the dry season ($P < 1.4 \cdot 10^{-6}$, Fig. 3.8a.). The proportion of coarse elements was $6 \pm 10\%$ (Fig. 3.7). Bulk density was 1.22 ± 0.10 $g\ cm^{-3}$. None of them varied with land use or season ($P > 0.5$, Figure 3.8b). Soil carbon content was $2.2 \pm 0.5\%$. Although it tended to be lower in mature rubber tree plantations than in young rubber tree plantations or fields without rubber tree, it was not significant when spatial auto-correlation was considered in the model (Fig. 3.9a). C/N ratio was higher in the rainy season ($P < 2.1 \cdot 10^{-3}$, Figure 3.9b). The volume infiltrated in 10 min was very variable within each field, and did not vary significantly with land use (Figure 3.10).

3.2.5 Interactions between weeds and soil properties

I then investigated the variations of soil characteristics with plant cover characteristics: living plants density, litter biomass, living plants biomass, and weeds richness separately for the dry and rainy season. Main results are summarised in Table 3.2 and the results of the model selection can be found in Table 3.3 (dry season) and Table 3.4 (rainy season). Land use (both annual land use and the presence of RTs) were included in the models, but if their interactions with plant variables are not significant their effect is not discussed again here, as it was detailed above.

In the dry season, carbon content tended to increase with living plants biomass (square-root transformed, $P = 1.4 \cdot 10^{-2}$, higher than the significance threshold for multiple testing correction). C/N did not vary with any plant variable. The corrected humidity index significantly decreased with plant density in fields with no annual crop and significantly increased with plant density in upland rice fields (interaction annual crop:plant density; $P = 6.8 \cdot 10^{-4}$). The bulk density tended to decrease with plant density in young rubber tree plantations, but not in fields with no rubber trees or in mature rubber tree plantations (interaction plant density:RT, $P = 4.0 \cdot 10^{-2}$, not significant after multiple testing correction). The volume infiltrated in 10 min tended to decrease with litter biomass ($P = 2 \cdot 10^{-2}$, not significant after multiple testing correction). In the rainy season, C content tended to decrease with

Figure 3.6: Variability of a. soil humidity and b. corrected humidity index with the sampling period. Each point represents the averaged humidity or corrected humidity index for one field at one sampling date. a. Effects of sampling periods, all included or only dry seasons included: $P < 10^{-6}$. b. Effects of sampling periods, all included: $P < 10^{-6}$; only dry seasons included: $P = 8 \cdot 10^{-2}$.

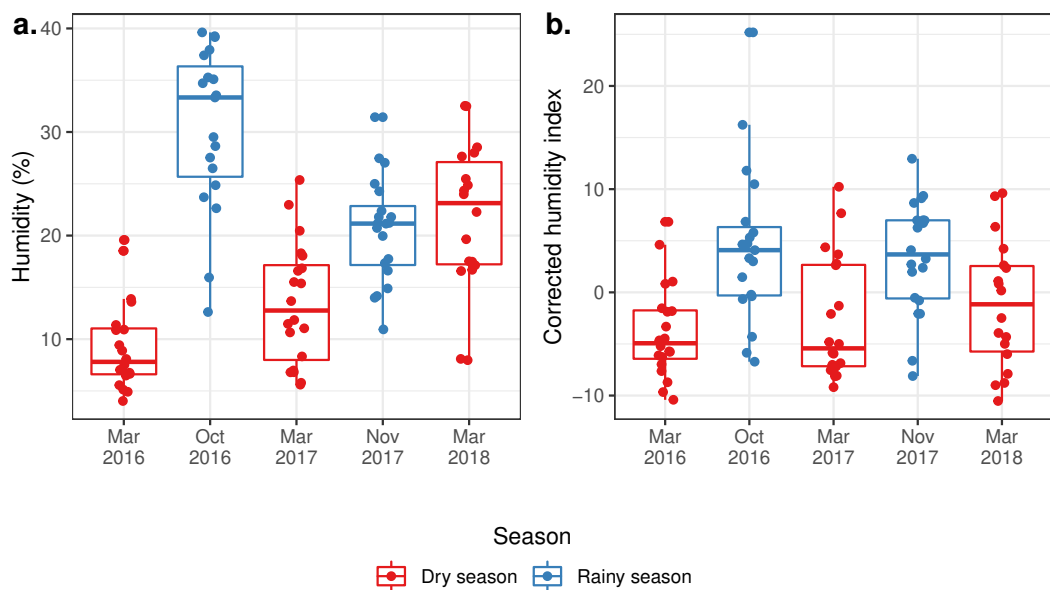


Figure 3.7: Variations of soil coarse elements with land use. Annual land uses correspond to colours and the presence of trees is represented as the x-axis. Each point represents the average value of the considered variable in one field within one sampling period. The effects of annual crop and presence of trees were not significant.

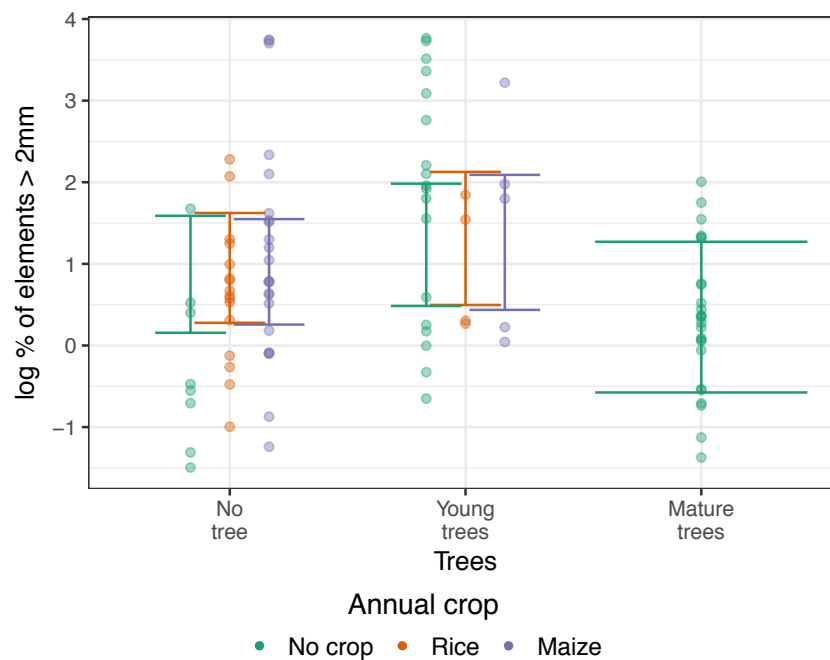
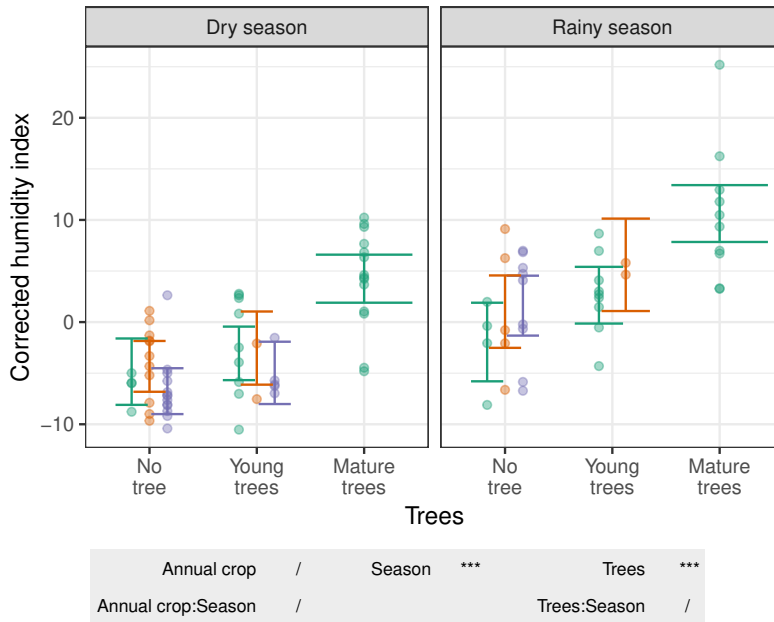


Figure 3.8: Variations of a. corrected humidity index, and b. bulk density with land use and season. Annual land uses correspond to colours and the presence of trees is represented as the x-axis. Each point represents the average value of the considered variable in one field within one sampling period. Tables under each plot present the simplified results for each multivariate ANOVA. *: $P < 5 \cdot 10^{-2}$; **: $P < 10^{-2}$; ***: $P < 10^{-3}$; n.s.: $P > 5 \cdot 10^{-2}$; /: removed from model during stepwise model selection.

(a) Soil humidity.



(b) Soil bulk density.

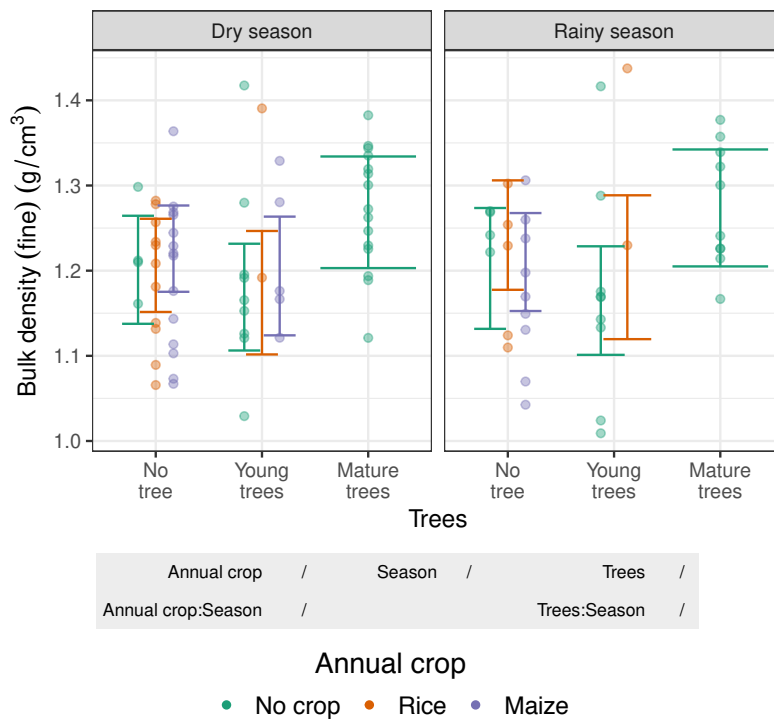
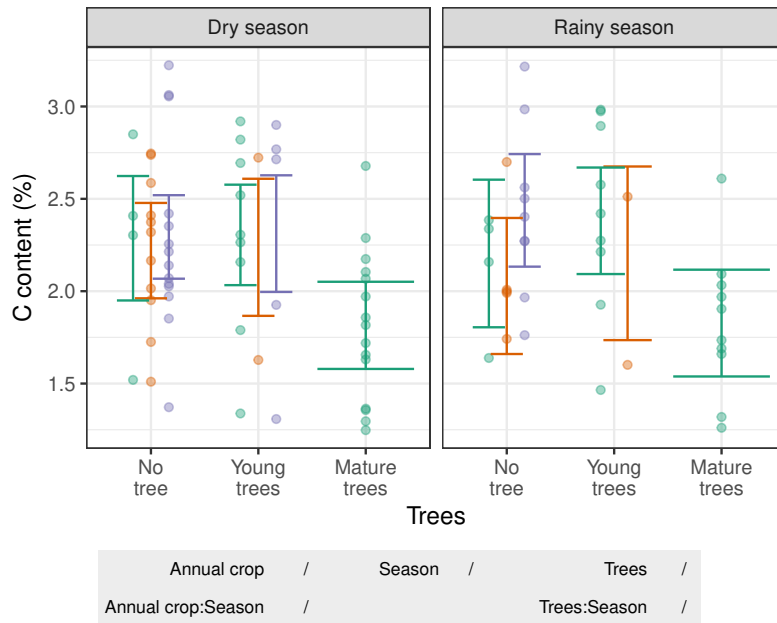


Figure 3.9: Variations of a. C content and b. C/N ratio with land use and season. Annual land uses correspond to colours and the presence of trees is represented as the x-axis. Each point represents the average value of the considered variable in one field within one sampling period. Tables under each plot present the simplified results for each multivariate ANOVA. *: $P < 5 \cdot 10^{-2}$; **: $P < 10^{-2}$; ***: $P < 10^{-3}$; n.s.: $P > 5 \cdot 10^{-2}$; /: removed from model during stepwise model selection.

(a) C content.



(b) C/N ratio.

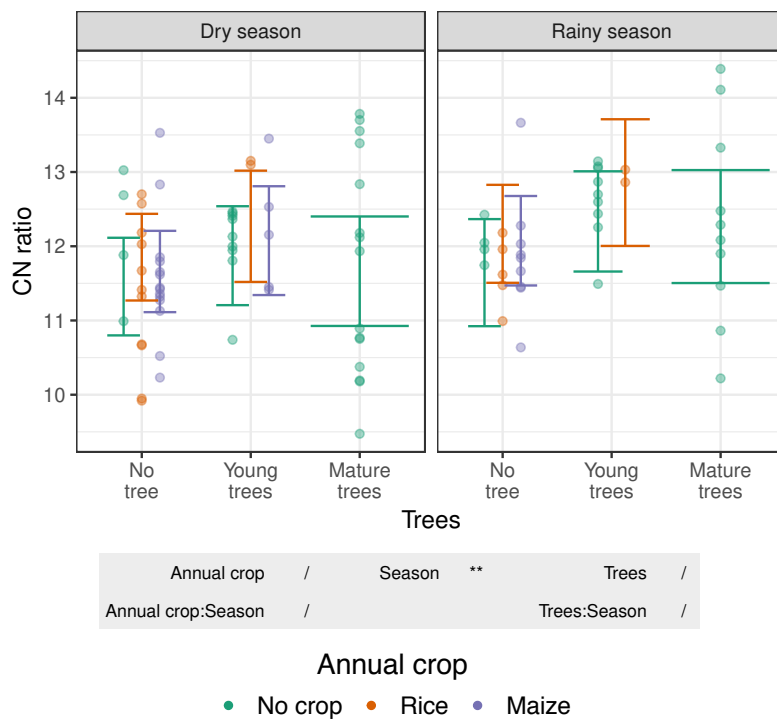
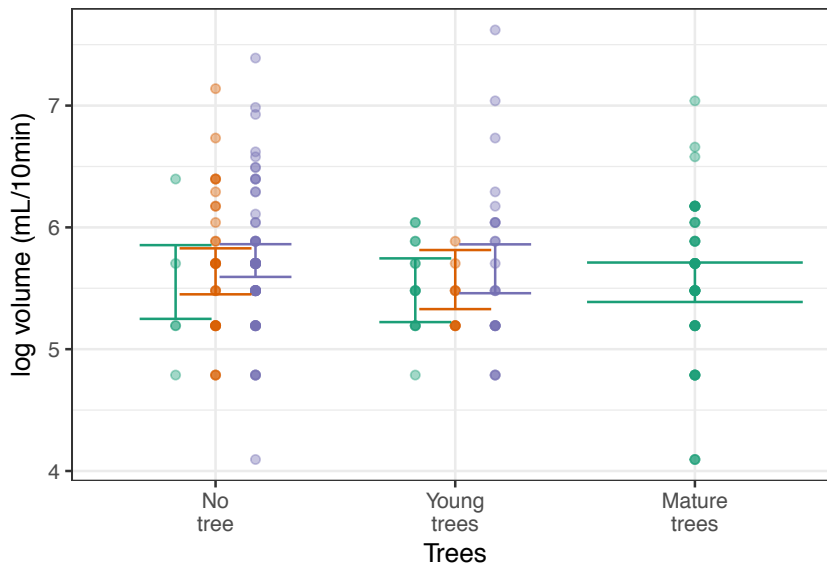


Figure 3.10: Variations of volume infiltrated in 10 min with land use, in the dry season. Annual land uses correspond to colours and the presence of trees is represented as the x-axis. Each point represents the value obtained from one infiltration test. The table under the plot presents the simplified results for each multivariate ANOVA. *: $P < 5 \cdot 10^{-2}$; **: $P < 10^{-2}$; ***: $P < 10^{-3}$; n.s.: $P > 5 \cdot 10^{-2}$; /: removed from model during stepwise model selection.



plant density in rice fields and to increase in maize fields or fields with young rubber tree (interaction plant density:annual crop, $P = 3.5 \cdot 10^{-2}$; interaction plant density:RT, $P = 2.3 \cdot 10^{-2}$, not significant after multiple testing correction). The corrected humidity index increased with plant density in fields with no rubber trees only (interaction plant density:RTs; $P = 7.6 \cdot 10^{-4}$). C/N ratio and bulk density did not vary with any plant variable.

3.3 DISCUSSION

In this chapter, I investigated the interactions between plant-related variables and soil physicochemical characteristics and how land use variables - the presence of rubber trees and the nature of the current annual land use - affect these interactions.

3.3.1 Multiple testing and new P-value threshold

I presented raw P-values, as calculated by each model. However, Wright (1992), among others, showed that it was necessary to control for inflated type-I error when conducting multiple testing. I took a very conservative approach similar to Bonferonni's correction by decreasing the P-value significance threshold from $5 \cdot 10^{-2}$ to $4.2 \cdot 10^{-3}$, which resulted in some of my results to become non-significant.

Those results (with $5 \cdot 10^{-2} > P > 4.2 \cdot 10^{-3}$) are less reliable than those obtained with very low P-values. Yet I considered that they are still worth presenting in this manuscript and discuss these tendencies below.

Table 3.2: Summary of the results obtained from plant-soil interaction models. Dark green (respectively dark red) arrows denote reliable positive (resp. negative) effects, significant after multiple testing corrections ($P < 4.2 \cdot 10^{-3}$). Light green (respectively light red) arrows denote positive (resp. negative) tendencies, not significant after multiple testing corrections ($5 \cdot 10^{-2} > P > 4.2 \cdot 10^{-3}$).

<i>Dry season</i>				
Response variable	Living plants biomass	Plant density	Herbaceous richness	Litter biomass
C content	↑			
C/N ratio				
Corrected humidity		↓ (no crop) ↑ (rice)		
Bulk density		↓ (young RT)		
Volume infiltrated				↓
Hydraulic conductivity		↓ (no crop) ↑ (rice)	↓ (rice) ↓ (no rubber tree)	↓
<i>Rainy season</i>				
Response variable	Living plants biomass	Plant density	Herbaceous richness	Litter biomass
C content		↑ (Maize, young rubber tree) ↓ (Rice)		
Corrected humidity		↑ (no rubber tree) ↓ (Young rubber tree, Mature rubber tree)		

Table 3.3: Results of multiple ANOVA regressions - Dry season. SS: sum of squares. Chisq/F value: test statistic, depending on whether the final model includes quantitative variables. Df: degree of freedom. P: P-value, based on the test statistic. Estimates are calculated based on marginal effects, i.e. averaged on all the other variables kept in the model. Plant density was log-transformed and biomasses were square-root transformed. Different letters in the estimate column denote significant pairwise interactions ($P < 5 \cdot 10^{-2}$).

Response variable	Explanatory variable	SS	Chisq/F	Df	P	Estimate	R ²
C content	<i>Living plant biomass</i>	0.56	6.4	1	1.4e-2	$2.2 \pm 0.9 \cdot 10^{-3}$	38
	AC	0.60	6.9	1	1.6e-2	$7.4 \pm 2.8 \cdot 10^{-1}$	
C/N ratio	AC	1.6	4.4	1	3.6e-2	$4.8 \pm 0.2 \cdot 10^{-2}$	30
Corrected humidity index	<i>Plant density</i>	102	8.4	1	5.5e-3		74
	<i>Annual land use</i>	22	0.9	2	0.41		
	RT	178	7.3	2	1.6e-3		
	<i>Plant density:Annual land use</i>	205	8.4	2	6.8e-4		
Bulk density	AC	13	1.0	1	0.31		
	<i>Plant density</i>	0.00	0.04	1	0.83		36
	RT	0.04	3.07	2	$5.4 \cdot 10^{-2}$		
	<i>Plant density:RT</i>	0.00	0.19	1	0.66		
Volume infiltrated (log)	<i>Plant density:RT</i>	0.05	3.41	2	4.0e-2		
	<i>Litter biomass</i>	1.34	5.1	1	0.026		9
Hydraulic conductivity	AC	0.48	1.8	1	$-5.8 \cdot 10^{-1}$		
	NA						

3.3.2 *Plant communities*

The species accumulation curves showed that although we relatively well described the herbaceous communities as a whole, we probably missed some species in individual land uses despite our relatively extensive sampling protocol. This result could be expected from the usual distribution of species in tropical areas, with few dominant species but many rare ones (de Rouw et al. 2015) which makes it difficult to thoroughly describe the whole communities.

In terms of plant communities composition, the relatively low amount of variance explained by the first axes of the redundancy analysis had two main causes. Firstly, the abundance matrix was a sparse matrix (with many zeros), resulting in lower explained variance (Legendre and 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 plant 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); and disturbances are known to have a long-lasting effect on weed communities, in particular through seedbank (Renne and Tracy 2007). We showed that mature rubber tree plantations had very specific weed assemblages compared to other land uses, and were for instance characterised by ferns such as *Thelepterys subelatus* and *Selaginella helferi*. This was likely due to higher soil water content and lower light availability than in annual crops.

3.3.3 *Weed biomass, density and richness*

In terms of biomass and species richness, my 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 9 species in paddy rice to 22 for mature rubber tree plantations (Gnanavelrajah and Shrestha 2007; Shrestha et al. 2010). Average living biomass in the present study was much lower under mature rubber tree plantations (0.2 kg m^{-2}) than in fields with annual crops (0.9 kg m^{-2}). 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. However, the observed biomasses were much higher than those recorded under similar crops in Eastern Thailand (0.18 kg m^{-2} in mature rubber tree 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). Indeed, I found that both living plant biomass and plant density increased with species richness. While the communities were in general over-dominated by *Ageratum* and *Conyza*, less abundant species probably had some influence on total biomass, which

might explain this result. These secondary species might play an important role in the functioning of the ecosystem (Mariotte et al. 2016).

3.3.4 *Soil physical properties and erosion*

I did not find variations of the proportion of coarse elements or of soil density with land use. The bulk density in our sampled plantations ($1.22 \pm 0.10 \text{ g cm}^{-3}$) was higher than reported in rubber tree monocultures in lowland Acrisols of Sumatra (Indonesia, 0.93 g cm^{-3} to 0.98 g cm^{-3} , Guillaume et al. (2016)) and similar to bulk density in mountainous rubber tree plantations on Ferralsols and Cambisols in Yunnan (China) (1.1 g cm^{-3} to 1.3 g cm^{-3} , de Blécourt et al. (2013)).

The interactions between plant density and soil water content are ruled by complex processes. High soil water content favours plant germination and 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. I showed that soil water content was low in upland rice fields during the dry season but increased with weed density; it also increased with weed density in fields with no rubber trees in the rainy season. This suggests either that under these conditions, water availability is a limiting factor for plant growth (in the dry season); or that weeds limit evaporation more efficiently than they increase transpiration; or that weed limit crust formation and favour infiltration and thus water storage in the soil. Under such conditions, allowing weeds to grow might thus increase water availability for crops. In mature rubber tree plantations, high relative air humidity under the canopy decreases the atmospheric evaporative demand in respect to open-field situations, which explains much higher soil humidity. 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 rubber tree plantations, weed cover is thus likely to decrease erosion. In humid plantations, humidity decreased with plant density in the rainy season; thus soil cover can decrease runoff. In open fields, at the end of the dry season, weed cover can slightly increase soil humidity and decrease aggregates slaking during the first rains which in turn tends to decrease crust formation, runoff and erosion (Patin et al. 2012).

Organic C content is known to increase aggregation, porosity, and the stability of aggregates, as confirmed by my finding that bulk density decreases with carbon and nitrogen content. However, contrarily to previous studies (Guillaume et al. 2016), I did not find any variation of C content or C/N ratio with land use, maybe because the mature rubber tree plantations sampled in this study were relatively young (around 12 years old, compared to 17 on average in Guillaume et al. (2016)) and only the first to be planted in the study area. Considering that C content did not vary with the season, the increase of the C/N ratio in the rainy season was surprising. It was likely due to an increase in the quantity of organic matter in the soil (due to the degradation of crop roots and aerial parts), combined with a decrease of nitrogen content (which might have been consumed by the crop).

While none of these trends were detectable, their combination might have led to significant variations of the C/N ratio.

Abundant soil cover by weeds has been shown to favour higher organic C and N contents (Abraham and Joseph 2016). Considering the timescale of my study, it is more likely that the tendency of C content to increase with living plants biomass in the dry season results from erosion mitigation rather than actual carbon storage in the soil. Indeed, C and N content observed at a given time are a residual from quantities removed by erosion processes, added by plants (e.g. root decay) and transformed by micro-organisms over the previous years. Thus soils that have undergone low erosion rates and retain high soil organic carbon content might now favour abundant weed assemblages. This is particularly true during the dry season when measurements are probably less disturbed by recent fertiliser applications than in the rainy season. However, past fertilisation levels might also have influenced plant communities. I chose not to investigate this possibility because of the uncertainty about the amount of fertilizer used (collected from farmers' reports and not checked on-field). A longer-term study of the history and past management of the fields might be necessary to investigate more in-depth the interactions between weeds and 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). Diverse communities also decrease soil erosion (Seitz et al. 2016). It is thus surprising that I did not detect major changes in soil properties with species richness, and likely due to the strong dominance of *A. conyzoides* and *C. sumatrensis* in the communities.

3.3.5 *Management and erosion control*

Despite low water availability during the dry season, weed biomass at the end of the dry season was high, which may constitute an important asset to protect soil from the high erosivity of the first rains at the beginning of the rainy season. 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 rubber tree (Abraham and Joseph 2016), its acceptance might be easier for rubber than for upland rice or maize farmers.

3.3.6 *Comparison with previous results*

This chapter is the continuation of the study described in Neyret et al. (2018). In this article, we presented results obtained in the first sampling period only (March 2016), studying a chronosequence of four land uses in a well-balanced design. The present

work extended this work by including more land use types and observations in the rainy season. It confirms the results already published in terms of differences in living plants and litter biomass, plant species composition and soil humidity with land use; as well as variations of plant richness that were ambiguous in the initial study. It also confirms the high specificity of weed communities under rubber tree plantations. As in Neyret et al. (2018), the present results show that soil humidity is the main soil characteristic that is associated with weed communities, although the exact relationships were different, probably due to the different way that land use types were integrated into the models.

3.4 CONCLUSION

I found variations in both weed abundance (biomass, plant density) and community composition with land use. Soil water content was the highest in mature rubber tree plantations and varied differently with weed density depending on the land use, which suggests that different types of weed communities might have different impacts on soil properties. Fine-scale soil characterisation, as well as a better comprehension of field history and management practices, are needed to understand better soil-weeds interactions. Besides, erosion processes take place at various timescales: continuous monitoring of soil erosion and weeds cover is needed on an annual basis to appreciate the seasonal variation of these processes; this will be investigated in Chapter 6. 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.

In this study, I have focused on the impact of weed communities characteristics on soil properties. However, rather than one-directional effects, soil properties probably feedback on plant assemblages. The differences found in plant-soil interactions in the various land uses might stem from variations in weed communities composition. To further investigate these inter-relations, I will in the next Chapters quantify the effects of land use and soil on plant communities composition, but also put these assemblages in a wider context of temporal and spatial variability.

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Conclusion en français

Dans cette étude, j'ai montré qu'il existait des variations d'abondance des adventices (biomasse, densité de plantes) et de composition des communautés en fonction de l'usage du sol. L'humidité du sol était la plus élevée dans les plantations d'hévéa matures et présentait des relations différentes avec la densité des adventices en fonction du type d'usage du sol. Cela suggère que différents types de communautés d'adventices pourraient avoir des impacts différents sur les propriétés du sol. Une caractérisation fine des sols, ainsi qu'une meilleure compréhension de l'historique des champs et de leurs pratiques de gestion, sont nécessaires pour mieux comprendre les interactions sol-adventices. En outre, les processus d'érosion se déroulent à différentes échelles de temps: un contrôle continu de l'érosion du sol et de la couverture adventices est nécessaire sur une base annuelle pour apprécier la variation saisonnière de ces processus; cela sera étudié au chapitre 6. Enfin, des recherches interdisciplinaires portant sur les processus décisionnels des agriculteurs, et sur le compromis entre rendement et protection des sols, seront essentielles pour faire face aux menaces actuelles sur la durabilité des plantations.

Dans cette étude, je me suis concentrée sur l'impact des caractéristiques des communautés d'adventices sur les propriétés du sol. Cependant, plutôt que des effets unidirectionnels, il existe certainement des rétroactions des propriétés du sol sur les assemblages de plantes. Les différences trouvées ici entre les interactions plantes-sol dans les divers usages du sol pourraient provenir de variations dans la composition des communautés adventices. Afin d'approfondir l'étude de ces interactions, je vais dans les prochains chapitres quantifier les effets de l'usage du sol et du sol sur la composition des communautés végétales, mais également placer ces assemblages dans un contexte plus large de variabilité temporelle et spatiale.

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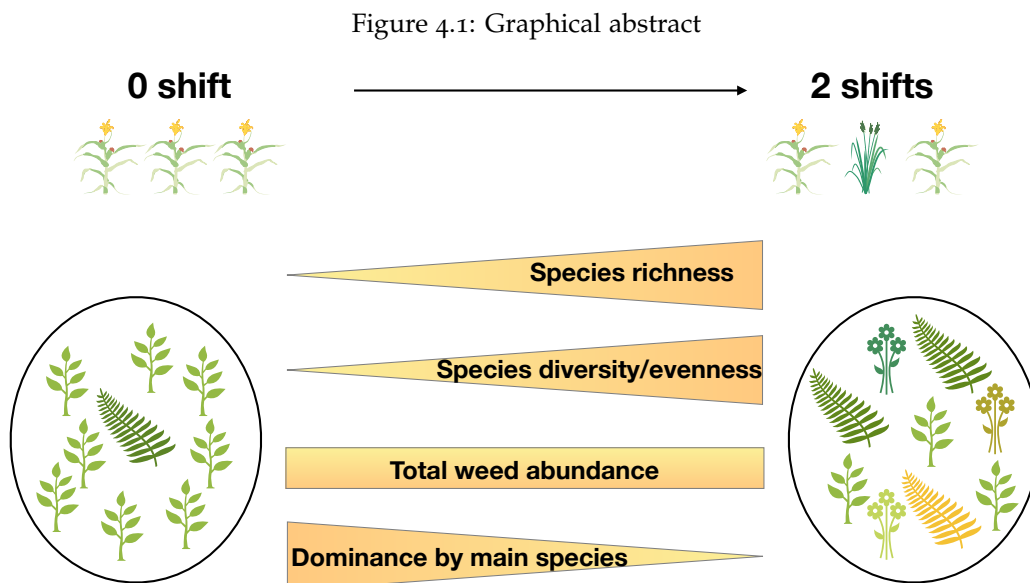
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Table 3.4: Results of multiple ANOVA regressions - Rainy season. SS: sum of squares. Chisq/F value: test statistic, depending on whether the final model includes quantitative variables. Df: degree of freedom. P: P-value, based on the test statistic. I provide estimates calculated based on marginal effects, i.e. averaged on all the other variables kept in the model. Plant density was log-transformed and biomasses were square-root transformed. Soil variables which did not vary with any plant variable were omitted.

Response variable	Explanatory variable	SS	Chisq/F	Df	P	Estimate	R ²
C content	<i>Plant density</i>	0.25	1.8	1	0.19	$2.2 \pm 0.9 \cdot 10^{-3}$	38
	<i>Annual crop</i>	0.01	0.03	2	0.97	$7.4 \pm 2.8 \cdot 10^{-1}$	
	RT	1.1	3.8	2	3.5e-2		
	AC	0.35	2.4	1	0.13	$-3.3 \pm 2.1 \cdot 10^{-1}$	
	<i>Plant density:Annual crop</i>	1.9	6.41	2	5.1e-3	Plant density:Rice $-5.2 \pm 1.9 \cdot 10^{-4}$ Plant density:No crop $-8.4 \pm 9.0 \cdot 10^{-2ab}$ Plant density:Maize $6.2 \pm 2.5 \cdot 10^{-b}$	
	<i>Plant density:RT</i>	1.3	4.32	2	2.3e-2	Plant density:No rubber tree $-2.1 \pm 1.5 \cdot 10^{-1ab}$ Plant density:Mature RT $-1.0 \pm 1.6 \cdot 10^{-4}$ Plant density:Young RT $3.1 \pm 1.6 \cdot 10^{-b}$	
N content	RT	0.01	3.4	2	3.5e-2	Mature rubber tree $1.5 \pm 0.1 \cdot 10^{-4}$ Young rubber tree $1.9 \pm 0.1 \cdot 10^{-1ab}$ Mature RT $1.9 \pm 0.1 \cdot 10^{-b}$ $1.5 \pm 4.1 \cdot 10^{-1}$	22
	AC	0.00	0.1	1	0.71		
CN content	RT	5.0	4.2	2	2.4e-2	No rubber tree 12 ± 1 Mature rubber tree 12 ± 2 Young RT 13 ± 2 $8.3 \pm 1.8 \cdot 10^{-1}$	22
	AC	9.3	20	1	6.5e-5		
	<i>Plant density</i>	179	11	1	2.1e-3		60
Corrected humidity index	RT	446	13	2	4.5e-5		
	AC	0.1	0.0	1	0.93		
	<i>Plant density:RT</i>	291	9.1	2	7.6e-4	Plant density:Mature rubber tree -2.0 ± 1.0 Plant density:Young rubber trees -1.9 ± 1.0 Plant density:No rubber tree 3.9 ± 1.1	^a ^a ^b

THE NUMBER OF LAND USE SHIFTS IMPACTS WEED DIVERSITY

In this chapter, I investigate the effect of crop succession on the diversity of plant communities. I quantify the temporal variability of land uses as the number of land use shifts during the three years preceding sampling and show that this temporal variability has a larger impact on plant richness and diversity than land use identity. More temporally diverse fields harboured more diverse, even communities which were less dominated by single species.



Introduction en français

Dans les zones tempérées, il a été montré que l'intensification de l'agriculture affecte fortement les communautés adventices en favorisant les espèces les plus compétitives imitant la culture principale (Fried et al. 2009; Fried et al. 2010; Fried et al. 2015) et en diminuant la diversité et l'abondance des adventices (Squire et al. 2000; Hyvonen et Salonen 2002; Baessler et Klotz 2006; Fried et al. 2009; Hyvönen et al. 2011). Le fonctionnement des écosystèmes repose sur la présence d'un nombre d'individus et d'une diversité suffisants pour fournir des services écosystémiques complémentaires. La diminution de la diversité et de l'abondance des adventices met donc en péril leurs services écosystémiques (Matson et al. 1997; Tscharrntke et al. 2005), telles que la conservation des sols (Durán Zuazo et Pleguezuelo 2008), la lutte antiparasitaire (Crowder et Jabbour 2014), la filtration de l'eau et le soutien de la biodiversité dans les niveaux trophiques supérieurs (Marshall et al. 2003; Petit et al. 2011). Les adventices ont également été proposées comme espèces indicatrices - c'est-à-dire comme des espèces reflétant l'état biotique ou abiotique de l'environnement - pour déterminer l'impact environnemental des pratiques agricoles.

Diverses études ont proposé de mettre en place des rotations culturales plus variées pour lutter contre les adventices avec moins d'herbicides (Kegode et al. 1999; Petit et al. 2011) et pour favoriser la diversité des communautés adventices tout en réduisant leur capacité à entrer en compétition avec les cultures (Liebman et Dyck 1993). Doucet et al., 1999; Squire et al., 2000; Ulber et al., 2009). Des expériences à la ferme ont montré que, en zone tempérée, diversifier les rotations culturales avait généralement un effet positif sur la diversité des plantes et des sols. Cela peut être dû, par exemple, à des différences de date de semis et à l'utilisation d'herbicides spécifiques aux cultures (Doucet et al. 1999; Cardina et al. 2002; Ulber et al. 2009). Ces études ont étudié l'effet de différents types de rotations ou du nombre de cultures cultivées dans une rotation donnée. Cependant, il peut exister une confusion entre les effets dus au nombre de changements de cultures ou dus au nombre de cultures différentes présentes dans la rotation. Jiang et al. (2016) ont montré que les rotations dans les rizières d'Asie du Sud-Est affectaient fortement la diversité fongique et bactérienne. Cependant, à ma connaissance, l'effet de la diversité temporelle des cultures sur la diversité et l'abondance des adventices dans les systèmes agricoles d'Asie du Sud-Est reste peu étudié (voir cependant Shrestha et al. (2010)). Une meilleure compréhension des relations entre les rotations culturales et la biodiversité non cultivée est particulièrement critique dans les zones montagneuses, où la biodiversité a été fortement affectée par les récentes modifications des pratiques agricoles (Rerkasem et al. 2009).

Dans ce chapitre, je cherche à déterminer l'effet de la diversité temporelle de l'usage des sols à court terme sur la richesse, la diversité, l'abondance et la composition des communautés d'adventices dans un paysage agricole fragmenté du nord de la Thaïlande. J'ai quantifié la diversité temporelle de l'usage du sol en mesurant soit le nombre de changements d'usage du sol, soit le nombre de types d'usage du sol différents au cours des trois saisons de culture précédant l'échantillonnage. Bien que la présente étude se concentre sur la diversité temporelle, le type d'usage du sol affecte également les communautés adventices (Chapitre 3) et est inclus dans les modèles. Ce chapitre résulte d'une coopération avec Nathalie Colbach (Agroécologie, AgroSup Dijon, INRA, Univ. Bourgogne, Univ. Bourgogne Franche-Comté).

In temperate areas, agricultural intensification has been shown to strongly affect weed communities, by favouring species that are more competitive and mimic the main crop (Fried et al. 2009; Fried et al. 2010; Fried et al. 2015) and overall by decreasing in-field weed diversity and abundance (Squire et al. 2000; Hyvönen and Salonen 2002; Baessler and Klotz 2006; Fried et al. 2009; Hyvönen et al. 2011). Ecosystem functioning depends on the presence of enough individuals and a sufficient diversity to provide complementary services. The current decrease in weed diversity and abundance thus endangers their associated ecosystem services (Matson et al. 1997; Tschardt et al. 2005), such as soil conservation (Durán Zuazo and Pleguezuelo 2008), pest control (Crowder and Jabbour 2014), water filtration or nutrient cycling (Gholamhoseini et al. 2013a; Gholamhoseini et al. 2013b; Yagioka et al. 2015), and support of biodiversity at higher trophic levels (Marshall et al. 2003; Petit et al. 2011). Weed communities have also been proposed as indicators of the health and resilience of agroecosystems and can be used as indicator species - i.e. species that reflect the biotic or abiotic state of the environment or provide evidence of the impact of environmental conditions - to help assessing the ecological impacts of farming practices.

Crop rotation, or more generally crop temporal diversification (as opposed to continuous monoculture), is known to improve soil health and fertility (Watson et al. 2002), can mitigate erosion rates (Morgan 2005) and decrease crop disease risk (Colbach et al. 1994). Various studies have proposed to implement more diverse crop rotations to control weeds with lower herbicide inputs (Kegode et al. 1999; Petit et al. 2011) and to favour weed communities diversity while decreasing their ability to compete with the crop (Liebman and Dyck 1993; Doucet et al. 1999; Squire et al. 2000; Ulber et al. 2009). Farm experiments have shown that in temperate areas, diverse crop rotations usually had a positive effect on plant and soil diversity, due for instance to variations of crop sowing date and to the use of crop-specific herbicides (Doucet et al. 1999; Cardina et al. 2002; Ulber et al. 2009). Most of these studies investigated the effect of different rotations or of the number of crops grown in rotation. However, it is not clear whether the effect is due to the number of land use shifts (e.g. related to disturbances, the number of times that the crop changed) or the number of different crops present in the rotation.

Jiang et al. (2016) showed that rotations in upland rice fields of East Asia strongly affected fungal and bacterial diversity. However, to our knowledge, little is known about the effect of temporal diversity of land uses on weed diversity and abundance in mountainous Southeast Asian agricultural systems (but see Shrestha et al. (2010) in Southeastern Thailand). A better understanding of the relationships between crop rotations and non-cultivated biodiversity is particularly critical in mountainous areas, where biodiversity has been strongly affected by recent modifications of farming practices (Rerkasem et al. 2009).

In this chapter, I aimed at determining the effect of short-term land use temporal diversity on the richness, diversity, abundance and composition of weed communities in a fragmented agricultural landscape of mountainous Northern Thailand. I measured land use temporal diversity as either the number of land use shifts or the number of different land uses in the three growing seasons preceding the sampling. While the focus of this study was temporal diversity, land use identity also affects weed communities (Chapitre 3) and was included in the models. This chapter

results from a collaboration with Nathalie Colbach (Agroécologie, AgroSup Dijon, INRA, Univ. Bourgogne, Univ. Bourgogne Franche-Comté).

4.1 MATERIAL AND METHODS

4.1.1 *Diversity indices*

I used multiple descriptors of weed communities that provided complementary information (Table 4.1). Weed abundance (measured as weed biomass and density) provided information on the productivity of the ecosystem and the potential aggressiveness of weed communities towards the crop. The number of weed species is a simple measure of plant richness, which we complemented by diversity and dominance indices – describing respectively the evenness of the whole community and the strength of the dominance by the main species. Diversity and dominance are important indicators of an ecosystem's resistance and resilience, as more even communities are likely to be more stable and resilient. Besides, two communities with similar richness and diversity can harbour distinct species pools, and I also investigated whether land use temporal diversification affected the identity of weed species using abundance matrices. Abundance matrices were Hellinger-transformed (Legendre and Gallagher 2001).

I classified the species according to a Relative Importance index R_i calculated for each species i as the average of its frequency (f_i , number of plots where species i is present) and relative abundance (p_i , where abundances of herbs and shrubs/trees are all normalised in individuals per square meter).

$$RI_i = \frac{1}{2}(f_i + p_i)$$

4.1.2 *Quantification of land use sequence variability*

I summarised land use as two variables, an "annual land use" variable describing which type of annual land use (maize, upland rice, or no annual crop) and the presence or absence of young rubber tree (Table 4.2). Mature rubber tree plantations, as perennial crops with no temporal variability, were excluded from this chapter. Land use temporal variability can be quantified in two complementary ways, either focusing on the frequency of disturbances or the total number of land uses in a sequence. I used both indices: I calculated on the one hand the number of land use shifts in the three planting seasons preceding sampling ("number of land use shifts", Fig. 4.2, Table 4.3) and, on the other hand, the number of land use types found in the field in the three planting seasons preceding sampling ("number of land use types", Fig. 4.2).

For instance, maize-maize-maize sequences account for 0 shifts and 1 land use type; maize-rice-maize sequences account for 2 shifts and 2 land use types; while maize-rice-no crop accounts for 2 shifts and 3 land use types. Sampling conducted in the rainy season (end of the planting season) and in the next dry season (before the start of the planting season) had the same number of land use shifts and number of past land use (Fig. 4.2). For some fields, I was able to describe the land use

Table 4.1: Selected plant communities characteristics.

Type of data	Name	Calculation	Biological meaning	Details on calculation
Diversity	Species richness	S (number of species present in the field)	Simple biodiversity indicator. Provides information about the local species pool	
	Shannon index	$H = -\sum p_i \log(p_i)$ with p_i the relative abundance of species i within the field	Diversity index, which takes into account both the number of species and their evenness. H tends to 0 when one species is ultra-dominant in the community. It tends towards $\ln(S)$ when the S species are present in equal abundance in the community.	Calculated separately for herbs and shrubs/trees as well as for all species together
	Berger-Parker index	$D = p_{i,max}$ with $p_{i,max}$ max the relative abundance of the most abundant species within the field	Dominance index, measuring the strength of the dominance of the most abundant species. Tends to 1 in monospecific communities and to $1/S$ when the S species are present in equal abundance in the community.	
Abundance	Plant biomass	Biomass (g) per square meter	Information on ecosystem productivity	Measured for herbaceous, shrub and tree species together
	Plant density	Number of individuals per square meter	Weed reproduction success, competition, soil moisture	
Composition	Community composition	Number of individuals per species per field	Indications on how species are associated	Measured for herbaceous, shrub/tree species separately

history only from 2014 onwards, in which case the first sampling point was not used (Table 4.3).

Maize was the most represented land use in the dataset. In order to validate my main results regarding the impact of land use shifts, irrespective of the identity of the current land use, all analyses were conducted twice: i/ including all available data; and ii/ including only fields with maize as the current crop (i.e. maize only or young rubber tree plantations with maize intercrop). For these analyses, we compared only maize fields with no land use shift ($n = 17$) or two land use shifts ($n = 7$) because maize fields with only one shift were too few ($n = 3$).

4.1.3 Statistical analyses

I built models for each plant community characteristic (as response variables) described in Table 4.1. For univariate responses (e.g. richness, diversity, dominance, abundance) I used linear mixed models (function *lmer*, package *LME4*). Each model included the following explanatory variables:

- Temporal land use variability: measured either as the number of land use shifts (levels: 0, 1 or 2) or the total number of land use types (1, 2 or 3) in the three preceding sampling seasons (2 Df, Degrees of freedom);
- Season: end of the dry season or end of the rainy season (1 Df);
- Interaction between land use variability and season (2 Df);
- Annual land use type: maize, rice or fallow (2 Df);
- Presence of trees: with or without rubber trees (1 Df);
- Spatial autocorrelation: see part 4.1.3.a (1 Df).

In my dataset, the treatment of interest (land use variability) was not independent of the field itself or the land use. Indeed, we conducted botanical inventories repeatedly in the same fields and the number of land use shifts in one site were not independent from one year to another. In order to take into account this non-independence, I used field-level random effects in the models. Plant densities (always strictly positive) were log-transformed, and biomasses square-root transformed, to ensure normality of the residuals. I conducted pairwise comparisons between each level of land use temporal variability (e.g., for the number of land use shifts, 0 v. 1, 0 v. 2 and 1 v. 2 shifts; and for the number of land use types, 1 v. 2, 1 v. 3, and 2 v. 3 land use types) while keeping the other explanatory variables constant (*emmeans* function). The significance of each variable in the full model was assessed using ANOVA type II or III tests (i.e. testing the effect of each variable "after" the other fixed effects; function *Anova*, package *CAR*).

For multivariate response matrices, which were the abundance matrices of shrubs/trees and herbaceous species, I conducted redundancy analyses. The matrices were Hellinger-transformed to correctly represent species' unbalanced abundances (Legendre and Gallagher 2001). I also removed from the redundancy analysis three ubiquitous herbaceous species that were likely to mask the effect of interest variables. I included all the explanatory variables described above, save the

Table 4.2: Description of land use identity based on an "annual crop" variable and a "presence of trees" variables. "*" indicates possible presence of small longan or rubber saplings.

Annual crop identity → Presence of trees ↓	Maize	Rice	No annual crop
No trees	Maize monoculture* (n = 22)	Rice monoculture* (n = 13)	Fallow* (n = 4)
Trees	Young rubber with maize intercrop (n = 5)	Young rubber with rice intercrop (n = 4)	Young rubber without intercrop (n = 18)

Figure 4.2: Quantification of land use temporal variability as either the number of shifts or the number of land uses, over three growing seasons (example land use sequence: maize - maize - maize - rice - fallow). Larger symbols indicate the land use type at the time of sampling, while smaller symbols indicate previous land uses.

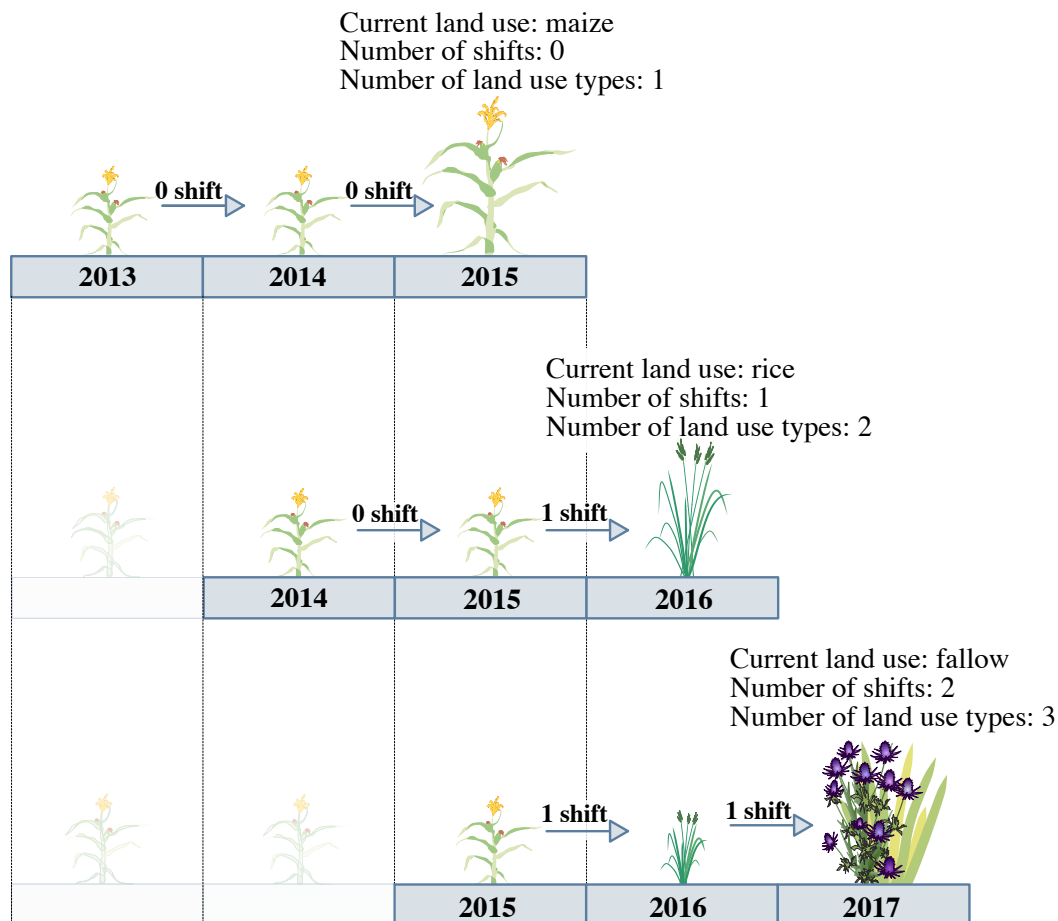


Table 4.3: Crop sequences between 2013 and 2017. Shaded boxes: unknown. The number of land use shifts is calculated based on the land use identities of the three previous growing seasons (see Fig. 4.2).

Field	Land use sequence					Number of land use shifts *		
	2013	2014	2015	2016	2017	2013-2015	2014-2016	2015-2017
1		Maize	Maize	Maize	Rice		0	1
2	Maize	Maize	Maize	Maize	Fallow	0	0	1
3	Maize	Maize	Maize	Maize	Rice	0	0	1
4	Maize	Maize	Maize	Maize	Rice	0	0	1
5	Rice	Maize	Maize	Maize	Fallow	1	0	1
6		Maize	Rice	Rice	Fallow		1	1
7	Maize	Maize	Rice	Maize	Maize	1	2	1
8		Rice	Rice	Maize	Rice		1	2
9	Maize	Maize	Rice	Maize	Rice	1	2	2
10		Rice	Rice	Fallow	Fallow		1	1
11	Rubber tree + Maize	Rubber tree + Maize	Rubber tree + Maize	Rubber tree + Rice	Rubber tree + fallow	0	1	2
12	Rubber tree + Maize	Rubber tree + Maize	Rubber tree + Maize	Rubber tree + Rice	Rubber tree + fallow	0	1	2
13	Rubber tree + Maize	Rubber tree + Maize	Rubber tree + Maize	Rubber tree + Fallow	Rubber tree + Fallow	0	1	1
14	Rubber tree + Maize	Rubber tree + Maize	Rubber tree + Maize	Rubber tree + Fallow	Rubber tree + Fallow	0	1	1
15	Rice	Rubber tree + Rice	Rubber tree + Maize	Rubber tree + fallow	Rubber tree + Fallow	2	2	1

*The land use shift countings of the periods 2013-2015; 2014-2016; and 2015-2017 correspond respectively to the weed sampling in March 2016; November 2016 and March 2017; November 2017 and March 2018.

interaction between temporal variability and season. I tested the significance of each variable with a permutation-based test ($n = 999$). Again, the focus variable was land use temporal variability. Thus, in order to test the differences of species composition between each level of land use temporal variability, I first partialled out the effects of season, land use and space and then conducted pairwise comparisons between each level of land use temporal variability using the *pairwise.factorfit* function (Package *RVAIDEMEMOIRE*). As conducting multiple pairwise comparisons increases the risk of false discovery (i.e. considering that a difference is significant while it is only due to chance), I corrected the P-values for multiple comparisons using the *fdr* method.

4.1.3.A Spatial autocorrelation

For all models, I also included a spatial autocorrelation variable, which I integrated differently depending on the response.

When the response was univariate (e.g. diversity, richness) the spatial autocorrelation was determined with the following steps:

1. I fitted a multivariate regression with all fixed effects included, and with no random effect.
2. I calculated the spatial correlogram based on the residuals of this regression and the significance of the correlation for each distance class (function *correlog*).
3. If the correlation was significant only for a distance of 0 m, then the autocorrelation was only within each field, from one sampling period to another. This would be taken into account by random effects in the final model, so I kept no spatial autocorrelation variable.
4. Else, I calculated the autocovariate with the minimal, non-null distance yielding a significant correlation as the neighbourhood radius.
5. I computed a new multivariate ANCOVA including all the fixed effects, the autocovariate and random effects.

When the response was multivariate (abundance matrices), I first calculated the spatial polynomials to the third degree (e.g., with X the Easting and Y the Northing: X, X², Y, Y², XY, etc.). After scaling these new variables, I conducted an RDA with the abundance matrix as the response variable and all the spatial polynomials as explanatory variables. I finally conducted stepwise model regression, and only the selected variables were integrated into the final model.

4.1.3.B Indicator species analysis

My last objective was to determine whether certain species were specifically associated with either high or low land use variability. In this regard, I identified groups of indicator species related to each number of land use shifts (resp. land use types). As proposed by Cáceres and Legendre (2009), indicator species are species that can be used as ecological indicators of environmental and ecological conditions or biodiversity. Their association to a given environment (here, the number of land use types or land use shifts) is composed of two components, calculated independently for each species. Component "A" is the probability that a given site belongs to

the target environmental group (i.e. "field with three land use shifts in the past three years") given the fact that the species has been found. This is the specificity of the species as an indicator of the environmental group. Component "B" is the probability of finding the species in sites belonging to the environmental group. This is called the fidelity of the species as an indicator of the target environmental group. I used the INDICESPECIES package (function *multipatt*, *IndVal* method).

4.2 RESULTS

4.2.1 Land use sequences

From 2014 to 2018, we observed a total of 17 distinct land use sequences (Table 4.3, Fig. 4.3), with a repartition of land use sequences that varied with time: for instance the sequence M - M - M (i.e. only maize monoculture, in pink) was observed only during the first sampling period, while sequences including at least one fallow (in purple) appeared later in the study. Young rubber tree plantations were intercropped with rice or maize during two to four years before the shade from the canopy prevented further intercropping. For the representation of land use sequences, I classified land use sequences based on the presence of rice or fallow in the sequence. The number of land use shifts was not independent of land use type: maize fields were more often associated with no land use shift than upland rice fields or fields without annual crop (χ^2 test, $P < 10^{-6}$). Some farmers reported that the decision to grow maize (cash crop) or rice (subsistence crop) depended on both market and familial factors: a family running out of rice would be more likely to grow rice the next year, while the market price of maize might determine the planting of maize fields. This decision was also likely to depend on the start of the rainy season, as maize needs only part of the rainy season to complete its growth.

4.2.2 Plant communities richness

We found a total of 64 herbaceous species, and 88 tree, shrub, sub-tree or liana species among which 63 and 86 (respectively) were identified at least to the genus level.

We measured species richness, diversity and abundance at one given season and compared it to the preceding land use sequence. Species richness at the field level varied from 7 to 26 (median 17) in the dry season and 7 to 31 (median 18) in the rainy season. We identified three groups of species based on breaks in the Relative Importance index bar plot (Fig. 4.4). Three herbaceous species (*Ageratum conyzoides*, *Conyza sumatrensis* and *Mitracarpus hirtus*) were ubiquitous, with a Relative Importance Index > 0.4 . They were removed from later analyses of community composition. We identified 21 intermediate species with a RI comprised between 0.1 and 0.4. The least common species, among which 19 included only one individual, had a RI lower than 0.1 and comprised most shrub and tree species.

Total species richness did not vary with land use shifts in the dry or the rainy season ($P > 0.05$, Table 4.4). However, fields with two land use shifts had significantly higher herbaceous species richness (12.8 on average) than fields with no land use shift (8.2, $P < 0.05$), while fields with one land use shift had intermediate herbaceous

Figure 4.3: Number of fields characterised by a given land use sequence during the three year preceding sampling, over the three periods investigated: 2013-2015, 2014-2016, 2015-2017. Colours indicate the sequence type (e.g. including only maize, rice, or fallow). M: maize; Ri: rice, YR: young rubber trees.

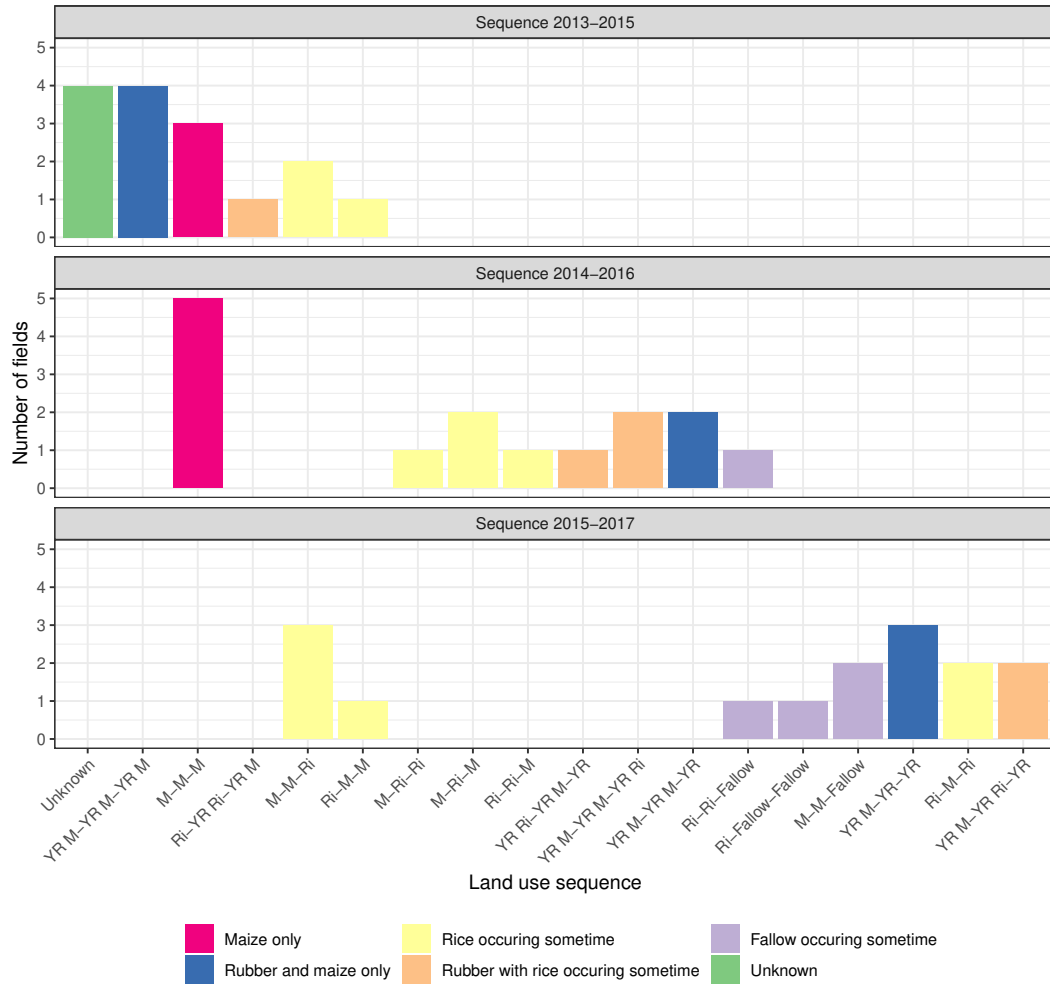
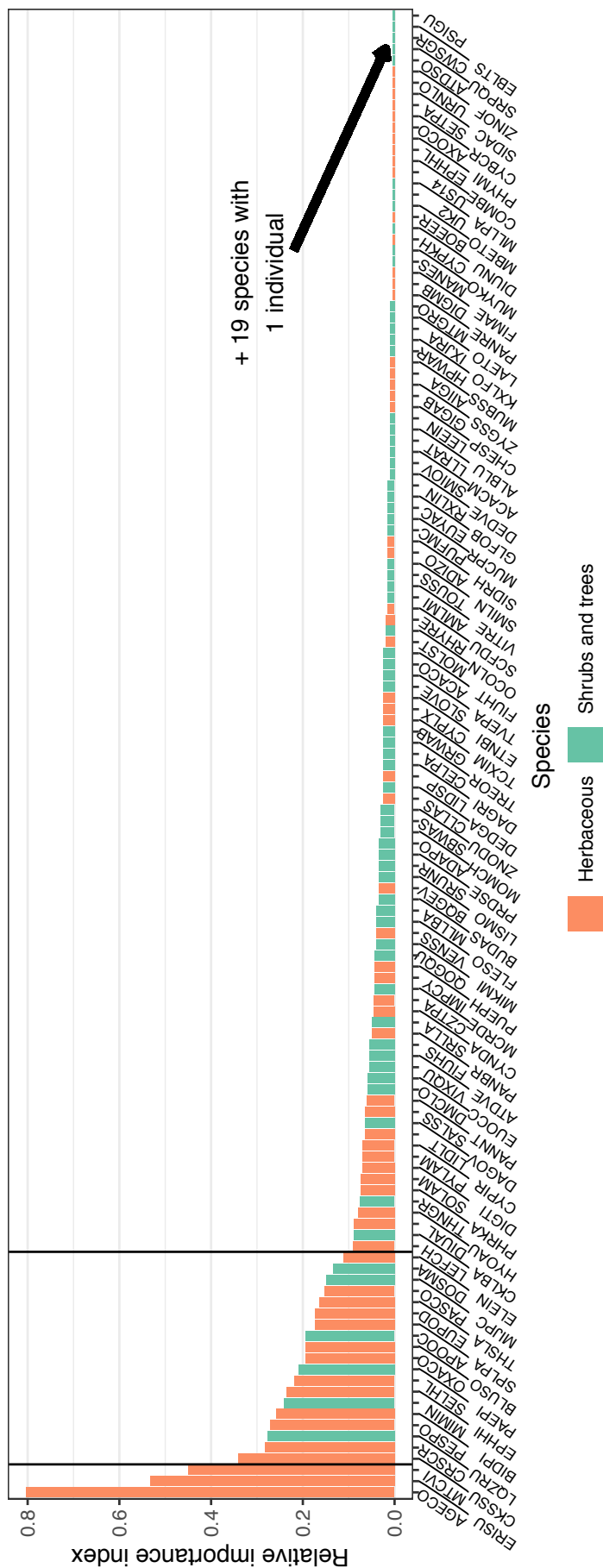


Table 4.4: Effects of crop type and crop variability on plant richness, diversity and abundance. R²: pseudo-R-squared of the total model, i.e. including random effects. *: P < 0.05. **: P < 0.01. ***: P < 0.001. Significance letters are defined based on a p-value threshold of 0.05.

	Number of shifts	Season	Number of shifts*Season	Spatial	Annual crop	Presence of trees	Annual crop * Presence of trees	Number of shifts	Estimate (dry season)	Estimate (rainy season)	R ² (%)
	Partial R ²	Partial R ²	Partial R ²	Partial R ²	Partial R ²	Partial R ²	Partial R ²				
Richness (all species)	3 ns	0 ns	8 ns	2 ns	1 ns	1 ns	1 ns	0	15.9 (11.6 - 20.2) ^a	13.2 (7.8 - 18.5) ^a	38
								1	15.9 (13.1 - 18.6) ^a	18.9 (16 - 21.8) ^a	
								2	18 (13.9 - 22.2) ^a	18.7 (14.2 - 23.1) ^a	
Richness (herbaceous species)	12 *	1 ns	0 ns	4 ns	3 ns	6 ns	0 ns	0	8.2 (5.3 - 11.2) ^a	8.6 (5 - 12.1) ^a	57
								1	11.9 (9.9 - 13.9) ^{ab}	12.7 (10.6 - 14.7) ^a	
								2	12.8 (9.9 - 15.6) ^b	13.3 (10.2 - 16.3) ^a	
Richness (tree/shrub species)	1 ns	0 ns	14 *	22 *	0 ns	21 *	2 ns	0	7.4 (4.6 - 10.2) ^a	4.3 (0.8 - 7.8) ^a	48
								1	4 (2.2 - 5.7) ^a	6.2 (4.3 - 8.1) ^a	
								2	5.5 (2.8 - 8.2) ^a	5.6 (2.7 - 8.6) ^a	
Dominance (all species)	11 *	22 ***	2 ns	1 ns	3.	4 ns	2 ns	0	0.7 (0.6 - 0.9) ^a	0.9 (0.7 - 1.1) ^a	48
								1	0.6 (0.5 - 0.7) ^{ab}	0.7 (0.6 - 0.8) ^a	
								2	0.5 (0.3 - 0.6) ^b	0.7 (0.5 - 0.8) ^a	
Dominance (herbaceous species)	14 **	15 **	2 ns	4 ns	6 *	1 ns	3 ns	0	0.8 (0.7 - 1) ^a	0.9 (0.7 - 1.1) ^a	56
								1	0.6 (0.5 - 0.7) ^{ab}	0.7 (0.6 - 0.8) ^a	
								2	0.5 (0.4 - 0.6) ^b	0.7 (0.5 - 0.8) ^a	
Shannon (all species)	9 *	16 **	3 ns	1 ns	0 ns	0 ns	3 ns	0	1 (0.7 - 1.3) ^a	0.8 (0.3 - 1.2) ^a	34
								1	1.2 (1 - 1.4) ^{ab}	0.9 (0.7 - 1.2) ^a	
								2	1.6 (1.3 - 1.9) ^b	1.1 (0.7 - 1.5) ^a	
Shannon (herbaceous species)	13 **	8 *	4 ns	5 ns	2 ns	2 ns	4 ns	0	0.7 (0.3 - 1) ^a	0.6 (0.3 - 1) ^a	52
								1	1 (0.8 - 1.2) ^{ab}	0.9 (0.6 - 1.1) ^a	
								2	1.4 (1.1 - 1.7) ^b	1 (0.7 - 1.4) ^a	
Shannon (tree/shrub species)	0 ns	0 ns	0 ns	1 ns	2 ns	18.	0 ns	0	0.7 (0.2 - 1.1) ^a	0.7 (0.1 - 1.2) ^a	49
								1	0.6 (0.3 - 0.9) ^a	0.6 (0.3 - 0.9) ^a	
								2	0.6 (0.2 - 1) ^a	0.5 (0.1 - 1) ^a	
Biomass*	1 ns	10.	6 ns	1 ns	8 ns	13 ns	4 ns	0	8.9 (4.9 - 13) ^a	3.6 (-1.4 - 8.6) ^a	35
								1	7.6 (5.1 - 10.2) ^a	7.3 (4.6 - 10) ^a	
								2	7.9 (4 - 11.8) ^a	5.4 (1.3 - 9.6) ^a	
Abundance**	0 ns	10 *	2 ns	0 ns	2 ns	0 ns	4 ns	0	5.3 (4.4 - 6.2) ^a	5.9 (4.8 - 7) ^a	28
								1	5.5 (5 - 6.1) ^a	5.9 (5.3 - 6.5) ^a	
								2	5.1 (4.2 - 5.9) ^a	6 (5.1 - 6.9) ^a	

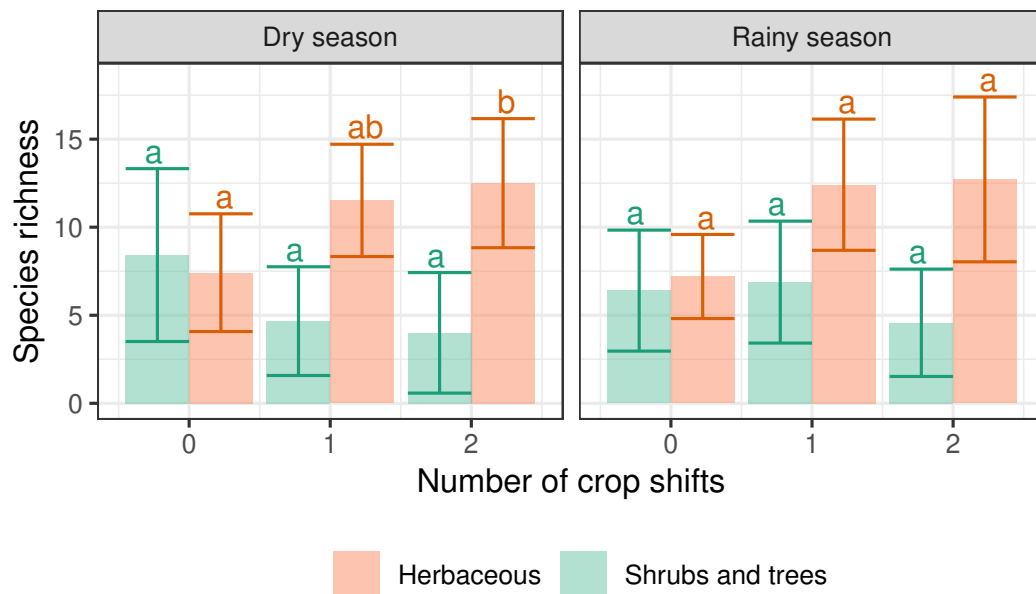
* gm⁻², square root-transformed
 ** plantm⁻², log-transformed

Figure 4.4: Relative Importance index of identified species. Three groups of species, separated by vertical lines, can be distinguished: *A. conyzoides*, *C. sumatrensis* and *M. hirtus* are the three dominant, ubiquitous species; followed by intermediate and rare species.



species richness (Fig. 4.5). The number of land use shifts did not affect herbaceous species richness in the rainy season, nor trees and shrubs species richness either during the dry or the rainy season (Table 4.4, Fig. 4.5). The number of land use shifts explained more variation in herbaceous species richness than land use identity (as accounted by partial R^2 , Table 4.4). Similar results were obtained when considering only fields that were planted with maize (i.e. maize alone or rubber trees intercropped with maize, Table S4.2, Figure S4.1).

Figure 4.5: Variations of species richness per field with the number of land use shifts. Bars represent the mean \pm standard deviation. Different letters indicate significant differences within each group in the models presented in Table 4.4 ($P < 0.05$).



4.2.3 Plant communities abundance

Weed biomass (square root-transformed) and weed density (log-transformed) did not vary with the number of land use shifts nor the number of land use types (Table 4.4).

4.2.4 Plant communities diversity

In the dry season, herbaceous communities were more even when the number of land use shifts increased, with Shannon H' index ranging on average from 0.7 in fields with no land use shift to 1.4 in fields with two land use shifts ($P < 1 \cdot 10^{-3}$, Table 4.4). The same trend was observed for evenness in the total community (shrubs/trees included) but not for shrubs/trees communities only. Communities were generally highly dominated by the main species, but this dominance was weaker when the number of land use shifts increased. Indeed, in fields with no shift, Berger index was 0.7 on average, which indicates that the most abundant species represented 70% of all individuals. Conversely, dominance index was only 0.5 in fields with two land use shifts ($P < 5 \cdot 10^{-2}$, Table 4.4). The number of land

use shifts explained more variation in both evenness and dominance variability than land use identity (higher partial R^2 , compare Tables and 4.4 and S4.1). The same trends for evenness and dominance were observed when considering the number of crops instead of the number of crop shifts, but with lower explanatory power (Table S4.1). It was also the case when taking into account only fields with maize as the current annual crop (Table S4.2).

4.2.5 *Plant communities composition*

I did not find a clear variation in herbaceous nor shrubs and tree communities with the number of land use shifts when partialling out the effects of land use and season (Table 4.5). However, there was a significant variation of both herbaceous and shrub and tree communities with the number of land use types (Table 4.6), although the models explained only 17% and 10% (respectively) of the total variation. Pairwise comparisons showed that for both herbaceous and shrub/tree communities, each number of land use types had significantly different communities from the others ($P < 0.04$ for herbaceous species, $P < 0.02$ for shrub and tree species, data not shown). I thus did not conduct indicator species analysis with the number of land use shifts, but rather with the number of land use types, to identify the species associated to the different number of land use type. I found that few species were indicators of one or two land use types in the past three years, and seven species were significantly associated with fields with three land uses (Table 4.7). For example, the fern *Thelepterys subelatus* was a good indicator of fields with 3 land use types in the previous three years because all sites including the species had 3 land use types (B component = 1.00), although it did not occur in these fields only (A component = 0.74). This species is known in Laos as an indicator of environments with high humidity, shade, and that have not burnt (de Rouw, personal communication). *Phyllanthus amarus* and *Digitaria radicata* occurred almost only within these fields, although not in all. On the contrary, *Lepisanthes rubiginosa* was always found within fields which had had only one or two crops in the three previous years.

4.3 DISCUSSION

The number of land use shifts was an important factor in the determination of herbaceous, but not shrub and trees, species diversity. I also demonstrated that the effect of land use shifts is usually stronger than that of the number of land uses. Previous studies have mainly focused on the effect on weeds of a given rotation (e.g. fixed crop types: corn–soybean, corn-soybean-hay Cardina et al. (2002)) or the switch to low-input systems Barberi et al. (1997). The present study is, to my knowledge, the first to differentiate the effects of land use temporal variability from that of land use identity on weed diversity in Southeast Asia.

4.3.1 *Diversified land use sequences*

From land use history data spanning over 5 years, I showed that farmers often cultivated maize for several years in a row, with occasionally upland rice to break

Table 4.5: Results of the redundancy analyses conducted separately for herbaceous and tree-shrubs communities. The number of land use shifts, the season, the annual land use identity and the presence of trees are used as explanatory variables for the Hellinger-transformed abundance matrix. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Selected spatial polynomials included $(X, Y, Y^2, Df = 2)$ for herbaceous species and $(X, Y, X^2, Y^2, Df = 3)$ for tree and shrub species, and their participation to explained variance was summed.

Explanatory variable	Df	Herbs	Shrubs
		% of total explained variance	% of total explained variance
N land use shifts	2	12.4 .	14.2
Season	1	23.6 **	3.5
Annual land use	2	7.0 *	17.7 .
Presence of trees	1	17.9 **	55
Spatial polynomials	2 3	39.1 ***	20.5 ***
Residuals (%)		71	77

Table 4.6: Results of the redundancy analyses conducted separately for herbaceous and tree-shrubs communities. The number of land use types, the season, the annual land use identity and the presence of trees are used as explanatory variables for the Hellinger-transformed abundance matrix. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Selected spatial polynomials included $(X, Y, Y^2, Df = 2)$ for herbaceous species and $(X, Y, X^2, Y^2, Df = 3)$ for tree and shrub species, and their participation to explained variance was summed.

Explanatory variable	Df	Herbs	Shrubs
		% of total explained variance	% of total explained variance
N land use types	2	14.0 *	15.6
Season	1	22.9 **	3.4
Annual land use	2	20.3 **	19.3 *
Presence of trees	1	6.5	9.1 .
Spatial polynomials	2 3	36.2 ***	52.4 *
Residuals (%)		70.0	76.9

Table 4.7: Indicator species of different numbers of land use types. Component 'A' is the specificity of the species as an indicator of each field's number of land use types. Component 'B' is the probability of finding the species in sites belonging to the site group, i.e. the fidelity of a species to a given number of land uses. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

Species associated with fields with 1 land use type			
	A	B	
<i>Antidesma velutinosum</i>	0.92	0.35	*
Species associated with fields with 3 land use types			
	A	B	
<i>Thelopterys subelatus</i>	0.73	1.00	***
<i>Phyllanthus amarus</i>	0.82	0.71	***
<i>Digitaria radicata</i>	0.88	0.57	***
<i>Thysanolaena latifolia</i>	0.70	0.71	**
<i>Panicum notatum</i>	0.84	0.43	**
<i>Adiantum zollingeri</i>	1.00	0.29	**
<i>Leptochloa panicea</i>	0.77	0.43	*
Species associated with fields with 1 or 2 land use types			
	A	B	
<i>Lepisanthes rubiginosa</i>	1.00	0.63	**
<i>Mimosa invisa</i>	1.00	0.57	*
Species associated with fields with 1 or 3 land use types			
	A	B	
<i>Cyclea barbata</i>	0.91	0.33	*

the maize monoculture. Conversely, upland rice was only cultivated for 2 years in a row. This was related to both socio-economic (e.g. market prices, labour availability) and agricultural strategies. Weed control is also a determining decision factor, as weed infestation usually prevents cultivating rice more than 2-3 years in a row while maize is much more robust to weeds (Sankaran and de Datta 1986) and allows the use of herbicides later in the season due to the use of herbicide-resistant varieties. For instance, with no use of herbicides, weeds under continuous upland rice have been shown to become uncontrollable within three years (de Rouw 1995) and to require that 54% of the total labour in rice fields be spent on weeding (out of 306 days per hectare of total labour, average of 8 publications data based on field countings in Laos, de Rouw, unpublished). In this area, the expansion of rubber trees is still relatively new, with the oldest plantations being planted at the beginning of the 2000s. Intercropping under young rubber trees whose canopy was still open enough (up to usually 4 to 5 years) allowed farmers to optimise their income and probably followed similar decision factors, although we did not directly test this hypothesis.

These strategies led to the emergence of two groups of land use sequences among the fields I investigated. One mostly consisted of continuous maize cultivation (either continuous maize monoculture or young rubber trees with continuous maize intercrop) and the other with alternating cultivation of maize and rice. Thus, the fields with no land use shifts consisted only of maize fields, which is why I also conducted analyses using only maize fields data.

4.3.2 *The number of land use shifts increases herbaceous richness and diversity*

My results show that in addition to a few dominant and ubiquitous species, weed flora in the study site comprised many secondary or rare species, including a large part occurring only once. This result is typical of tropical agroecosystems, where many rare species can be found: for instance, in a study over 3 years comprising 199 plots of annual crops, fallow or forest, de Rouw et al. (2015) found that only 42% of 459 different species appeared more than three times. I demonstrated that land use temporal diversification had a positive effect on herbaceous species richness and diversity. As I showed in Chapter 3 that rice fields had on average higher plant richness than maize fields, and as rice fields were usually more temporally diverse, the increase of plant richness with the number of land use shifts might be related to a “rice” effect as well as to a “number of land use shifts” effect. Nonetheless, the positive effect of land use shifts on plant richness was supported even when considering only maize fields, i.e. when removing any possible confusion with the annual crop. Moreover, the effect of the number of land use shifts was stronger than that of land use identity and the number of land uses in the past three growing seasons. Previous studies, mostly in temperate areas, indeed found that increasing number of land use shifts had a positive effect on weed richness and diversity (Liebman and Dyck 1993; Doucet et al. 1999; Squire et al. 2000; Ulber et al. 2009). However, most found that this was only a marginal effect compared to current land use identity or management practices (Barberi et al. 1997; Smith and Gross 2007). For instance, Doucet et al. (1999) found that crop sequence had a weaker impact on weed density than land use identity and a very low effect on plant diversity. Using a simulation approach, Bürger et al. (2015) showed that while tillage was the main

factor affecting weed diversity, the simplification of crop rotations also reduced biodiversity, especially in regions already harbouring low diversities. The outcome of such studies investigating the effects of temporal diversity on plants depends on the timescale of the study. Such effects are likely to be noticeable only when looking at the total weed flora within a field, by looking either at the seedbank or at the flora over multiple years, as opposed to looking at the flora within a single year only (Dessaint et al. 1997). A longer-term study of Huai Lang agro-ecosystem could thus provide further confirmation of our results.

Such increase of weed richness in diversified land use sequences can have multiple causes. Firstly, the fact that plant richness and diversity responded more to the number of land use shifts than the number of land use types suggests that disturbance, and not only the diversity of land uses, favours weed diversity. Weed species respond to a variety of factors, such as the type and dose of herbicides, fertilisers, light availability, or soil preparation. The two main cereal crops in our study - upland rice and maize - differed in their associated farming practices. From direct observations and interviews with farmers, it appeared that herbicide application should differ between rice and maize, especially because of the use of resistant maize allowed the application of glyphosate after maize germination; however I did not detect, numerically, any significant difference in the type or amount of herbicides reported by the farmers (see Chapter 2).

Rice and maize had different sowing and harvesting times, which have been shown to be major determinants of weed communities functional composition (Gunton et al. 2011). For instance, maize has a much shorter growing period, which leaves the fields almost fallow-like with dry maize stalks during a large part of the year. Rice and maize also create different light conditions, which is known to be an important determinant of weed growth (Holt 1995; Colbach et al. n.d.): while rice grows very densely, quickly covering the ground and limiting weed growth, maize leaves most of the soil bare and triggers the growth of photosensitive species. For instance, *A. conyzoides* and *C. sumatrensis* have been shown to have much higher germination rates under full sun (de Rouw et al. 2013). Similarly, rice and maize residues are likely to create different humidity conditions which could favour the germination of different fractions of the seedbank. Thus, variable land uses correspond to variable germinating and growing conditions for weeds, and a selection of different species from one season to another. This can, in turn, allow the maintenance of diverse communities over time (Gaba et al. 2013). The Resource Pool Diversity (RPD) hypothesis (Smith et al. 2010) likewise suggests that diversified crop rotations lead to more diverse soil resources, both directly (through crop specific requirements, root exudates, etc.) and indirectly, through crop-related farming practices (e.g. varying fertiliser inputs). However, in my study area, the fertilisation regimes of maize and rice were relatively similar and finer measurements of maize and rice nutrient uptakes would be necessary to test the validity of this theory in our system.

Contrarily to herbaceous species, trees and shrubs richness and diversity did not respond to changes in the number of land use shifts or the number of land use types. This is due to the weaker response of trees and shrubs to year-to-year shifts, compared to herbaceous species which grow and reproduce more quickly. Indeed, perennial species have more underground reserves from which they can directly

regrow. This makes them less dependent on local conditions and farming practices to establish in a given field.

4.3.3 *The number of land use shifts does not affect weed abundance*

I did not detect changes in weed biomass or density with land use temporal variability, which suggests that weed pressure did not increase with the number of land use shifts or the number of land use type. Conversely, I observed a weaker dominance of the main species, i.e. a lower proportion of individuals belonging to the most abundant species, with an increasing number of land use shifts. The two main species (*Ageratum conyzoides* and *Conyza sumatrensis*) are highly competitive weeds due to allelopathy, resistance to glyphosate (for *C. sumatrensis*) and high seed production (Itoh et al. 1992). In more temporally diverse fields, they are confronted with a continuously varying and unpredictable environment. This might hinder their expansion and reproduction, diminishing their competitive ability and creating opportunities for new species to germinate from the seedbank or to establish from neighbour communities. Land use temporal variability thus prevents the selection of species functionally close to the crop, reduces their ability to compete with the crop (Liebman and Dyck 1993; Smith et al. 2010) and promotes weed diversity, which has been shown to decrease their competitiveness (Storkey and Neve 2018).

4.3.4 *The number of land use types, not land use shifts, affects plant communities*

Contrarily to herbaceous species richness and diversity, which varied more with the number of land use shifts than the number of land use types, I showed that the composition of herbaceous plant communities varied only with the number of land uses - although this effect was not significant when considering maize fields only. Some species were significantly associated with the highest number of land use types in the past three years.

These results suggest that different mechanisms drive the changes in the diversity and composition of plant communities. Plant richness is related both to the frequency of disturbance in the field: a change in the local conditions disturbs the dominant species, and the diversification of resources favours niche diversification, both of which increase species diversity. On the contrary, in our case the number of land use types probably affected plant communities composition only through its dependence with the type of annual crops (e.g. maize v. rice).

4.4 CONCLUSION

Weed management should not aim at suppressing weeds, but rather at promoting diversified and less competitive communities. In this study, I demonstrated that the temporal diversification of land uses increased the diversity of herbaceous plant communities. The implementation and maintenance of diverse crop rotations, as opposed to continuous monocultures could provide a basis for a better use of weeds' ecosystem services and biodiversity conservation.

In this study, I have investigated within-field farming practices, showing that temporal diversity affected weed communities. However, plant communities do not respond only to farming practices but also to other local (e.g. soil, slope) or landscape characteristics, through seed dispersal among different habitat patches. In the next chapter, I quantify the relative impact of land use, soil and landscape factors in the determination of plant communities.

Conclusion en français

La gestion des adventices ne devrait pas viser à les supprimer complètement, mais plutôt à promouvoir des communautés diversifiées et moins compétitives. Dans cette étude, j'ai montré que la diversification temporelle des usages du sol augmente la diversité des communautés de plantes herbacées. La mise en place et le maintien de rotations culturales diverses, par opposition aux monocultures continues, pourraient servir de base à une meilleure utilisation des services écosystémiques des adventices et à la conservation de la biodiversité.

Dans cette étude, j'ai montré que la diversité temporelle des cultures affectait les communautés adventices. Cependant, les communautés végétales ne réagissent pas uniquement aux pratiques agricoles, mais également à d'autres caractéristiques locales (telles que le sol, la pente) ou paysagères, par la dispersion des graines entre différentes parcelles d'habitat. Dans le chapitre suivant, je quantifie l'impact relatif des facteurs liés à l'usage du sol, au sol et au paysage dans la détermination des communautés végétales.

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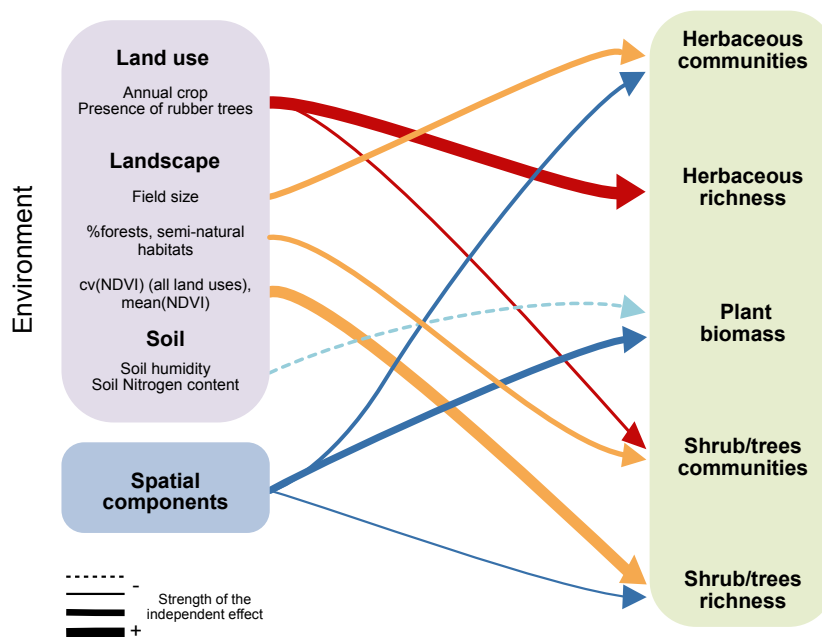
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RELATIVE EFFECTS OF LAND USE, LANDSCAPE, SOIL AND SPATIAL COMPONENTS ON WEED COMMUNITIES

In this chapter, I quantify the relative impact of landscape (defined as the land use composition and configuration of the neighbouring area), local soil variables, land use and spatial components (combinations of spatial coordinates) on the richness and composition of weed communities. I show that landscape is the main factor affecting the composition and richness of herbaceous and shrub/tree communities as well as plant biomass; but that its effect is rarely independent but rather joint with that of other explanatory variables. I also show that species sorting and mass effect are the main meta-community types structuring shrubs and trees as well as herbaceous communities.

Figure 5.1: Graphical abstract.



Introduction en français

La structure des communautés végétales peut être principalement expliquée par des facteurs environnementaux tels que le climat ou le substrat rocheux (Hanzlik et Gerowitt 2011; Hyvönen et al. 2011; Borgy et al. 2015) qui déterminent un pool régional d'espèces. La présence effective d'une espèce à un endroit donné dépend toutefois de multiples autres facteurs et notamment des conditions biotiques et abiotiques locales. Les communautés locales forment des méta-communautés, c'est-à-dire des ensembles de communautés reliées par la dispersion de multiples espèces qui peuvent interagir (Leibold et al. 2004). La dispersion entre communautés affecte la diversité des espèces locales à la fois directement, par exemple en modifiant l'abondance d'une espèce dans une communauté locale par dispersion, et indirectement, en modifiant les interactions entre les espèces. Elle peut être plus ou moins limitée par des facteurs internes (par exemple la production de graines) et externes, tels que la présence de barrières (par exemple des routes) ou de vecteurs (oiseaux, insectes, mammifères) de dispersion.

Déterminer les processus qui structurent une méta-communauté peut renseigner sur les effets relatifs de la compétition, des composants spatiaux et des ressources biotiques ou abiotiques sur la biodiversité dans un milieu donné. Les modèles traditionnels incluent le modèle de méta-communauté neutre (N), qui stipule que la dispersion est le facteur limitant déterminant la structure des méta-communautés. Le modèle de tri des espèces (SS) suppose des capacités de dispersion élevées dans un environnement hétérogène, qui entraîne un tri des espèces via des gradients de ressources. L'existence de dynamiques puits-source ou la présence de niches spatiotemporelles (ou "patches") donnent lieu à des mécanismes de méta-communautés à effet de masse (ME) ou dynamiques de patch (PD). La comparaison des effets des composantes spatiales (liées à la dispersion) et de l'environnement (sol, type d'utilisation des sols, etc.) peut être utilisée pour identifier les principaux processus structurant la méta-communauté (Cottenie 2005).

Dans un contexte agricole, les espèces présentes dans un champ donné ne dépendent pas seulement de caractéristiques locales mais aussi des caractéristiques du paysage, à savoir la nature, la structure et la composition des habitats environnants. Diverses études, en système tempéré, ont montré que la complexité du paysage est généralement favorable à la diversité et à l'abondance des mauvaises herbes (Gabriel et al. 2005; Gaba et al. 2010; Petit et al. 2016). Le contexte et la structure du paysage du nord de la Thaïlande sont très différents: les très petits ou petits champs (<2,56 ha) représentent 28% de la superficie agricole en Europe, contre 70% en Asie (Lesiv et al. 2019). Une taille de champ plus petite est associée à une hétérogénéité accrue en raison de la densité plus importante des bordures de champ. Les effets de la composition et de la configuration du paysage devraient donc être différents à Huai Lang par rapport aux études publiées précédemment.

Dans ce chapitre, j'utilise les données des inventaires floristiques réalisés en saison sèche pour quantifier les impacts relatifs de l'identité de l'usage des sols, du sol, du paysage et des composantes spatiales sur la diversité, l'abondance et la composition des adventices herbacées et ligneuses. Je décris le paysage en utilisant à la fois des descripteurs de composition et de configuration ainsi que des caractéristiques de santé de la végétation dans une "zone voisine" de 200 m de rayon autour de chaque point d'échantillonnage. Les objectifs de cette étude étaient les suivants: i/ identifier, dans chaque tableau explicatif (utilisation des sols, sols, paysages) les variables affectant les communautés de mauvaises herbes; ii/ déterminer, en utilisant des méthodes de partition de variance, les effets totaux et indépendants de ces tableaux explicatifs; et iii/ identifier les principaux processus qui façonnent la structure des méta-communautés herbacées et ligneuses. Cette étude s'appuie sur une coopération en cours avec Florence Dubs, de l'INRA de Versailles.

Patterns of plant biodiversity can be primarily explained by interlaced environmental factors, such as climate, bedrock or broad soil type (Hanzlik and Gerowitt 2011; Hyvönen et al. 2011; Borgy et al. 2015). These factors determine a regional pool of species. The actual presence of a species in a given location, however, depends on multiple other factors, including local abiotic conditions (e.g. topography) and the interaction of the species with others (Fig. 5.2). Besides, local communities are not isolated, but form meta-communities, i.e. sets of local communities that are linked by dispersal of multiple potentially interacting species (Leibold et al. 2004). The meta-community framework combines the study of local factors (both abiotic, such as environmental conditions, and biotic, such as competition) and regional factors (dispersal, immigration) to explain patterns of species distribution that happen in different spatial scales. Dispersal among communities is likely to affect local species diversity both directly, for instance by modifying the abundance of a species in a local community, and indirectly, through changes in species interactions. It can be more or less limited by internal factors (e.g. seed production) as well as external factors, such as the presence of dispersal barriers (e.g. roads) or dispersal vectors (birds, insects, mammals). Determining the processes driving a meta-community can inform us about the relative effects of competition, spatial components and biotic or abiotic resources in shaping biodiversity in a given set of conditions. Traditional models include the neutral meta-community model (N), which states that species are ecologically equivalent and that limited dispersion is the main parameter driving the structure of meta-communities. On the contrary, the species-sorting model (SS) is based on high dispersal abilities in a heterogeneous environment, which results in species sorting along resource gradients. Processes of sink-source dynamics or the presence of spatiotemporal niches (or "patches") result in mass-effect (ME) or patch dynamic (PD) meta-communities types. The comparison of the effects of spatial components (related to dispersal, corresponding to combinations of spatial coordinates and distance between communities) and environment (soil, land use type, etc. i.e. niche characteristics) can be used to identify the main drivers structuring the meta-community (Cottenie 2005).

In an agricultural context, the species that are found within a given field depend not only on local characteristics, such as soil, farming practices, current and preceding crop type, fertilisation and weeding regimes, or rotations (Cardina et al. 2002; Fried et al. 2008; Hyvönen et al. 2011), but also on landscape characteristics, i.e. the nature, structure and composition of the surrounding habitats. For instance, it has been shown that in temperate agroecosystems, field borders act as refuge habitats for weed species that are not adapted to agricultural areas (Fried et al. 2009). Multiple studies have investigated the effect of landscape complexity on bird, insect, and mammal species (Schweiger et al. 2005; Devictor et al. 2008), as well as plant species (Gabriel et al. 2005; Tschardt et al. 2005). They showed that landscape complexity is usually favourable to weed diversity and abundance (Gabriel et al. 2005; Gaba et al. 2010; Petit et al. 2016).

Most of these studies were conducted in temperate agroecosystems, which have undergone thorough modernisation and landscape homogenisation. The context and landscape structure of mountainous Northern Thailand is likely to be very different. For instance, Lesiv et al. (2019) showed that very small or small fields (<2.56 ha) represented 28 % of the agricultural area in Europe, while it represented 70 % in Asia. As a comparison, the median field size in our study area was 1.6 ha

Figure 5.2: Effect of soil, land use, landscape and spatial components on plant communities structure. General climatic and soil conditions (among others) determine the regional species pool. The local conditions (e.g. land use, local soil variables) determine the composition of local communities, which are also influenced by dispersal among local communities. This mechanism is influenced by landscape characteristics (e.g., presence of a natural barrier limiting dispersal between a and b) and spatial components (e.g. dispersal limited by the distance between c and d). All these communities related by dispersal form a meta-community.

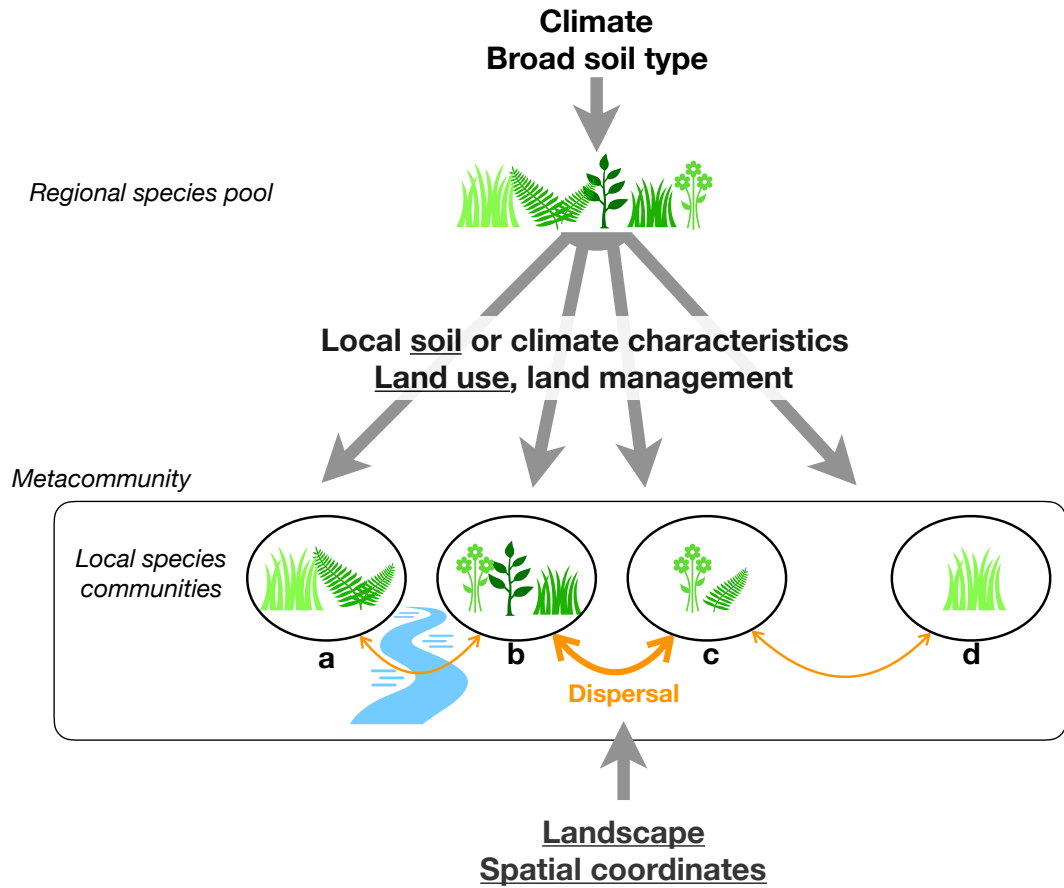


Figure 5.3: Comparison of landscape heterogeneity between (top) a typical European agricultural landscape (Payroux, Val-de-Sèvre, France, $46^{\circ}11' N$, $0^{\circ}28' W$, agricultural area studied in Gaba et al. (2010) and Petit et al. (2016)) and (bottom) a mountainous landscape of Southeast Asia (Huai Lang, Chiang Rai Province, Thailand, $20^{\circ}00'35''N$, $100^{\circ}10'26''E$). Source: Google Earth images.



(Fig. 5.3). Smaller field size is likely to be associated with increased heterogeneity due to the increased length of field borders. Besides, most agricultural areas in Europe are located in flatlands (pastures and grasslands excepted), whereas the uplands of mountainous Southeast Asia are both cultivated and steep. The effects of landscape composition and configuration and spatial components are thus expected to differ in these uplands compared to previously published studies, possibly leading to different meta-community processes. Besides, while previous studies have mostly focused on herbaceous species, shrub and tree species communities are likely to be affected by different dispersal and reproduction processes.

In this chapter, I use data from floral inventories conducted during the dry season 2016, 2017 and 2018 in Huai Lang to quantify the relative impacts of land use identity, soil, landscape and spatial components factors on weed (herbaceous species and tree/shrub species) diversity, abundance and composition. I describe landscape using both compositional (e.g. proportion of each land use) and configurational (e.g. edge length) descriptors as well as vegetation health characteristics in a 200 m-radius "neighbouring area" around each sampling point. The objectives of this study were i/ to identify, within each explanatory table (land use, soil, landscape) the variables affecting weed communities; ii/ to determine, using variance partitioning, the total and independent effects of these explanatory tables; and iii/ to identify the major processes shaping herbaceous and shrub/trees meta-communities structure. This study is based on an ongoing cooperation with Florence Dubs, from INRA Versailles.

5.1 METHODS

5.1.1 *Plant communities data*

I used abundance data (plant per m^2) for herbs, shrub and tree species for each field sampled in the dry season. I kept only species that were found in two samplings (either two different fields or one field on two years) or more. I additionally removed from the analysis one herbaceous species and two tree species that were specific to one location and overly affected the community structure. The abundance matrices were Hellinger-transformed. I measured species richness as the number of species kept in the final analysis (i.e. removing very rare species found in less than two samplings) within each field. Plant biomass was calculated as the average biomass of living plants measured in the five replicates within each field.

5.1.2 *Step 1. Variable identification within each explanatory table*

I conducted variable selection separately for each response table (herbaceous species communities, herbaceous species richness, shrub/tree composition and species richness, plant biomass). All numerical variables were scaled before the analysis.

Each explanatory table (land use, landscape, soil, and spatial components) and the process of variable selection within each is described below and summarised in Table 5.1.

5.1.2.A Landscape

The landscape dataset included variables describing landscape composition and configuration as well as a proxy of vegetation variability (mean and coefficient of variation of NDVI, $\text{mean}(\text{NDVI})$ and $\text{cv}(\text{NDVI})$) within a circular neighbouring area of 200 m radius, centred on the sampling point. The details of the landscape analysis can be found in part 2.2.7. Landscape compositional and configurational measures were constant across years: there was no land use change because only fields with annual crops or young fallow were susceptible to change among years and they were all pooled within a single "annual fields" class. NDVI measures were calculated on separate NDVI remote sensing images for each year and varied for each sampling period.

NDVI-related and compositional/configurational variables were treated separately. Within each of these sub-groups, I conducted the first variable selection based on Pearson correlation, in order to keep only variables with correlations smaller than 0.65 (Tables S5.2 and S5.3). For the compositional/configurational data table, all edge length and patch area variables were highly correlated to the proportion of land uses in the neighbour area; while landscape Shannon index was highly correlated to the number of land uses. I retained the proportion of each land use, the number of land uses and the field areas. None of the $\text{cv}(\text{NDVI})$ presented a correlation larger than 0.65, but as I included $\text{cv}(\text{NDVI}_{all})$ (cv of NDVI for all land uses) in addition to each land-use specific cv, I removed $\text{cv}(\text{NDVI}_{orchard})$ to avoid multicollinearity issues.

I then conducted a model selection including both NDVI-related and compositional/configurational variables (function *step*). The model was a redundancy analysis for herbaceous and shrub/trees communities matrix, and a mixed model for richness and biomass responses, with the field as a random effect. For the mixed model analyses, I also present the coefficient and significance (based on ANOVA type II tests) of each variable in the final model; partial R^2 for each variable was calculated using the *r2beta* function (package R2GLMM, standardised generalised variance method).

5.1.2.B Soil

The soil dataset included topsoil variables, soil type class (see part 2.2.5), and slope. Humidity, bulk density, carbon and nitrogen content varied from one year to another but pH, texture, soil class were measured only once and supposed to be almost constant from one year to another. I removed two variables (carbon content and the proportion of clay) who had correlation coefficients higher than 0.65 with other variables (Table S5.1). I then conducted a model selection including all soil variables (function *step*). The model was a redundancy analysis for herbaceous and shrub/trees communities matrices, and a mixed model for richness and biomass responses, with the field as a random effect. For the mixed model analyses, I also present the coefficient and significance of each variable in the final model.

5.1.2.C Spatial components

The spatial coordinates dataset consisted the UTM coordinates of all fields (X, Y) as well as polynomial combinations of these coordinates (XY, X^2 , Y^2 , X^2Y , Y^2X , X^2Y^2). I scaled these variables and then conducted a Principal Component Analysis,

retaining ten principal components. I then conducted a model selection including all spatial components (function *step*). The model was a redundancy analysis for herbaceous and shrub/trees communities matrix, and a mixed model for richness and biomass responses, with the field as a random effect.

5.1.3 Step 2. Variance partitioning

I thus obtained, for each response, four tables of explanatory variables: land use, landscape, soil, and spatial components. I conducted variance partitioning (package VEGAN, function *varpart*) to compute the independent, total and joint variance explained by each table and group of tables (Fig. 5.4). I used the UPSETR package to represent the results of variance partitioning analyses. I determined the significance of the independent effect for each individual data table using partial RDA. For instance, I measured the independent effect of landscape on the composition of herbaceous communities by partialling out the effects of spatial components, soil, and land use. The significance was tested on 5000 permutations.

5.1.4 Step 3. Determination of the dominant meta-community processes

In order to identify the main drivers of meta-communities, I then pooled all the landscape, soil, and land use variables selected in step 2 into an "environment" (E) table, based on Cottenie (2005). The spatial components constituted the spatial (S) dataset. I tested the following variance components based on redundancy and partial redundancy analyses:

(E): environmental variation (simple RDA);

(s): spatial variation (simple RDA);

(E | s): environmental variation without spatial components (RDA after partialling out spatial effects);

(s | E): spatial variation without environment (RDA after partialling out environmental effects).

5.2 RESULTS

5.2.1 Description of plant communities

There was high variability among both herbaceous plants and three/shrubs communities, with a few fields being very different from the others (Fig. 5.5a and 5.5b). For herbaceous plants, the two first axes of the PCA explained respectively 10.2% and 9.2% of the total variation. For shrub/tree communities, the first two PCA axes explained 8.2% and 6.9% of the total variability.

5.2.2 Mature rubber tree plantations are associated with low landscape heterogeneity

When compared to other land uses, mature rubber tree plantations had significantly larger areas ($P < 3 \cdot 10^{-5}$). The proportion of semi-natural habitats, riparian areas,

Figure 5.4: Principle of the variance partitioning analysis for 2 tables. The variance is partitioned into the variance explained by A only (independent R^2) (a), by B only (b), and jointly by A and B (ab). The total variance explained by A (total R^2) is the sum of (a) and (ab). The variance explained by neither A nor B (i.e. white area) is the residual part.

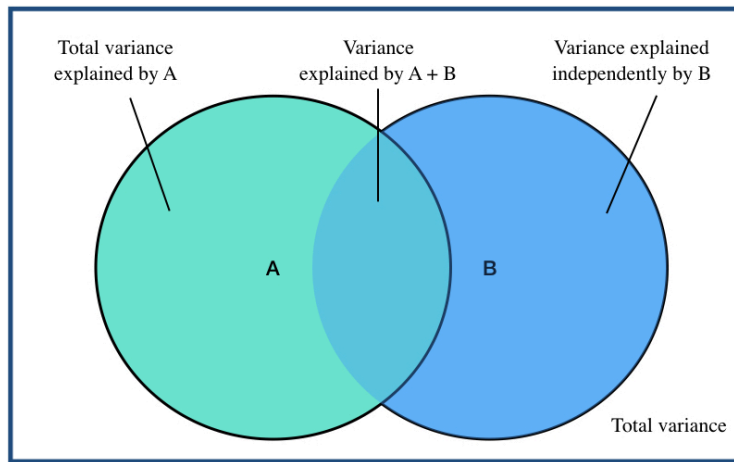
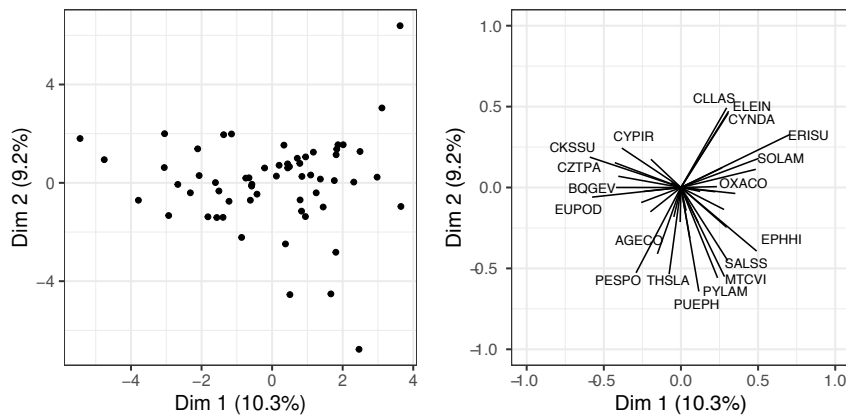
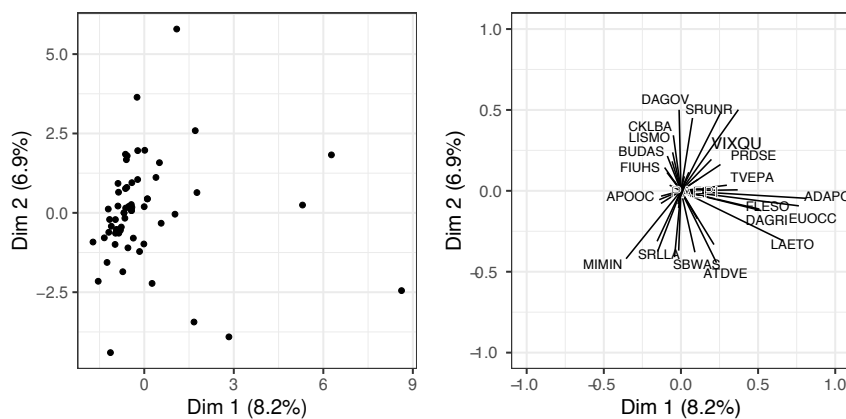


Figure 5.5: PCA on community abundance data. a: Herbaceous communities. b: shrub/tree communities. Left: individual-based representation, each dot represents one field. Right: species-based representation. Each arrow represents one species, only the 20 most influential species are labelled. Species names can be found in Table S2.1.

(a) PCA for herbaceous communities.



(b) PCA for shrub/tree communities



and the variability of NDVI (coefficient of variation for all land uses) also decreased significantly with the proportion of mature rubber tree plantations (not shown).

5.2.3 Single effects of soil and landscape on plant communities

In this part, all reported results correspond to models including only one explanatory variable (either landscape or soil).

5.2.3.A Herbaceous communities

I selected nine landscape variables as drivers of herbaceous communities composition, including seven variables describing landscape composition and configuration and two variables describing NDVI (Table 5.1, Fig. 5.6a). The first axis was mostly determined by the field size and the second axis by the mean(NDVI_{annual}). The model was highly significant and explained 44 % of the total variation of herbaceous communities. Nitrogen content, soil bulk density, humidity, pH, C/N ratio and silt content explained 33% of the variation in herbaceous species (Fig. 5.6c). The first axis was strongly anti-correlated to soil humidity, while the silt content drove the second axis. Seven spatial components explained 35% of the total variation (Fig. 5.6e).

5.2.3.B Shrub/tree communities

Seven landscape variables, including four describing the landscape composition and configuration, and three describing the NDVI, were selected as drivers of shrub/tree communities. (Figure 5.6b). The first axis was mostly anti-correlated to the proportion of rivers and orchards in the neighbouring area. The model explained 30% of the total variation in shrub/tree communities. The soil variables that best explained shrub/tree communities were the proportion of sand, soil humidity, and soil class (Fig. 5.6d). The model explained 17% of the total variation. Spatial components explained 23% of the total variation in shrub/tree communities (Fig. 5.6f).

5.2.3.C Herbaceous and shrub/trees richness and plant biomass

Herbaceous species richness decreased with field size, the proportion of orchards and the mean(NDVI_{annual}) in the neighbouring area (Table 5.2). The full model also included the proportion of semi-natural elements and the mean(NDVI_{riparian}) (insignificant effects, adjusted R²: 43%). In respect to local environment variables, herbaceous species richness increased with the proportion of sand and the local slope, but decreased with the soil bulk density and the proportion of coarse elements (adjusted R²: 37%, Table 5.2).

Shrub/tree species richness increased with mean(NDVI_{all}), cv(NDVI_{all}) and cv(NDVI_{mature.rubber}). It slightly decreased with mean(NDVI_{orchard}) and mean(NDVI_{forest}) and the proportion of young rubber tree plantations (adjusted R²: 49%, Table 5.2). Shrub/tree species richness increased with soil silt content and decreased with soil humidity. Soil class and the proportion of coarse elements, although kept in the final model, did not have significant effects *per se* (adjusted R²: 38%, Table 5.2).

Table 5.1: Variable selection process. Green: initial dataset, with all the variables that were measured. Orange: variables kept after removing variables with Pearson correlation coefficient > 0.65. Blue: final model after RDA or mixed model selection within each explanatory dataset. X: Easting; Y: Northing.

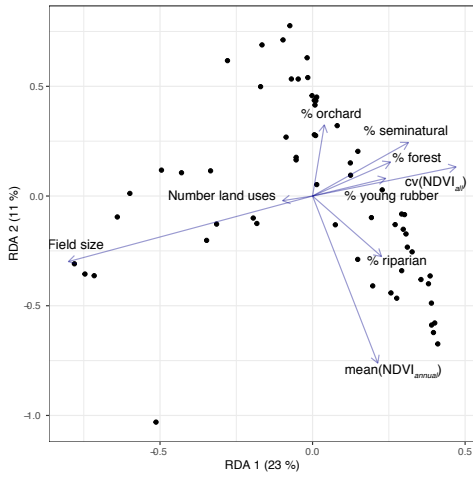
	Land use	Landscape	Local factors	Spatial components	
		Composition and configuration Number of land uses Shannon index Field area Total edge length of each land use % in the landscape of each land use Mean patch area of each land use	NDVI-based mean(NDVI _{all}) cv(NDVI _{all}) mean(NDVI _i) cv(NDVI _i)	Humidity N content C content C/N ratio % sand % clay Slope Soil class Bulk density % coarse elements pH	X, Y, XY, X ² , Y ² X ² Y, XY ² X ² Y ²
		<i>Keep only correlations among numeric variables <0.65</i>			PCA
	Presence of trees Annual land use	% annual fields % forest % riparian vegetation % semi-natural: % orchard % young rubber tree Field area Number of land uses	cv(NDVI _{all}) mean(NDVI _{annual}) mean(NDVI _{orchards}) mean(NDVI _{young.rubber}) cv(NDVI _{annual}) cv(NDVI _{forest}) cv(NDVI _{mature.rubber}) cv(NDVI _{riparian}) cv(NDVI _{semi-natural}) cv(NDVI _{orchard}) cv(NDVI _{young.rubber})	N content Humidity pH Bulk density % coarse elements % sand % silt Soil class Slope C/N ratio	Transformed into Dim1... to Dim5 (dimensions of the PCA)
Response variable	<i>Creation of the final model: selected variables after model selection within each explanatory table</i>				
Herbaceous communities composition	Presence of trees Annual land use	% forest % riparian vegetation % semi-natural % orchard % young rubber tree Number of land uses Field size	mean(NDVI _{annual}) mean(NDVI _{riparian}) cv(NDVI _{all})	Humidity N content pH % silt Bulk density C/N ratio	Dim.1 Dim.3 Dim.4 Dim.5 Dim.6 Dim.8 Dim.9 Dim.10
Shrub/trees community composition	Presence of trees Annual land use	% annuals % forest % riparian vegetation % orchards % orchards	mean(NDVI _{annual}) cv(NDVI _{mature.rubber}) cv(NDVI _{young.rubber})	Humidity % sand Soil class	Dim.1 Dim.2 Dim.3 Dim.4 Dim.5 Dim.6
Herbaceous species richness	Presence of trees Annual land use	% semi-natural Field size % orchards % orchards	cv(NDVI _{riparian}) mean(NDVI _{annual})	Bulk density Slope % coarse elements % sand	Dim.2 Dim.4 Dim.5
Shrub/trees species richness	Presence of trees Annual land use	% young rubber tree	mean(NDVI _{orchard}) mean(NDVI _{annual}) cv(NDVI _{forest}) cv(NDVI _{mature.rubber}) cv(NDVI _{all}) cv(NDVI _{forest})	Soil class Humidity % silt Soil class	Dim.1 Dim.1
Biomass	Presence of trees Annual land use	% annuals % riparian vegetation % orchards Field size	mean(NDVI _{forest}) cv(NDVI _{semi-natural})	N content Slope Soil class Humidity	Dim.5 Dim.8

Table 5.2: Effect of the selected variables within the landscape and soil tables on herbaceous plants richness, shrubs/trees plant richness, and plant biomass. Each model included either the landscape or the soil data tables as explanatory variables. *** $P < 0.001$; ** $P < 0.01$, * $P < 0.05$, . $P < 0.1$.

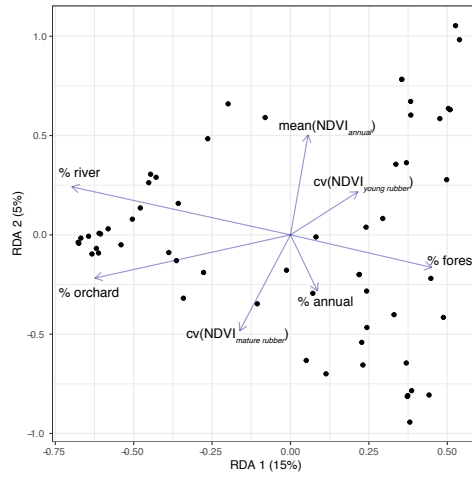
Landscape			Soil		
Response: Herbaceous richness					
	Coeff.	Partial R ²		Coeff.	Partial R ²
Field size	-1.4	13 *	% sand	2.7	28 ***
% orchards	-1.2	10 *	Slope	2.1	20 **
mean(NDVI_{annual})	-1.1	10 *	Bulk density	-1.6	16 **
% semi-natural	1.1	8 .	% coarse elements	-1.7	11 *
cv(NDVI_{riparian})	-0.9	7 .			
Total R ² _{adj} = 43%			Total R ² _{adj} = 37%		
Response: Shrubs and trees richness					
	Coeff.	Partial R ²		Coeff.	Partial R ²
cv(NDVI_{all})	2.0	37 ***	Humidity	-1.9	30 ***
mean(NDVI_{annual})	1.6	24 ***	% silt	1.6	23 ***
mean(NDVI_{orchard})	-1.2	13 **	Soil class		11 .
cv(NDVI_{mature.rubber})	1.0	9 *	% coarse elements	-0.76	6 .
% young rubber	-0.8	8 *			
cv(NDVI_{forest})	-0.9	7 *			
Total R ² _{adj} = 49%			Total R ² _{adj} = 37%		
Response: Biomass					
	Coeff.	Partial R ²		Coeff.	Partial R ²
Field size	-35	29 ***	Humidity	-24.8	15 **
% riparian	38.4	21 ***	N content	20.5	15 *
% orchards	-21.4	13 **	Soil class		17 .
% annuals	-25.7	13 **	Slope	21.4	9 .
mean(NDVI_{forest})	-21.9	13 **			
cv(NDVI_{semi-natural})	19.9	10 *			
Total R ² _{adj} = 43%			Total R ² _{adj} = 29%		

Figure 5.6: Effects of landscape (a, b), soil (c, d), and spatial components (e,f) on herbaceous (right: a, c, e) shrubs and trees communities (left: b, d, f). The redundancy analyses were conducted on the Hellinger-transformed abundance matrices. Each dot represents one field.

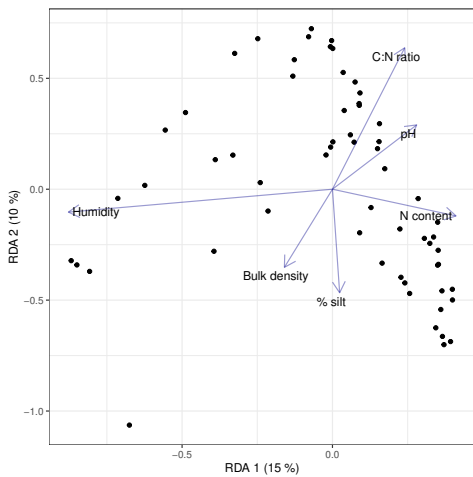
(a) Landscape effect on herbaceous communities.



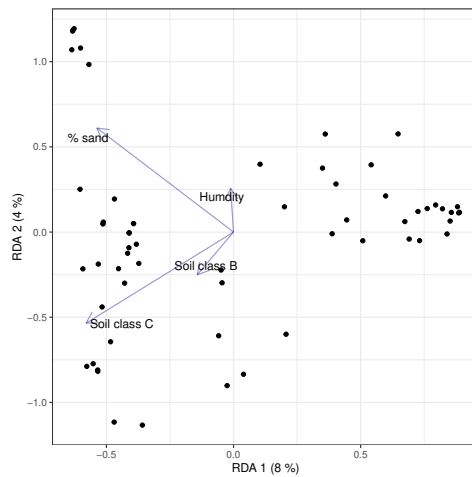
(b) Landscape effect on shrub/tree communities.



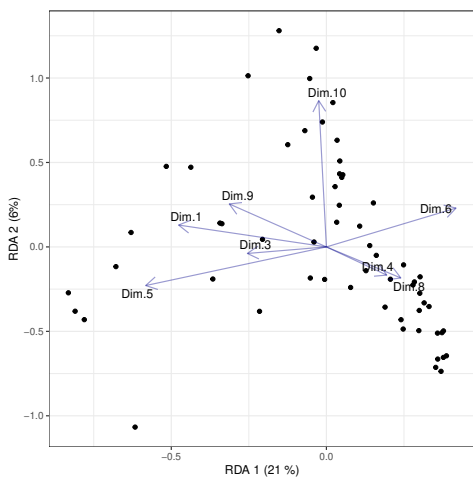
(c) Soil effect on herbaceous communities.



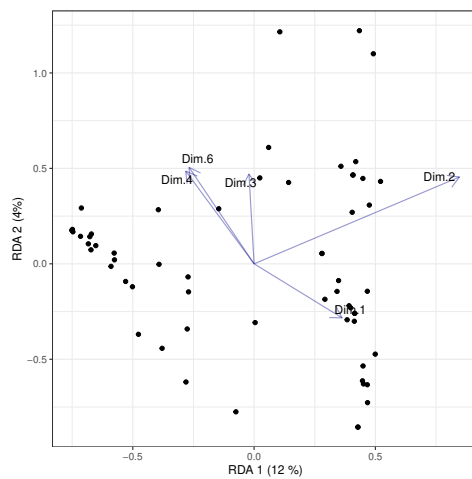
(d) Soil effect on shrub/tree communities.



(e) Spatial components effect on herbaceous communities.



(f) Spatial components effect on shrub/tree communities.



Weed biomass increased with $cv(NDVI_{semi-natural})$ and the proportion of riparian vegetation. It decreased with the field size, the proportion of orchards and annual fields and with $mean(NDVI_{forest})$ (adjusted R^2 : 43%, Table 5.2). In respect to soil variables, it increased with nitrogen content and decreased with soil humidity. The full model also included soil class and slope (adjusted R^2 : 29%, Table 5.2).

5.2.4 *Total and independent effects of soil, landscape, land use and spatial components on weed communities*

The following paragraphs describe the results of variance partitioning for each response table. The total and independent effects of each explanatory table are summarised in Figure 5.7.

5.2.4.A Herbaceous communities

We found that landscape (as described in Table 5.1) was the main determinant of the composition of herbaceous plant communities (independent effect: adjusted $R^2 = 9\%$; total effect: 32%). Local environment, land use and spatial components all had a total variance of 25% (Fig. 5.8a). Soil variables and land use had no independent explanatory power and participated to the total variation mostly in conjunction with other data tables. The full model explained 48% of the variation in the composition of herbaceous communities.

5.2.4.B Shrub/tree communities

Landscape was also the main determinant of the composition of shrub/tree communities, with a total explained variance of 21% and an independent effect variance of 7%, followed by spatial components. A large part (9%) of the explained variance was due to the combination of landscape, spatial components and soil variables (Fig. 5.8b). The full model explained 28% of the variability in the composition of shrub/tree communities.

5.2.4.C Herbaceous and shrub/trees richness and plant biomass

Landscape had the highest total effect on herbaceous species richness (37%), but its independent effect was negligible. Land use had the largest independent effect (14%). The model explained 52% of the total variability of herbaceous species richness. Landscape and soil had the largest total effects on shrub and tree species richness (42% and 29% respectively). After landscape, land use was the main independent effect. The full model explained 45% of the variability of shrub and tree species richness. Finally, landscape had the largest total effect (32%) on plant biomass, but this was mainly due to its joint effect with soil or land use and its independent effect was negligible. Spatial components and soil had the largest independent variance.

5.2.5 *Identification of the dominant meta-community processes*

I then investigated the main meta-community processes driving herbaceous and shrub/tree communities. Land use, soil, and landscape variables were merged

Figure 5.7: Summary of the variance partitioning analyses. 5.7a: total and 5.7b: independent variance components (measured as adjusted R^2) of each explanatory table on the different response variables.

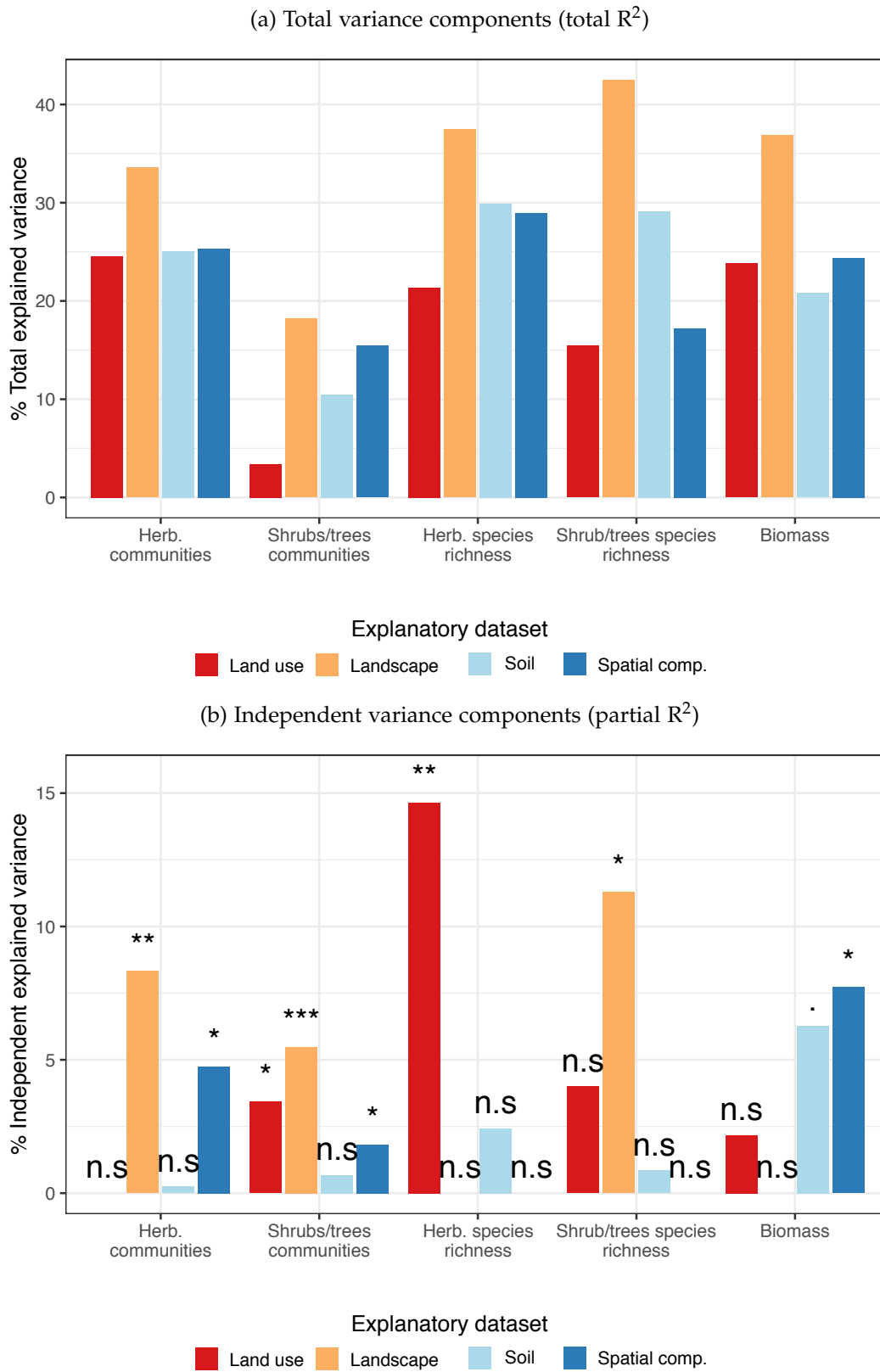


Figure 5.8: Variance partitioning of the composition of a. herbaceous and b. shrub/trees communities among the four explanatory tables (see Table 5.1). The vertical bars represent the independent variance components (measured as partial R^2) explained by each variable and the variance components explained by groups of two or more variables; the considered variables are indicated by a dot in the lower part of the graphic. Negative variance components were represented as 0 variance. The horizontal bars in the bottom left area represent the total variance component explained by each explanatory data table.

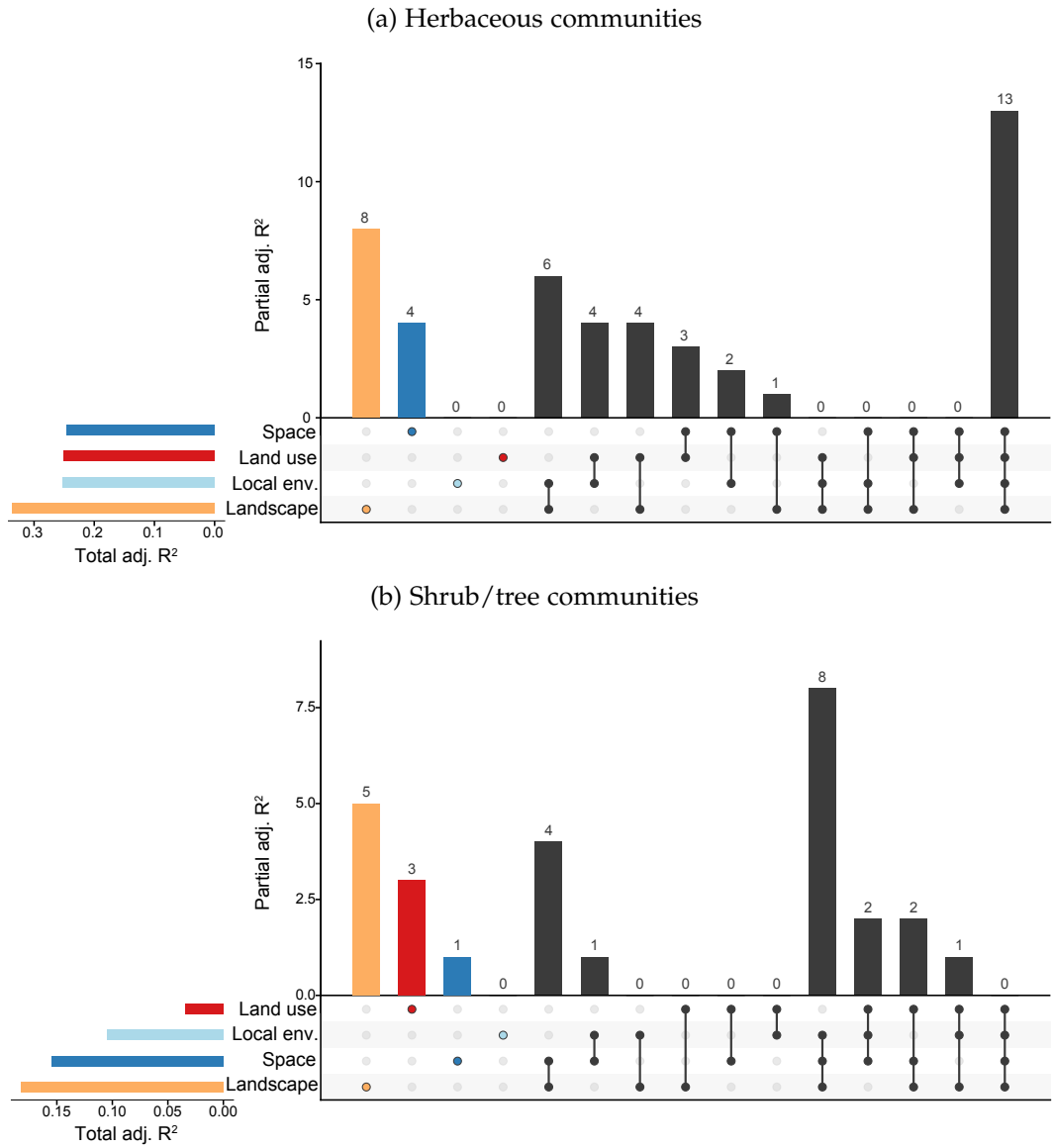
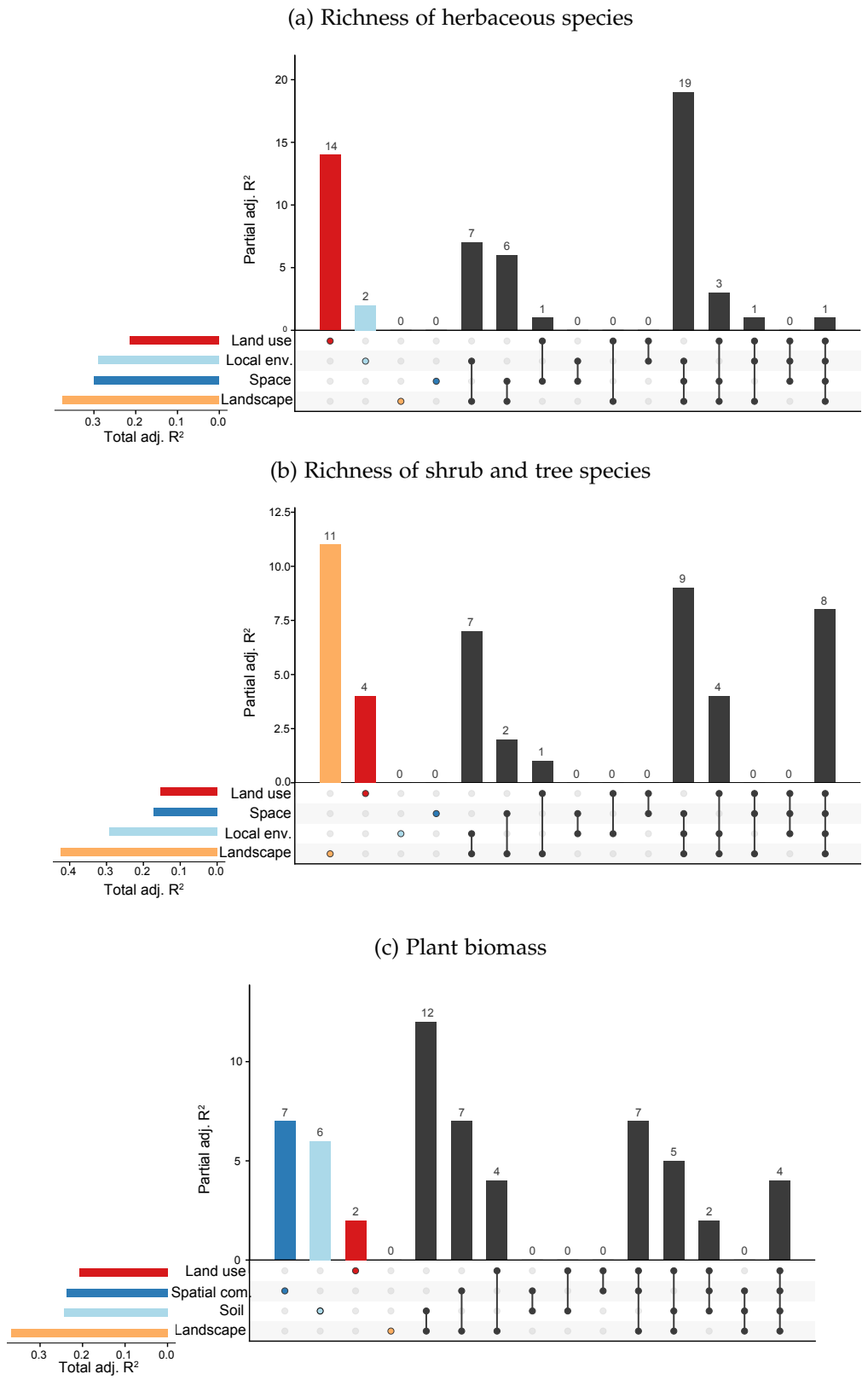


Figure 5.9: Variance partitioning of a. herbaceous species richness, b. shrub and tree species richness, and c. plant biomass among the four explanatory tables (see Table 5.1). The vertical bars represent the independent variance components (measured as partial R^2) explained by each variable and the variance components explained by groups of two or more variables; the considered variables are indicated by a dot in the lower part of the graphic. Negative variance components were represented as 0 variance. The horizontal bars in the bottom left area represent the total variance components explained by each explanatory data table.



into a "global environment" table. Table 5.3 shows the results of the partial RDAs, comparing the effects of this global environment and spatial components. The total effects of both the spatial and environmental tables, as well as their effects when partialling out the other table were significant for both herbs and shrubs/trees communities.

Table 5.3: Results of the partial RDA analyses to determine meta-community types. The components are the environment [E], the spatial components [S], the environment independent of the spatial components [E|S], and the spatial components independent of the environment [S|E]. [E] and [S] were tested with simple RDAs including only the considered table while [E|S] and [S|E] were tested with partial RDAs. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

Response	Variance component	Significance
Herbaceous	E	***
	E S	***
	S	***
	S E	*
Shrubs and trees	E	***
	E S	***
	S	***
	S E	**

5.3 DISCUSSION

5.3.1 *Differences between herbaceous and shrubs/trees communities*

The final model explained the composition of herbaceous communities much better than the composition of shrub/tree communities. As herbaceous species are relatively short-lived and form a rich seedbank, their communities are likely to be dynamic and to respond quickly to environmental conditions, either related to soil, farming practices, or landscape, with an overall low resistance to disturbance. They are also likely to have higher resilience, i.e. to recover more quickly by rapid germination. On the contrary, shrub and tree species usually live longer and have slower growth rates. Thus, past weeding practices (e.g. cutting or herbicide application) are likely to affect these communities for a longer period. As the interviews led with farmers did not provide precise data on these practices, we did not include these parameters in our analysis. This might explain why the shrub/tree communities were less explained by our analyses.

5.3.2 *Relative effects of soil, landscape, and land use*

I showed that the soil, which in this study was mostly represented by soil variables, had relatively low independent effects on the composition, richness, and abundance of plant communities. Indeed, although I did find significant relationships between soil characteristics and plants (e.g. positive relationship between biomass and soil N content as well as soil humidity), these factors had insignificant independent

effects when considering also the other explanatory tables. This was surprising, considering the importance of soil (pH and texture in particular) in the determination of weed communities composition and richness (Fried et al. 2008; Hanzlik and Gerowitt 2011; de Mol et al. 2015). This might be explained by two factors. Firstly, our field site was relatively small. Although the soil layering and the parental rock (described by soil class) was very variable, topsoil characteristics may not represent this variability because they respond to shorter-term processes than bedrock formation and evolution. Secondly, other soil parameters which I have not taken into account may be needed to better characterise the plant communities; external factors modifying the biological, physical and chemical characteristics of soils (e.g. nutrient content linked to fertilising practices) might also override the effect of the factors included in the present analysis.

I found that landscape had a large total effect on all considered response variables. For the composition of herbaceous communities, selected variables included both variables related to the general characteristics of the landscape, such as the number of land uses or the field size, and variables describing the presence of specific land use types in the neighbouring area. Field size and the number of land uses are descriptors of the local habitat complexity. Their effect on the composition of plant communities shows that landscapes of varying heterogeneity support different species assemblages. The effect of the presence of specific land uses such as the proportion of semi-natural elements or riparian vegetation on communities composition is probably related to the dispersal of some species from local "source" habitats in the landscape. This is supported by the positive effect of riparian areas, and the negative effect of field size, on herbaceous species richness - although the independent effect of landscape on herbaceous species richness was negligible. Botanical inventories of these specific landscape elements would be necessary to confirm this hypothesis.

On the contrary, the composition of shrub/tree communities was determined mostly by the presence of specific land uses or NDVI measures and were less dependent on landscape heterogeneity. Shrub/tree richness significantly increased with $cv(NDVI)$, which is also a proxy of land cover heterogeneity. This suggests that for instance, mosaic landscapes including diverse types of vegetation (trees, annual fields at different growth stages) harboured more diverse communities than homogeneous landscapes.

5.3.3 *Identification of metacommunity processes*

These results support the mosaic concept (Duelli 1997), which is based on meta-community dynamics and states that in agroecosystems, species diversity increases with habitat variability (e.g. number of land uses) and heterogeneity (number of patches). Meta-community processes can be identified based on the relative role of spatial and environmental factors in determining the composition and structure of communities (Cottenie 2005). I showed that in the case of both herbaceous and shrub/tree communities, i/ the environmental, ii/ the spatial, iii/ the environmental (independent of spatial components), and iv/ spatial components (independent of environment) were all significant (Table 5.3). According to Cottenie (2005), this identifies the meta-community type as dominated by "Species Sorting" and "Mass Effect" processes. In the mass effect perspective, the species can be

rescued from local exclusion in environments to which they are not adapted by immigration from neighbour communities in which they thrive. This is particularly relevant in the context of agroecosystems: species that are not agrotolerant can still be found, in low abundance, within agricultural fields because they disperse from neighbour environments to which they are better adapted (Fried et al. 2009). This is consistent with our findings that the presence of certain habitats, such as riparian vegetation areas or semi-natural elements, significantly affects local biodiversity within agricultural fields.

5.3.4 *Scales of landscape and biodiversity*

Investigating the effects of landscape on biodiversity necessarily raises questions about the scale of investigation. Firstly, the definition of the scale of "landscape" is vague and differs from one study to another. Duelli (1997) recommends working at scales of at least 1 km² to describe landscape variability: as such, Gabriel et al. (2005) investigated landscape sectors with diameters ranging from 1 km to 5 km. However, Gaba et al. (2010) and Petit et al. (2016) investigated the effect of landscape on plant communities in scales ranging 0.1 km to 1 km radiuses. The scale of interest is likely to depend on regional characteristics: indeed the dispersal ability of local species, the presence of dispersers, the topography and wind or runoff run all affect the dispersal and patterns of distribution of biodiversity. Besides, the relationship between landscape heterogeneity and biodiversity can be understood differently depending on the scale of biodiversity monitoring, i.e. local diversity (α -diversity) within a given field, or heterogeneity within the landscape (β -diversity), or even global biodiversity (γ -diversity) within the whole region. Based on the high heterogeneity of the studied landscape and results from previous studies (e.g. Gaba et al. (2010)) I chose to limit this study to the comparison of local (α) diversity with landscape descriptors measured within a 200 m-radius neighbouring area. This is also consistent with the relatively low dispersal ability of arable weeds, which usually disperse seeds close to the mother plant (Benvenuti 2007). One of the main perspectives of this study is thus to extend the analysis to other scales, ranging for instance between 100 m to 500 m. This would provide interesting insights into the possible variation in meta-community processes and dynamics with scale.

5.4 CONCLUSION

Overall, these results demonstrate that conservation actions in mountainous agroecosystems of Southeast Asia should not only focus on field-scale management, but take a more global approach of landscape management by maintaining diverse habitats and semi-natural areas in the landscape. The expansion of rubber tree plantations, which often cover large areas, is thus likely to have both direct (shadow, intense management) and indirect (through landscape homogenisation) effects on plant communities. Further investigation is required to determine the optimal scale of landscape management for conservation actions in such heterogeneous and mountainous agroecosystems.

In this chapter and the preceding study, I have shown that local as well as landscape management impacted plant communities. In the first result chapter, I also demonstrated that plant communities and soil characteristics were strongly interrelated; thus, the changes in plant communities associated with the switch to rubber tree plantations is likely to have a strong impact on soil conservation. In the last chapter of this manuscript, I will investigate the effect of rubber tree plantations on soil erosion and the mitigation of soil degradation by plant cover in rubber tree plantations.

Conclusion en français

Ces résultats démontrent que les actions de conservation dans les systèmes agricoles montagneux de l'Asie du Sud-Est ne doivent pas seulement se concentrer sur la gestion à l'échelle du champ, mais adopter une approche plus globale de la gestion du paysage en maintenant divers habitats et zones semi-naturelles. L'expansion des plantations d'hévéa, qui couvrent souvent de grandes superficies, est donc susceptible d'avoir des effets à la fois directs (ombre, gestion intense) et indirects (par l'homogénéisation du paysage) sur les communautés végétales. Des études additionnelles sont nécessaires pour déterminer l'échelle optimale de gestion du paysage pour les actions de conservation dans ces agroécosystèmes hétérogènes et montagneux.

Dans ce chapitre et le précédent, j'ai montré que la gestion locale ainsi que la gestion du paysage avaient un impact sur les communautés végétales. Dans le premier chapitre de résultats, j'ai également démontré que les communautés de plantes et les caractéristiques du sol étaient fortement interdépendantes; ainsi, les changements dans les communautés végétales associés à la transition vers les plantations d'hévéas auront probablement un impact important sur la conservation des sols. Dans le dernier chapitre de ce manuscrit, j'examinerai l'effet des plantations d'hévéa sur l'érosion des sols et l'atténuation de la dégradation des sols par le couvert végétal.

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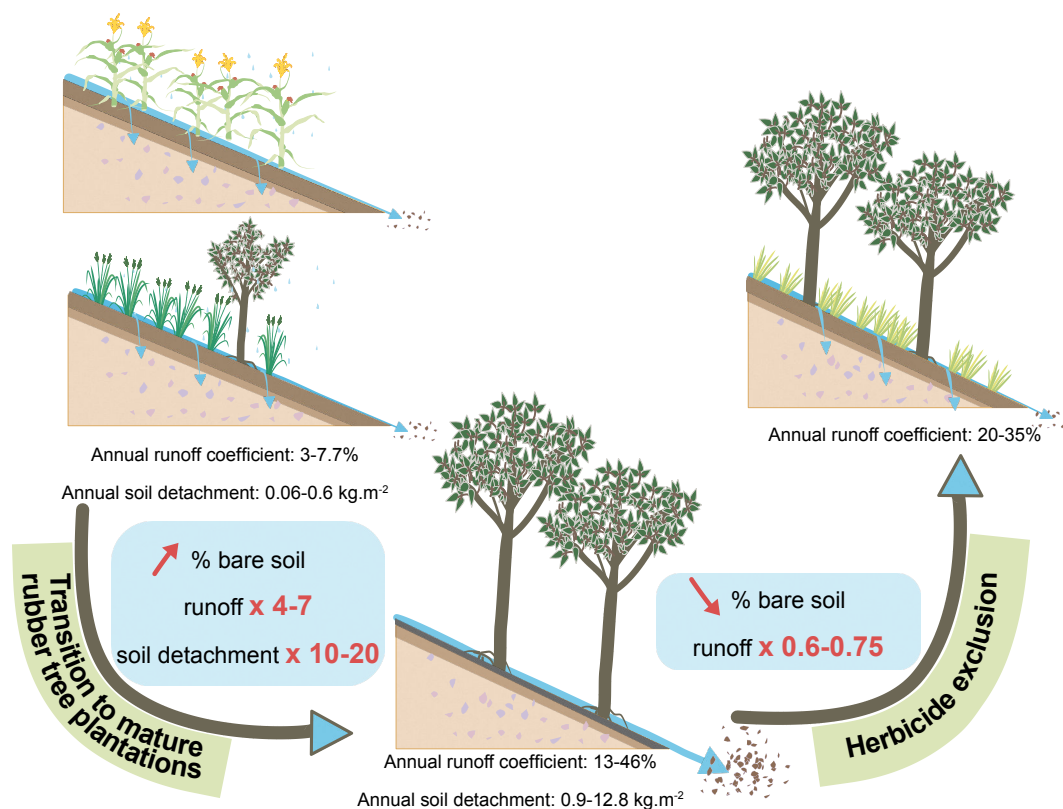
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THE EFFECT OF RUBBER TREE PLANTATIONS ON SOIL EROSION

In this chapter, I investigate the effects of the transition from annual crops to rubber tree plantations on runoff and soil detachment. I first show that rubber tree plantations strongly increase runoff and soil detachment compared to maize or young rubber tree plantations, due to an important soil surface degradation during the rainy season. I then demonstrate that restoring a natural weed cover under mature rubber tree plantations significantly reduces soil degradation risks.

Figure 6.1: Graphical abstract



Introduction en français

L'Asie du Sud-Est est doublement exposée à la dégradation des sols en raison de conditions météorologiques extrêmes et de changements rapides d'usage des sols (Borrelli et al. 2017; Panagos et al. 2017; Van Lynden et Oldeman 1997). En effet, comme dans de nombreuses zones tropicales, la conservation des sols en Asie du Sud-Est est particulièrement menacée par des conditions météorologiques défavorables. Par exemple, la base de données mondiale sur l'érosivité des précipitations (Global Rainfall Erosivity Database) classe cette zone parmi les régions présentant la plus forte érosivité due aux précipitations ($> 7400 \text{ MJ ha}^{-1} \text{ yr}^{-1}$, Panagos et al. (2017)), et certains modèles prévoient une augmentation de l'érosivité du fait des changements climatiques (Plangoen et Udmale 2017). Dans la région, la déforestation et l'intensification agricole ont exacerbé la dégradation de l'environnement, en particulier dans les zones montagneuses aux pentes abruptes. Plus récemment, des organisations et programmes nationaux et internationaux tels que l'UNCCD et REDD+ ont encouragé le remplacement des cultures annuelles par des cultures pérennes, telles que les plantations de teck ou d'hévéa, avec l'objectif d'accroître les revenus des agriculteurs et d'étendre le couvert forestier dans les zones montagneuses. La replantation d'arbres dans ces zones dégradées devrait restaurer des conditions de sol favorables. Cependant, l'effet de l'expansion des monocultures pérennes est loin d'être consensuel. Alors que la repousse naturelle des forêts réduit l'érosion des sols, le remplacement des cultures annuelles par des plantations de teck au Laos a entraîné une forte augmentation du détachement des sols et des écoulements en surface (Patin et al. 2018; Ribolzi et al. 2017; Lacombe et al. 2016). La plupart des études portant sur les effets des plantations d'hévéa sur le sol les comparent à des forêts ou à d'autres plantations d'arbres (Liu et al. 2015; Li et al. 2012; Noguchi et al. 2003; Nurulita et al. 2016). Cependant, de nombreuses plantations sont plantées sur des terres auparavant arables (Holt et al. 2016): une estimation adéquate de l'impact de l'hévéa sur l'érosion des sols devrait donc inclure les cultures annuelles ainsi que les cultures pérennes.

Les processus d'érosion peuvent être mesurés et analysés à différentes échelles. À grande échelle, les variations du débit des rivières et de la redéposition des sédiments peuvent fournir des informations sur les processus d'érosion régionaux. Au niveau du bassin versant, les processus incluent la séparation de l'eau en flux de surface et souterrain; le détachement et la redéposition des sédiments; et la connectivité et la redistribution des eaux de ruissellement. Dans ce chapitre, je présente les résultats de deux études distinctes menées dans les bassins versants de Huai Lang. Les deux sont basés sur des parcelles d'érosion de 1 m^2 (Janeau et al. 2003). Cette échelle est utile pour étudier des processus très locaux de détachement de particules de sol et d'infiltration d'eau (par exemple, Lacombe et al. (2017)) et leur relation avec les caractéristiques locales de la surface du sol. La première étude a été menée en 2015 et 2016 et visait à quantifier les effets combinés des conditions météorologiques (précipitations, énergie cinétique de la pluie, indice de précipitation antécédentes), des conditions de surface du sol et de l'utilisation des sols (maïs, jeunes plantations d'hévéa avec culture en inter-rang et hévéas mature). Mon hypothèse était que les principaux facteurs affectant le ruissellement et le détachement seraient la présence d'arbres associée à un couvert de sol discontinu; et donc que les plantations d'hévéa matures (arbres hauts et sans culture intercalaire) entraîneraient un ruissellement et un détachement plus importants que les jeunes hévéas (avec culture intercalaire) et que le maïs. Au sein de ces différents usages de sol des sols, je visais à i/ quantifier précisément le ruissellement et le détachement du sol sur une base annuelle et mensuelle (expérience 2015) et ii/ comprendre les conditions météorologiques et de surface déterminant l'érosion du sol (expérience 2016). La deuxième étude a été menée en 2017 et 2018 dans des plantations d'hévéas matures uniquement. Elle visait à décrire la dynamique du couvert végétal dans ces plantations et à quantifier son impact sur le ruissellement sous différentes pratiques de désherbage. Dans cette étude, mon hypothèse était que l'abondance du couvert du sol réduirait le ruissellement et diminuerait la vulnérabilité des plantations d'hévéas aux fortes précipitations.

Southeast Asia is doubly exposed to land degradation, due to extreme meteorological conditions and to rapid land use changes (Van Lynden and Oldeman 1997; Borrelli et al. 2017; Panagos et al. 2017). Oldeman et al. (1991) classified all Southeast Asia as having medium to high land degradation rates due to water erosion. Indeed, as in many tropical areas, soil conservation in Southeast Asia is particularly imperilled by adverse meteorological conditions. For example, the Global Rainfall Erosivity Database classifies the area as one of the regions with the highest rainfall erosivity ($> 7400 \text{ MJ ha}^{-1} \text{ yr}^{-1}$, Panagos et al. (2017)), and some models predict that climate changes will cause a continued increase in rainfall erosivity (Plangoen and Udmale 2017). In the area, deforestation (among the highest rates in the world (Zhao et al. 2006; Sodhi et al. 2010)) and the intensification of agriculture exacerbated environmental degradation, especially in mountainous areas with steep slopes. Thus, more recently, national and international organisations and programmes such as UNCCD and REDD+ encouraged the replacement of annual crops by perennial cash crops, such as teak tree or rubber tree plantations. The objective was to increase farmers' income and to expand tree cover in mountainous areas. The replanting of trees in degraded areas was expected to restore favourable soil conditions and water resources. Yet, the effect of perennial monoculture expansion is far from consensual. While natural forest regrowth decreases soil erosion and streamflow, the replacement of annual crops by teak plantations in Laos led to a sharp increase of soil detachment and overland flow (Lacombe et al. 2016; Ribolzi et al. 2017; Patin et al. 2018). Most studies investigating the impacts of rubber tree plantations on soil compared the plantations to forests or other tree plantations (Noguchi et al. 2003; Li et al. 2012; Liu et al. 2015; Nurulita et al. 2016). Yet, many plantations are planted in previously arable lands (Holt et al. 2016): an adequate estimation of rubber tree impact on soil erosion should thus include annual as well as perennial crops.

Erosion processes can be measured and analysed at different scales. At the largest scale, variations in rivers flow, sediment loads and sediment redeposition (e.g. in dams) can provide information about regional erosion processes. At the catchment scale, processes include water partitioning into overland and underground flow; the detachment and redeposition of sediments downslope; and runoff connectivity and redistribution by topographical features such as gullies or terraces. The catchment scale is particularly appropriate for tackling long-term data, for instance regarding the impacts of land use changes on erosion processes (Valentin et al. 2008).

In this chapter, I report the results of two separate studies conducted in Huai Lang catchments. Both are based on 1 m^2 erosion microplots (Janeau et al. 2003). This scale is useful for investigating very local, fine-scale processes of soil particle detachment and water infiltration (e.g. Lacombe et al. (2017)) and their relation to local soil surface characteristics. It provides information on the processes initiating water erosion (splash detachment, and incipient interrill erosion) and therefore about the erosion potential of a particular field or land use. The first study was conducted in 2015 and 2016 and aimed at quantifying the combined effects of meteorological conditions (rainfall, rain kinetic energy, Antecedent Precipitation Index), soil surface conditions and land use (maize, young rubber tree plantations with intercrop, and mature rubber tree plantations). My hypothesis was that the main factors affecting runoff and detachment would be the presence of a high canopy associated with discontinuous soil cover; and thus that mature rubber tree plantations (high tree and no intercrop) would cause higher runoff and detachment

than young rubber tree (with intercrop) and maize. In the different land uses, I aimed i) to precisely quantify runoff and soil detachment on an annual and monthly basis (2015 experiment) and ii) to understand meteorological and surface conditions determining soil erosion (2016 experiment). The second study was led in 2017 and 2018 in mature rubber tree plantations only. It aimed at describing the dynamics of plant cover under rubber tree plantations and to quantify its impact on runoff under different weeding practices (with or without herbicide application). In this study, my hypothesis was that abundant soil cover would overall lower the runoff, and decrease the vulnerability of rubber tree plantations to large rain events.

6.1 MATERIAL AND METHODS

6.1.1 *Location of the erosion microplots*

Location of the microplots in the different experiments is shown in Fig. 6.2.

6.1.1.A Study 1: 2015 and 2016

In March 2015, microplots were installed in a maize field (M), a young rubber tree plantation with rice intercrop (YR) and a mature rubber tree plantation either within the rubber tree rows (OR_s , where canopy is dense and rainfall interception is high) or between the rows (OR_i , with sparser canopy and lower interception). Three replicates were installed for each situation. In 2016, we moved the microplots to fields with similar land uses (except that the intercrop under YR was maize), located closer to the automatic meteorological station presented hereafter. The slope for microplots ranged from 36 % to 67 % in 2015 and 55 % to 71 % in 2016. In both 2015 and 2016 mature rubber trees were approximately 13 years old with height of about 7 m. Tree planting was rather regular following a rectangular grid $3.5 \times 7.0 \text{ m}^2$. Young rubber trees were approximately 3-4 years old with height of approximately 2.5 m. Tree planting was slightly denser following a grid $3 \times 6.5 \text{ m}^2$. Personal observations (Neyret et al. 2018) showed that herbicides were sprayed once a year in young rubber tree plantations with intercrop (usually in June, i.e; about 1 month after the onset of the rainy season) and twice a year in maize fields (April-May at early stage of maize growth and June-July when maize growth reaches about 1 m height). Management of mature rubber tree plantations was more variable and owners reported no herbicide spraying in 2015 and one spraying in July 2016.

6.1.1.B Study 2: 2017 and 2018

In 2017, we redistributed the microplots in the two mature rubber tree plantations studied in 2015 (plantation OR2) and 2016 (plantation OR4). We initially aimed at finding another plantation as close as the weather station as OR4 but were unable to obtain permission from the owners. Baseline management differed between the two plantations, with no herbicide application reported by the owner of OR2 and one to two applications a year in OR4. We installed six microplots in each plantation between rubber tree rows (three in an area with herbicide spraying, three in an area

Figure 6.2: Location of the erosion microplots from 2015 to 2018. Blue (pink) symbols indicate microplots location in 2015 (2016 respectively). OR2 and OR4 are the two rubber tree plantations used in 2017 and 2018. Grey areas represent the different soil series.

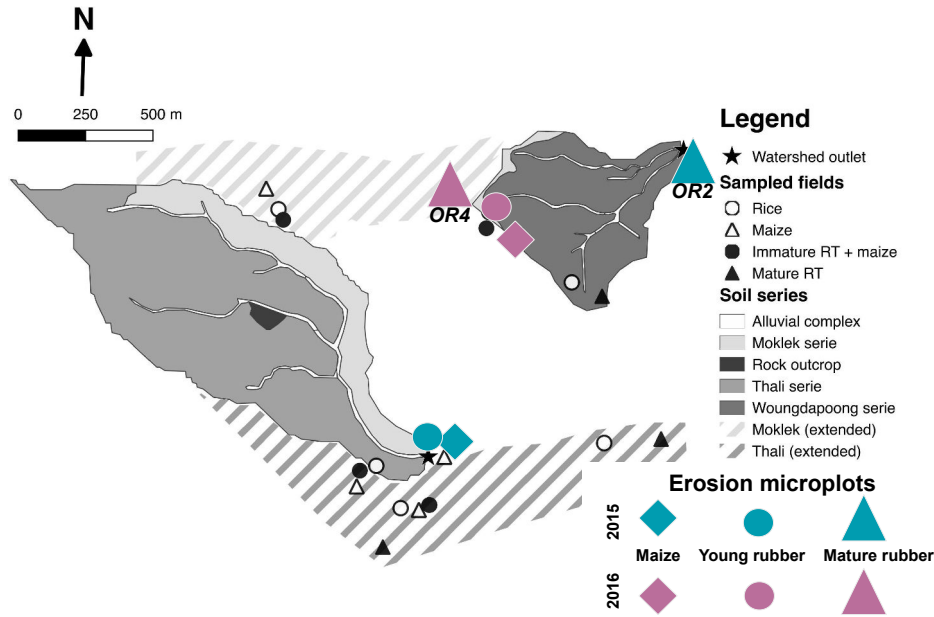


Table 6.1: Description of rainfall indices. (a) At the individual rain event level, i.e. directly calculated from rainfall data. (b) At the cumulative rain event level, i.e. indices calculated for each event generating runoff and taking into account rainfall history since the last event generating runoff. Rh_{n-1} : rainfall height of the previous rain event (mm). API_{n-1} : API at the beginning of the previous rain event. Δt : time since last rain event (days). Rainfall kinetic energy was calculated based on measurements made with a disdrometer in an experimental catchment located in Lao PDR, in a similar topographical and climatic context (Lacombe et al. 2017).

(a) Indices for single rain events			
	Name	Unit	Equation
Rh	Rainfall height	mm	
I_{30}	Maximum rainfall intensity (t = 30 minutes sliding window)	mm h^{-1}	$\max\left(\frac{Rh}{t}\right)$
EI_{30}	Storm rainfall erosivity	$\text{kJ mm h}^{-1} \text{m}^{-2}$	$I_{30} \times KE$
KE	Rainfall kinetic energy	kJ m^{-2}	$2.7952 + 11.953 \times \log_{10}(I_{30})$
(b) Indices for cumulative rain events (calculated since the last event generating runoff)			
	Name	Unit	Equation
Rc	Cumulative rainfall height	mm	$\sum_{\text{since last event}} Rh$
EC_{cum}	Cumulative kinetic energy	kJ m^{-2}	$\sum_{\text{since last event}} KE$
$EI_{30,max}$	Maximum EI_{30}	$\text{kJ mm h}^{-1} \text{m}^{-2}$	$\max_{\text{since last event}} EI_{30}$
R	Rainfall-runoff erosivity factor	MJ mm h^{-1}	$\sum_{\text{since last event}} EI_{30}/100$
API	Antecedent precipitation index		$(API_{n-1} + Rh_{n-1}) \times \exp\left(-\frac{\Delta t}{2}\right)$

without). The two areas within each plantation were 5 m to 10 m apart and at the same height along the hill slope.

6.1.2 *Meteorological monitoring*

An automatic weather station (Campbell BWS200) has been installed since March 2015 in the middle of a small flat grassland located at an elevation of 535 m AMSL. Meteorological parameters were measured on a 1-minute basis: temperature and air relative humidity with CS215 Sensor; wind speed and direction with Wind Sentry Sensor; rainfall with a tipping bucket rain gauge adjusted to tip once for each 0.2 mm of rain, (Campbell ARG100); sun plus sky radiation (300 nm to 1 100 nm) with a silicon photovoltaic detector (Campbell CS300). We calculated potential evapotranspiration using Monteith Penmann formula, taking into account longitude, latitude and elevation of the station and using wind, temperature, air humidity and solar radiation data.

The starting and ending time of an individual rain event was determined by a delay of at least 20 min between two bucket tips. A rain event starts at the tipping time following a period of 20 min without tip, includes all the following tips separated by less than 20 min and ends at the tipping time followed by a period of 20 min without tip. For each individual rain event I calculated the indices EI_{30} , KE and R established by Renard et al. (1997) to describe rainfall aggressiveness within the Revised Universal Soil Loss Equation (Table 6.1).

We also used two manual cumulative rain gauges located in open areas close to M and YR, and to OR_i and OR_s , respectively.

6.1.3 *Runoff and soil detachment monitoring*

Erosion microplots were 1 m² metallic frames, driven into the soil to a depth of 10 cm depth to avoid any influence of hypodermic lateral flow. They have been widely used in studies of soil detachment, notably in Southeast Asia (Janeau et al. 2003; Pierret et al. 2007; Podwojewski et al. 2008b; Patin et al. 2018). Their installation was realised carefully to avoid any disturbance on soil surface within the frame as well as vertical pathways between the frame and the soil (Fig. 6.3a). This allowed us to start monitoring just after installation from mid-May onwards for both years.

65 L buckets located downward each microplot allowed to collect the part of the rainfall which runs over the soil surface (overland flow), and the transported soil particles detached by splash erosion or by the velocity of the overland flow (Fig. 6.3b). The total volume of the overland flow was calculated from the measurement of water height in the collecting bucket. The concentration of soil particles was measured in a 300 mL aliquot which was filtered and dry-weighted at the Land Development Department laboratory in Chiang Mai, Thailand. The maximum frequency of overland flow sampling was once a day during very rainy periods. The samples often pooled several individual rain events which occurred during the period of time separating two consecutive samplings. I hence considered cumulated rainy events corresponding to the sum of the individual rain events which occurred during the period separating two consecutive samplings. As such, I calculated rainfall indices based on these cumulated rain events: cumulated rainfall height, cumulated kinetic energy, and maximum EI_{30} among the individual rainfalls that

Figure 6.3: Erosion microplots.

(a) Installation of an erosion microplot in plantation OR4.



(b) One installed microplot. The runoff collected from the metallic frame is collected in a large bucket.



occurred during the period of time separating two consecutive samplings. The calculation of these indices is described in Table 6.1b. For each cumulated rain event I also calculated the runoff coefficient which is the non-dimensional ratio between runoff volume collected for 1 m^2 (L m^{-2} and hence mm) divided by rainfall height (mm). Soil detachment (g m^{-2}) for each cumulated rain event generating runoff was calculated as the product of sediment concentration in the collected samples (g L^{-1}) by runoff volume (L m^{-2}). Table 6.2 provides a further description of the different plots.

6.1.3.A Year 2015 (monthly/annual scale)

The weather station was located 750 m at the north and 800 m at the west- south-west from M and YR sites and OR sites, respectively. I did not use the rainfall characteristics available at the automatic weather station (I_{30} , EI_{30} , EC) as the records in a rather remote location may be significantly different from actual conditions at (M, YR) and OR sites, especially in a mountainous environment. I only took into account the rainfall height recorded at the manual rain gauges located close to measurement sites. We measured the runoff volume in the collecting buckets after rainfalls at most once a day. When the volume accumulated reached at least 2 L, we emptied the bucket and sampled a 300 mL homogenised aliquot to measure sediment concentration. In these conditions, we were able to estimate precisely the monthly and annual soil detachment, but most sediment concentration measurements corresponded to multiple low rainfalls.

6.1.3.B Year 2016 (event scale)

As we found large differences in 2015 between rainfall measured at the automatic weather station and at manual rain gauges, we moved the plots closer to the station (Table 6.2). This change allowed to investigate more precisely the rainfall characteristics driving runoff and soil detachment. We also changed the sampling protocol to focus on daily rain events. After each event, and at most once a day, we measured runoff volume and we emptied the collecting bucket. We sampled a 300 mL homogenised aliquot only when the runoff collected in the bucket was larger than 2 L m^{-2} . Doing so runoff was only accumulated over the events occurring during one day. In contrast to 2015, all soil detachment measurements corresponded to daily events.

6.1.3.C Years 2017 and 2018 (event scale)

We kept the same protocol for runoff and soil detachment measurements as in 2016. We used manual rain gauge rainfall data for OR2 plantation (which was far from the weather station) and weather station rainfall data for OR4.

6.1.4 *Soil surface conditions*

6.1.4.A 2015 and 2016

We visually assessed the proportion of each soil surface type for each microplot in May or June and late August using the method proposed by Casenave and Valentin (1992)(Janeau et al. 2003; Chaplot et al. 2005; Podwojewski et al. 2008b).

Such assessment is both accurate and reproducible, particularly when applied by the same expert with training in visual estimation with percent cover charts (Malam Issa et al. 2011). The discriminated soil surface features included:

- Free aggregates (Fag) not anchored to the soil surface, and readily detached by gently brushing soil surface;
- Crusts resulting from the slaking of aggregates and the sealing of soil surface pores by the redistribution of fine particles. They include erosion crusts (ERO), gravel crusts (G) and structural crusts (ST);
- Litter and plant fragments lying directly on the soil surface.

The percentage of the soil surface covered by leaves and the height of the various stages of standing vegetation (crop, weed, bush, tree) were also estimated visually. It should be noted that overlap may exist between the soil cover and the different vegetation stages.

In 2016, oblique pictures of the microplots were also taken every week to provide qualitative indications of the dynamics of soil cover and were used to estimate surface conditions for one additional date (mid-October). As I had only two or three measures of soil cover each year and 3 microplots per land use, I had not enough statistical power to use soil cover as an explanatory variable of daily runoff or soil detachment. This data is thus only provided as a support for interpretation.

6.1.4.B 2017 and 2018

From 2017, in addition to soil surface type measurements, we took weekly standardised pictures of soil cover for each microplots, which corresponded to a bit more than 1180 pictures in total. I then analysed the image to measure the proportion of cover by living plants (see part 2.3.5).

6.1.5 *Data processing*

6.1.5.A Exclusion of very intense rain events

Some rain events were characterised by very high intensity or erosivity (EI_{30}). These intense events sometimes resulted in massive overland flows coming from the upper slope, accumulating sediments at the upper side of the frame and invading the microplot. In such conditions both runoff volume and soil detachment were clearly biased because they did not correspond to the rain directly falling within a controlled 1 m^2 area but to the flow running along on a hillslope of unknown area. I decided to discard all the "very intense events" characterised either by the 5% highest mean intensity or the 5% highest EI_{30} within each year. With exception to parts 6.2.1, 6.2.2.b, 6.2.3.a, these events were not included in the analyses. I provide figures and tables including these most intense events as supplementary material.

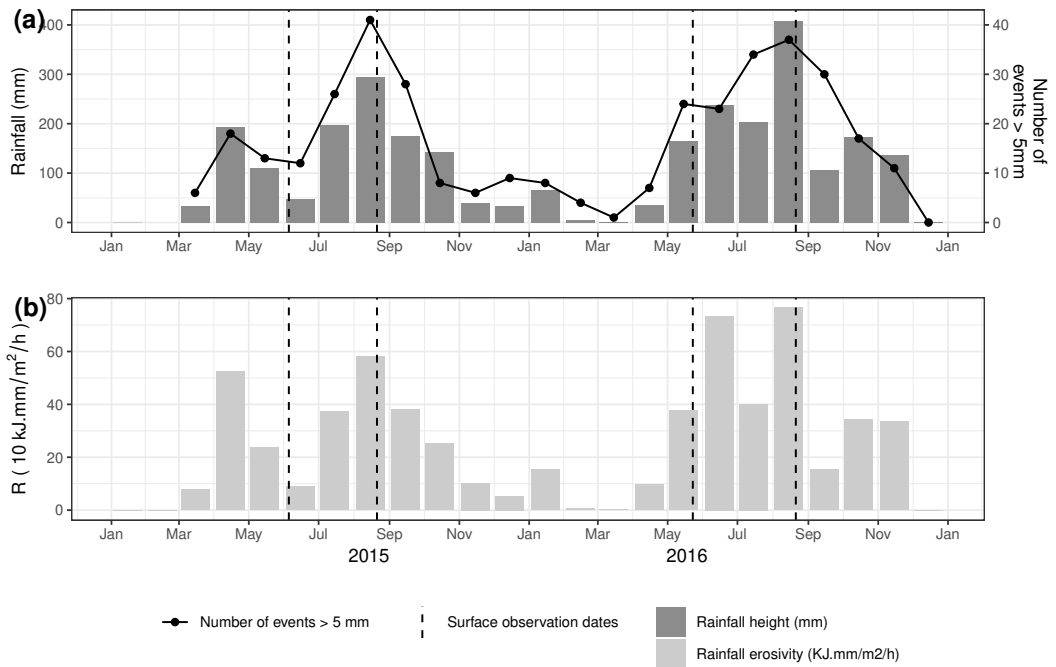
6.1.5.B Data transformation and analyses

Simple linear regressions require independence of the data and were not adapted to repeated measurements in the microplots. Thus, I used linear mixed models

Table 6.2: Plot characteristics in maize fields (M), young rubber tree plantations with intercrop (YR), and mature rubber tree plantations inter (OR_i) and within (OR_s) tree rows. Soil belonged to two soil series: Molklek (MI) and Wang Saphung (Ws).

Year	Land use	Soil series	Distance from weather station (m)	Average slope	Soil texture	Plantation code 2017-2018
2015	M	MI	750	57%	clay	} OR ₂
	YR	MI	760	62%	clay	
	OR _i	Ws	760	45%	clay	
	OR _s	Ws	760	57%	clay	
2016	M	Ws	170	65%	loam	} OR ₄
	YR	Ws	150	66%	clay-loam to loam	
	OR _i	MI	280	56%	clay to clay-loam	
	OR _i	MI	280	63%	clay to clay-loam	

Figure 6.4: Seasonal variations of rainfall height and erosivity in 2015 and 2016. 6.4a: monthly rainfall (light grey bars) and number of events >5mm (black dots). 6.4b: rainfall erosivity (R). Dashed vertical lines indicate dates of soil surface characterisation. Note that monthly records started in March 2015.



(R package NLME) with each microplot as a random effect to take into account the temporal dependence.

To investigate the relations between runoff, soil detachment and meteorological variables (first study), I discarded “small” events with rainfall height under 2 mm. Because meteorological variables (rainfall, rainfall erosivity, etc.) are not independent, and because I was interested in determining the best estimator of soil runoff and detachment, I chose to conduct simple regressions with only one explanatory variable. Fixed effects were rainfall characteristics (e.g. height, kinetic energy or intensity). Surface runoff and soil detachment were non-normal and with heterogeneous variance. I thus performed model-specific box-cox transformations:

$$y' = \begin{cases} \frac{y^\lambda - 1}{\lambda} & \text{if } \lambda \neq 0 \\ \ln(y) & \text{if } \lambda = 0 \end{cases} \quad (1)$$

With y the runoff or soil detachment, y' the transformed variable, and λ the optimised box-cox parameter (function *boxCox*, R package CAR). I then performed stepwise model selection based on AIC (function *stepAIC*, R package MASS). In this procedure, each variable is penalised by a factor 2, leading to likelihood ratio tests with $P = 0.15$. In order to apply stringent selection and to keep only variables significant at 5%, I used a penalty factor of 3.8 (quantile of the chi-square distribution for $P = 0.05$). The date was coded as day number since January 1st.

In the second study, in order to have a continuous estimation of soil cover for each microplot, I fitted one polynomial curve for each microplot, using a span of 0.6. For each point, the fit was done locally, based on the value of all neighbouring points with weight decreasing with the distance from the focal point (function *loess*). I fitted separate models between each herbicide spraying (e.g. five periods: January to June 2017, June to August 2017, August 2017 to June 2018, June to September 2018, and September to December 2018). I then tested the effect of treatment on monthly runoff coefficient, and of estimated soil cover on runoff coefficient of individual events, using mixed models. In both models, the plantation (OR2 or OR4) was included as a fixed effect while the month and the microplot were included as random effects.

6.2 RESULTS 1. COMPARISON OF RUNOFF AND SOIL DETACHMENT IN ANNUAL CROPS AND RUBBER TREE PLANTATIONS (2015-2016)

6.2.1 Meteorological conditions

The rainy season was both more intense and late in 2016 (May-November) than 2015 (April-October). In 2015, total rainfall measured from March was 1 256 mm in the maize field and young rubber tree plantation, and 1 310 mm in the mature rubber tree plantation. From May onwards (start of microplot monitoring) it was respectively 1 051 mm (M, YR) and 1 104 mm (OR_i, OR_s). The highest monthly rainfall peaked in August (276 mm) (Figure 6.4a). In 2016, total rainfall was 1 540 mm (May to December: 1 451 mm) and peaked in August (414 mm). Maximum

EI_{30} for single events were $17.2 \cdot 10^2$ and $19.7 \cdot 10^2 \text{ kJ mm m}^{-2} \text{ h}^{-1}$ in 2015 and 2016, respectively. The monthly erosivity factor R ($10^2 \text{ kJ mm m}^{-2} \text{ h}^{-1}$, corresponding to the monthly sum of EI_{30} divided by 100) peaked in April and August 2015 and June and August 2016.

The total number of individual rain events higher than 0.2 mm was larger in 2016 (221) than in 2015 (199), as was the number of events with cumulative rainfall height higher than 20 mm (20 and 15 respectively, Table 6.3). In total, from May onwards, we measured runoff for 50 (2015) and 63 (2016) "cumulated" rain events (see part 6.1.3).

6.2.2 Year 2015 (monthly and annual scale)

6.2.2.A Comparison of weather station and manual rain gauge data

In 2015, from May onward, 28 of 57 monitored rain events involved differences in measured rainfall height between at least one rain gauge and the automatic weather station which was greater than one third of the height measured at the station (Fig. S6.1). As a simple correction of intensity and kinetic energy (proportional to the rainfall height difference) was unlikely to faithfully represent local conditions in the plots, I decided not to use intensity nor kinetic energy calculated with rainfall height and intensity measured at the automatic weather station.

6.2.2.B Surface runoff, soil detachment and contribution of intense events

Yearly runoff and soil detachment for each microplot are summarised in Table 6.4. The 5% most intense events accounted for a large part of the runoff (up to 42% of the annual runoff, and 49% of soil detachment, for only 22-24% of total rainfall). These figures are in all likelihood significantly overestimated because the contributing areas were probably larger than 1 m^2 . Results for these "ungauged" events are presented in the supplementary information and were discarded in subsequent analyses. Annual runoff coefficient for individual microplots varied from 4.7 to 10.6% in M or YR and from 19% to 32% in OR_i or OR_s . Annual soil detachment varied from 0.08 kg m^{-2} to 0.63 kg m^{-2} in M and YR and from 1.9 kg m^{-2} to 3.9 kg m^{-2} in OR_i or OR_s .

6.2.2.C Impact of the land use on runoff and soil detachment

Figures 6.5a and 6.5b illustrate the temporal variations of runoff coefficient and soil detachment, depending on the land use. The bimodal shape of the rainfall, well marked in 2015, is clearly observed for soil detachment but not for runoff coefficient. Monthly runoff coefficient (averaged for the 3 replicates of each land use) in M and YR was the lowest in M microplots in July (2.6%) and peaked at 31% in M microplots in October when monthly rainfall height was low but rainfall erosivity density still high (Figure 6.4). Soil detachment remained generally very small in M and YR. Only one M microplot generated a cumulated detachment of 0.5 kg for 3 consecutive events in August and October (Fig. 6.5b).

Runoff coefficient ranged between 4.2% (July) and 56.1% (September) in OR_i , and between 5.3% (June) and 54.7% (October) in OR_s (Fig. 6.5a). It was low at the beginning of the rainy season (until August), with no difference between OR_i

Table 6.3: Cumulative rainfall height and kinetic energy separated by rainfall height in 2015 and 2016, from May onwards, in maize fields (M), young rubber tree plantations with intercrop (YR), and mature rubber tree plantations inter (OR_i) and within (OR_s) tree rows. In 2015, results are presented separately for M/YR and OR_i/OR_s because of rainfall spatial variability. The data including very intense events is provided in Table S6.1.

	2015				2016			
	(M YR OR _i OR _s)				< 25 mm	25-50 mm	>50 mm	Total
	< 25 mm	25-50 mm	>50 mm	Total				
Rainfall (mm)	394 407	241 294	130 149	766 851	500	499	406	1292
Kinetic energy* (kJ m ⁻²)	956 952	265 270	94 93	1314	1019	549	157	1725
n events	47	8	2		43	14	4	

* Calculated from the weather station.

Table 6.4: Annual runoff and soil detachment per microplot and per rainfall height (mm) in maize fields (M), young rubber tree plantations with intercrop (YR), and mature rubber tree plantations inter (OR_i) and within (OR_s) tree rows.

	Runoff (L m ⁻²)				Detachment (g m ⁻²)				
	<25	25-50	>50	Total	<25	25-50	>50	Total	
2015	M	5	20	12	36	1	30	87	118
		10	34	22	66	5	489	140	634
		17	38	24	79	8	111	168	287
		27	29	25	81	58	108	72	239
	YR	25	36	11	71	105	98	30	233
		12	20	12	45	9	60	8	78
	ORI	49	151	53	254	181	1375	309	1864
		65	180	25	270	322	2970	246	3539
	ORS	36	145	20	201	181	1808	566	2555
		58	111	62	231	522	2365	902	3790
		62	105	57	225	409	1979	1515	3902
		45	68	49	162	208	1037	1196	2441
2016	M	18	19	21	58	17	79	233	330
		19	24	20	63	45	125	149	320
		34	42	23	100	81	134	86	301
		23	31	29	82	34	86	122	242
	YR	24	33	28	86	45	103	62	209
		24	30	23	77	53	125	63	241
	ORI	115	163	190	467	549	1029	4096	5675
		192	237	173	602	1652	3615	7556	12823
	ORS	151	205	171	526	1322	2771	5530	9623
		125	152	166	443	844	1746	4123	6713
		93	119	162	374	646	1311	5062	7020
		130	167	163	460	942	1858	4762	7562

and OR_s ($P = 0.3$). It was significantly higher from September onwards, and the increase was more marked in OR_i than OR_s (Ancova: interaction land use:period, $P < 0.01$). Soil detachment reached values ranging from $0.5 \text{ kg m}^{-2} \text{ month}^{-1}$ to $2.5 \text{ kg m}^{-2} \text{ month}^{-1}$ (Fig. 6.5b). It was significantly higher in the late rainy season, after September, than in the early rainy season ($P = 0.003$), with no difference between OR_i and OR_s .

6.2.2.D Soil surface and soil cover conditions

Structural crust covered most of the soil surface in M and YR both in June and August (Fig. 6.6a), the rest of the surface consisting of either free aggregates or crop residues. However, especially in August, the soil surface in these fields was not bare but mostly covered either by weeds or the crop itself (Fig. 6.6b). In OR_s , structural crust also covered a large part of the soil. Rubber residues covered a significant part of the microplots in OR_s and completely covered the microplots in OR_i .

6.2.3 Year 2016 (event scale)

6.2.3.A Surface runoff and soil detachment

The 5% most intense events accounted for 4-46% of annual runoff and 9-38% soil detachment, but only 10% of total rainfall. After discarding these events, for which the contributing area was very likely biased, runoff coefficient for individual microplots varied from 4.4% to 7.7% in M and YR and from 29% to 47% in OR_i and OR_s . Soil detachment varied from $0.21 \text{ kg m}^{-2} \text{ yr}^{-1}$ to $0.33 \text{ kg m}^{-2} \text{ yr}^{-1}$ in M and YR and from $5.6 \text{ kg m}^{-2} \text{ yr}^{-1}$ to $12.8 \text{ kg m}^{-2} \text{ yr}^{-1}$ in OR (Table 6.4).

Average monthly runoff coefficient in M and YR remained stable throughout the rainy season, around 6% (Figure 6.7). From June, the runoff coefficient in OR_i and OR_s was always higher than in M or YR and increased steadily over the rainy season. It peaked in August after herbicide spraying (58% in OR_i , 43% in OR_s) and in November (68% and 67% respectively).

The minimal rainfall height generating soil detachment higher than 1 g m^{-2} was 11 mm in YR and M and 3.6 in OR_i and OR_s .

6.2.3.B Effect of rainfall characteristics on runoff and soil detachment depending on the land use

All rainfalls combined, runoff and soil detachment were significantly higher in OR_i and OR_s than in M and YR (Fig. 6.8a, 6.8b).

Runoff (boxcox-transformed) significantly increased with cumulative kinetic energy, all land use taken together. It increased with rainfall, maximum EI_{30} and API, with steeper slopes in OR_i and OR_s than in M and YR, although the interaction was barely significant for kinetic energy. It increased with date only in OR_i and OR_s . Runoff was best explained by rainfall or EI_{30} and land use ($R^2 = 72\%$ and 59% respectively, Fig. 6.8a), while API and calculated kinetic energy had a lower explanatory power (44% and 38% respectively, Table 6.5). When fitting models separately for land use types (i.e. separately for M/YR and OR_i/OR_s), rainfall, API and cumulative KE had similar explanatory power in M and YR than OR_i and OR_s (Table S6.4). However, maximum EI_{30} explained runoff slightly better in M and YR

Figure 6.5: Monthly runoff coefficient (a) and soil detachment (b) in maize fields (M), young rubber tree plantations with intercrop (YR), and mature rubber tree plantations inter (OR_i) and within (OR_s) tree rows in 2015. Monthly runoff coefficient was calculated as the cumulative runoff ($L m^{-2}$) divided by cumulative rainfall height mm for each month. Different letters indicate significant variations within each month. Intense events were excluded, the graph including very intense events can be found in Fig S6.2a and S6.2b.

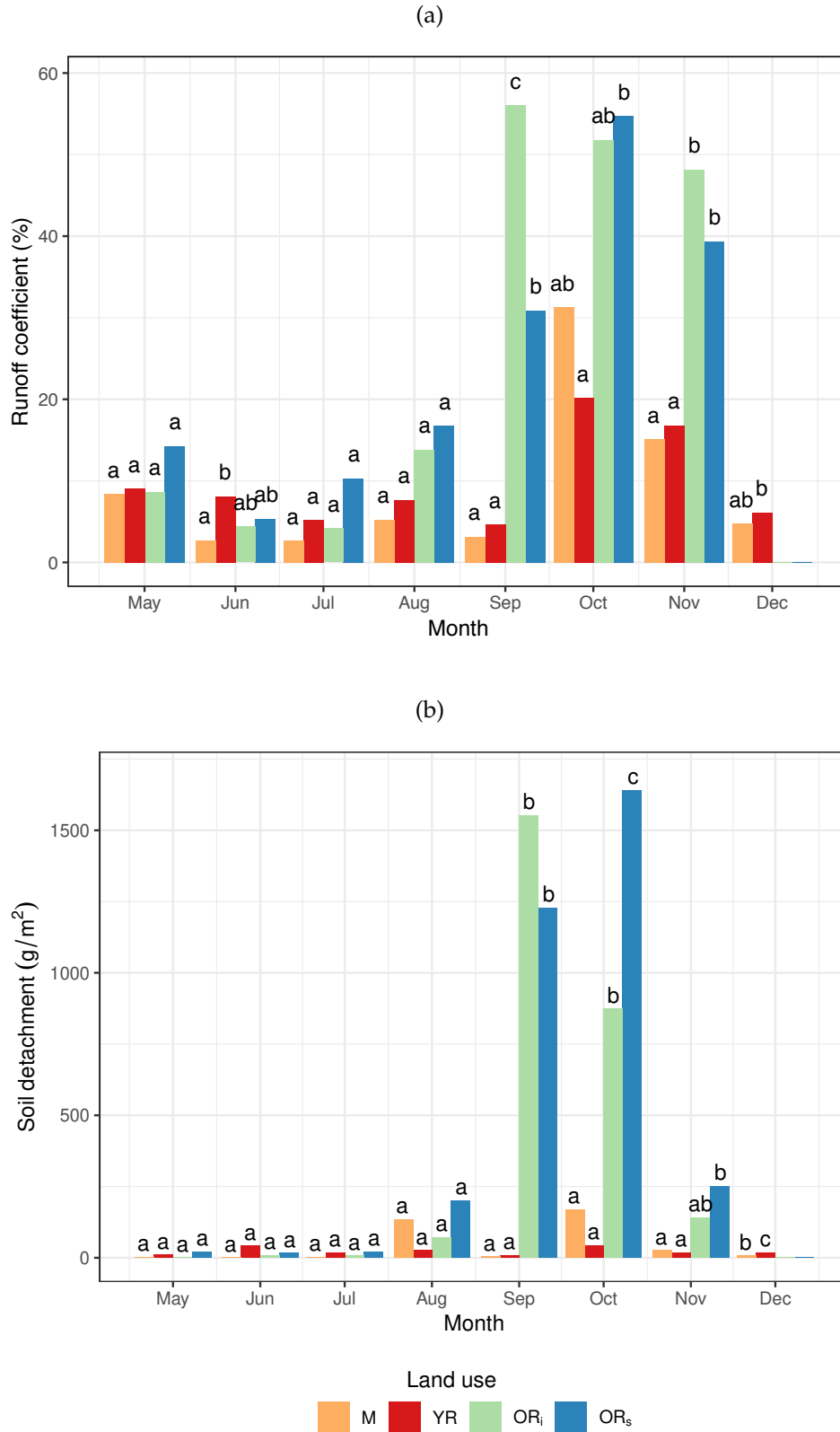
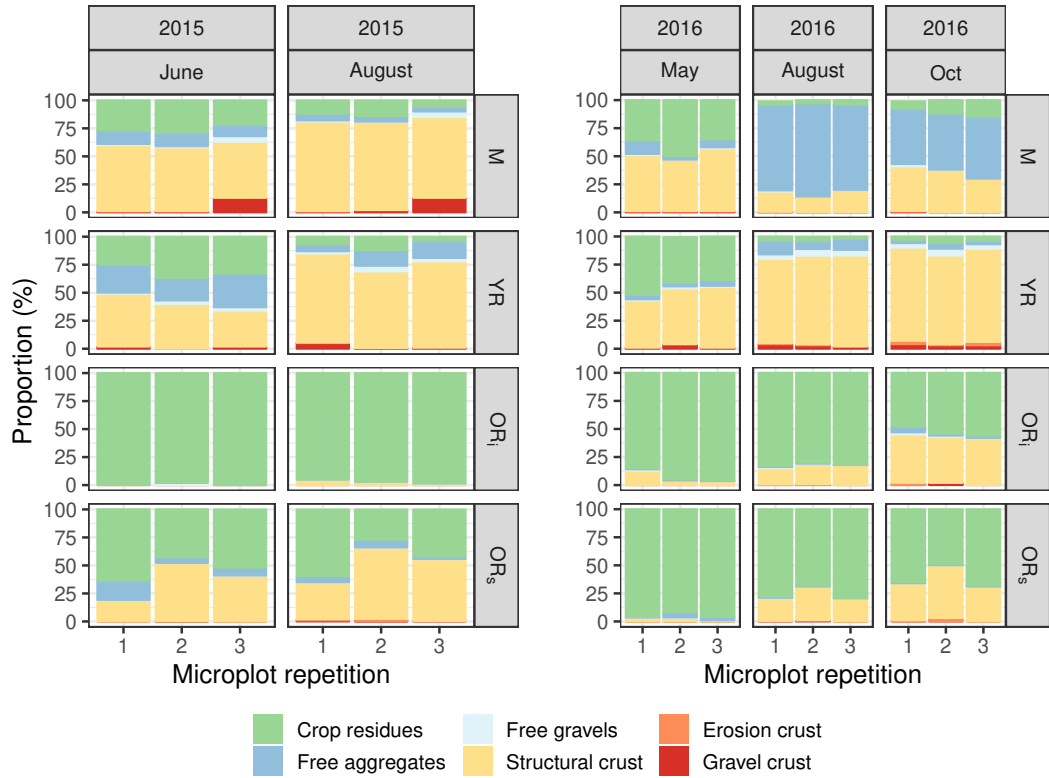


Figure 6.6: Variations of soil cover during the two years of experiment in maize fields (M), young rubber tree plantations with intercrop (YR), and mature rubber tree plantations inter (OR_i) and within (OR_s) tree rows. a) Variations of soil surface type. b) Variations of soil cover by crops and weeds measured independently from soil surface type. Crop cover in OR_i and OR_s correspond to canopy cover.

(a) Soil surface type.



(b) Soil cover.

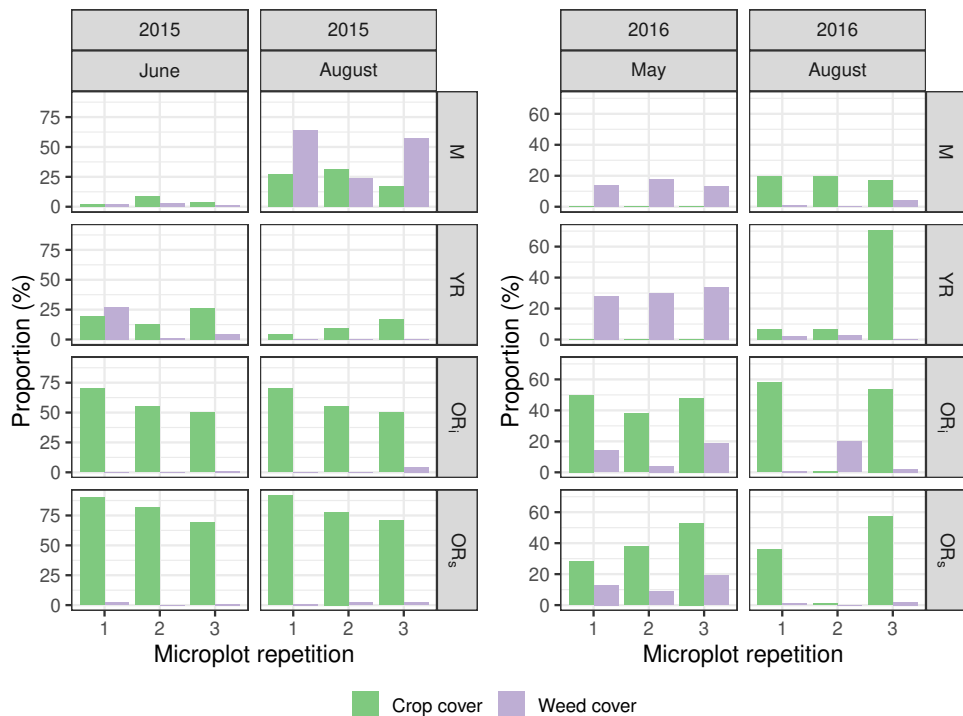
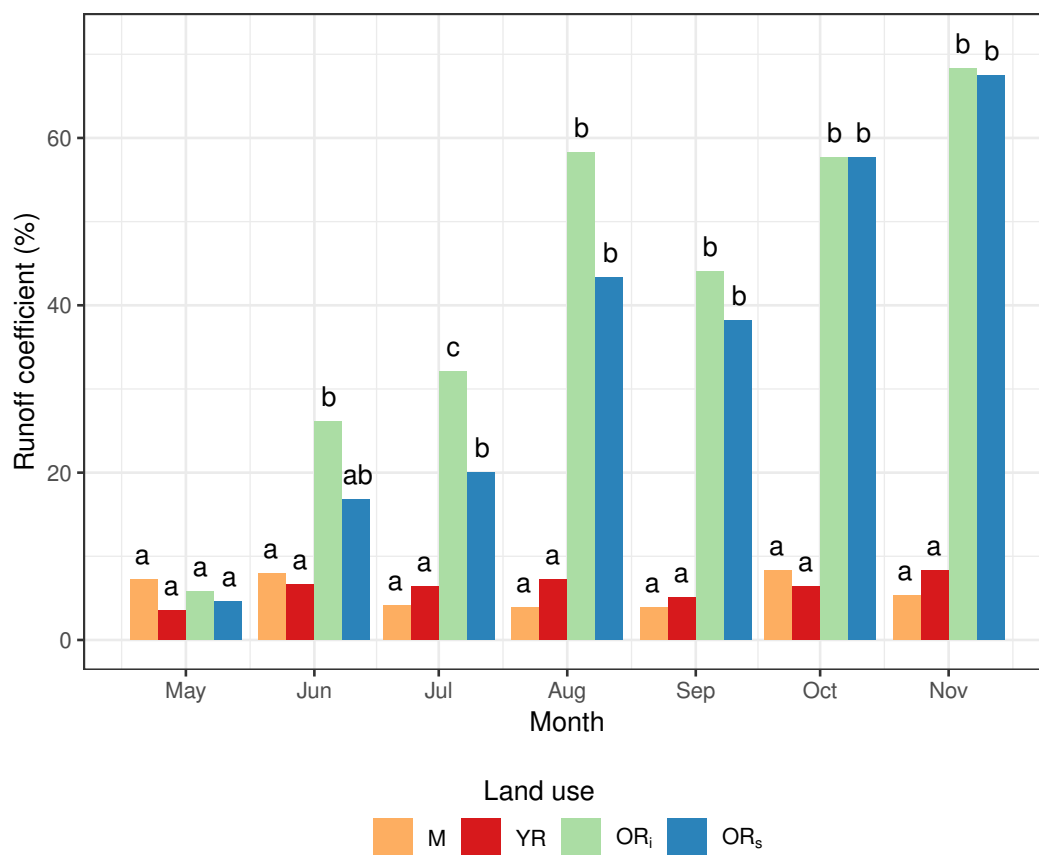


Figure 6.7: Monthly variations of surface runoff coefficient in 2016 in maize fields (M), young rubber tree plantations with intercrop (YR), and mature rubber tree plantations inter (OR_i) and within (OR_s) tree rows. Different letters indicate differences significant at 5% within each month. The graph including very intense event is presented in Fig. S6.3.



($R^2 = 54\%$) than OR_i and OR_s ($R^2 = 46\%$) while date explained runoff better in OR_i and OR_s ($R^2 = 12\%$) than M and YR ($R^2 = 1\%$, n.s. - Table S6.4).

Soil detachment (boxcox-transformed) increased with kinetic energy and EI_{30} regardless of the land use (Fig. 6.8b). It increased with date and rainfall, EI_{30} and API with steeper slopes in OR_i and OR_s than in M and YR. Soil detachment was best explained by rainfall and maximum EI_{30} ($R^2 = 49\%$ and $R^2 = 33\%$). When fitting separate models, all variables (except land use) explained soil detachment variations better under OR_i and OR_s than M and YR, especially rainfall ($R^2 = 47\%$ instead of 30%), API (18% instead of 4%), and date (21% instead of 4%, Table S6.4).

Log-transformed soil detachment increased linearly with log-transformed runoff ($P < 10^{-6}$); and it increased more in OR_i and OR_s (slope coefficient confidence interval: 1.70 g L^{-1} to 1.95 g L^{-1}) than in YR and M (slope coefficient confidence interval: 1.05 g L^{-1} to 1.52 g L^{-1} ; interaction: $P < 10^{-7}$; R^2 for fixed and random effects: 84 %; Fig. 6.9).

6.2.3.c Soil surface and soil cover conditions

At the onset of the rainy season, M and YR microplots were partly covered by crop residues (maize and rice, respectively). The rest of the surface was mostly structural crust. In the middle of the rainy season, the residues had mostly disappeared, leaving an almost continuous structural crust in YR and free aggregates in M, while the crop (maize or rice, respectively) provided a continuous cover (Fig. 6.6). In OR_i and OR_s microplots, rubber tree leaves covered 90 % of the surface at the beginning of the rainy season. It slightly decreased to 75 % in the middle of the rainy season. At the end of the rainy season, it decreased to about 50 % (Fig. 6.6). Uncovered surface mostly consisted of structural crust. Finally, at the end of the dry season, structural crust partly replaced free aggregates in M, while soil surface remained similar in YR. Soil cover by rubber leaves decreased to approximately 50% to 60% in OR_i and OR_s . For the three dates of observation, the variability between the plots was slightly higher for OR_s than for OR_i , but there was no significant difference between the average values.

Fig. 6.10 illustrates the trends of the soil cover dynamics. The photo series shows that in M and YR, soil surface remained covered by weeds, crop or crop residues throughout the rainy season, except at brief periods occurring at seeding and harvesting time. On the contrary, herbicide spraying in August in OR_i and OR_s had lasting effects, maintaining a quasi-null living plant cover until the end of the rainy season. Figure 6.7 also shows that the time of spraying corresponded to a leap in runoff coefficients.

6.3 RESULTS 2. MITIGATION OF RUNOFF BY WEED COVER UNDER RUBBER TREE PLANTATIONS (2017-2018)

6.3.1 Meteorological conditions

There was an important contrast between the meteorological conditions of 2017 and 2018, as 2017 had very high annual rainfall (1 864 mm in the weather station near OR_4 , 1 902 mm in the manual rain gauge near OR_2) and 2018 was very dry

Figure 6.8: Runoff and soil detachment variations with land use, rainfall characteristics and time since the onset of the rainy season in 2016 in maize fields (M), young rubber tree plantations with intercrop (YR), and mature rubber tree plantations inter (OR_i) and within (OR_s) tree rows. Runoff and detachment were transformed using model-specific box-cox transformations, which λ parameter is indicated in each subfigure. Graphs including very intense events are presented in Fig. S6.4a and Fig. S6.4b.

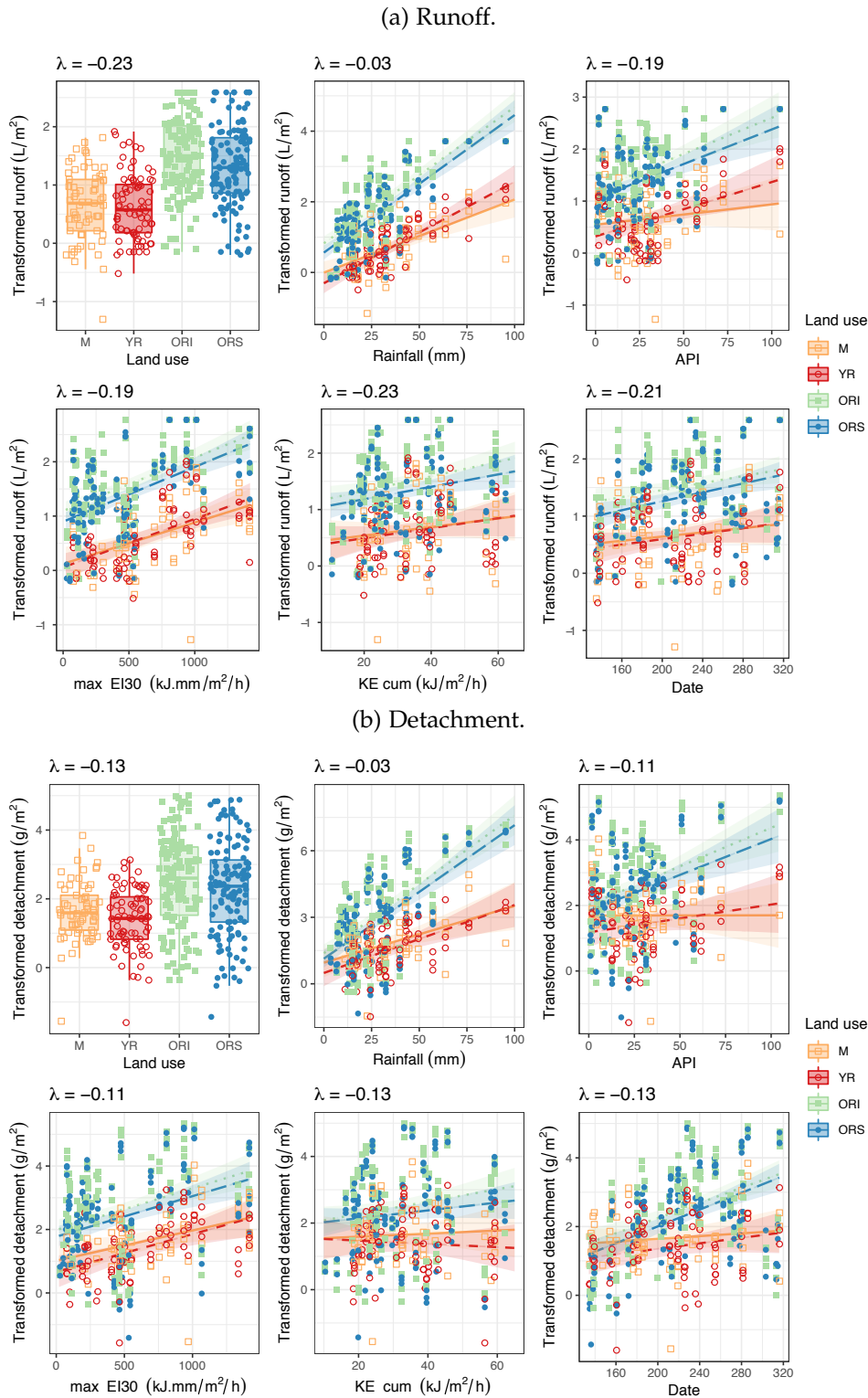


Table 6.5: Model selection for A. runoff and B. soil detachment, all land uses combined. y is A. transformed runoff or B. transformed detachment. x is the considered explanatory variable. a and b are the model coefficients. λ is the box-cox transformation parameter. Full models were simplified using stepwise regression. Indexed coefficients denote significant differences between land uses (a_i : interaction between x and land use; b_i : differences of land use intercepts). R^2 is calculated including both fixed and random effects. AIC: Akaike Information Criteria. API: Antecedent Precipitation Index. EI_{30} : rainfall intensity. KE: rainfall kinetic energy. Results for models including very intense events are presented in Table S6.3.

A. $Y = \text{Runoff (L m}^{-2}\text{)}$				
X	Model type	R^2 (%)	AIC	λ (conf. int)
Rainfall (mm)	$y = a_i x + b_i$	72	849	0.19 (0.17 0.21)
API	$y = a_i x + b_i$	44	916	0.09 (0.07 0.13)
Max EI_{30} ($\text{kJ mm m}^{-2} \text{h}^{-1}$)	$y = a_i x + b_i$	59	850	0.11 (0.07 0.13)
Cumulative KE (kJ m^{-2})	$y = ax + b_i$	34	881	0.05 (0.03 0.09)
Date	$y = a_i x + b_i$	30	907	0.07 (0.05 0.11)
B. $Y = \text{Detachment (g m}^{-2}\text{)}$				
X	Model type	R^2 (%)	AIC	λ (conf. int)
Rainfall (mm)	$y = a_i x + b_i$	45	1459	-0.03 (-0.07 0.01)
API	$y = a_i x + b_i$	19	1451	-0.11 (-0.15 -0.07)
Max EI_{30} ($\text{kJ mm m}^{-2} \text{h}^{-1}$)	$y = ax + b_i$	24	1412	-0.11 (-0.15 -0.07)
Cumulative KE (kJ m^{-2})	$y = ax + b_i$	13	1400	-0.13 (-0.17 -0.09)
Date	$y = a_i x + b_i$	26	1332	-0.13 (-0.15 -0.09)

Figure 6.9: Increase of log-transformed soil detachment with log-transformed surface runoff for all rain events causing detachment in 2016 in maize fields (M), young rubber tree plantations with intercrop (YR), and mature rubber tree plantations inter (OR_i) and within (OR_s) tree rows. The effects of log-transformed runoff and land use were significant ($P < 10^{-12}$). The slope coefficient in OR_i and OR_s (confidence interval: 1.70 g L^{-1} to 1.95 g L^{-1}) was significantly higher ($P < 10^{-7}$) than in YR and M (1.05 g L^{-1} to 1.52 g L^{-1}). R^2 for fixed and random effects was 85%. The graph including the most intense events is presented in Fig. S6.5.

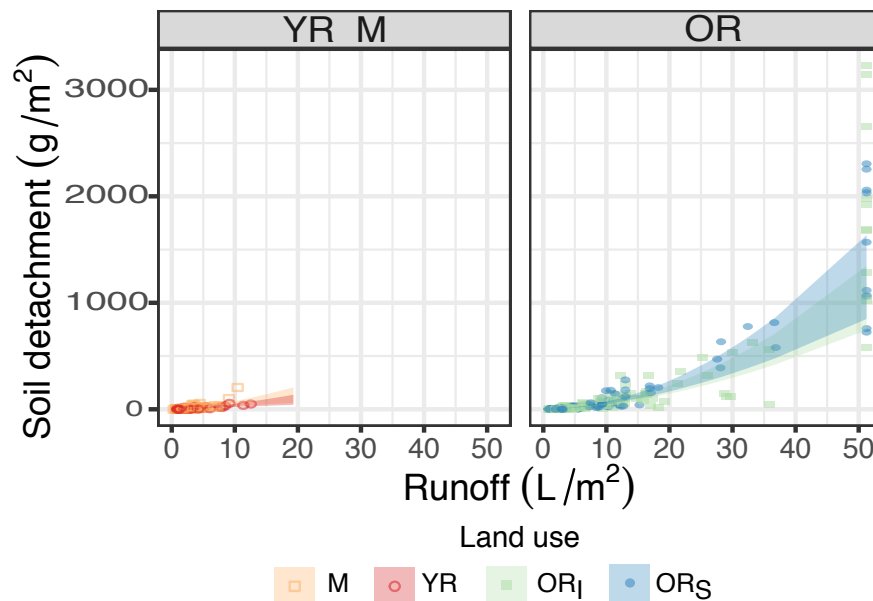
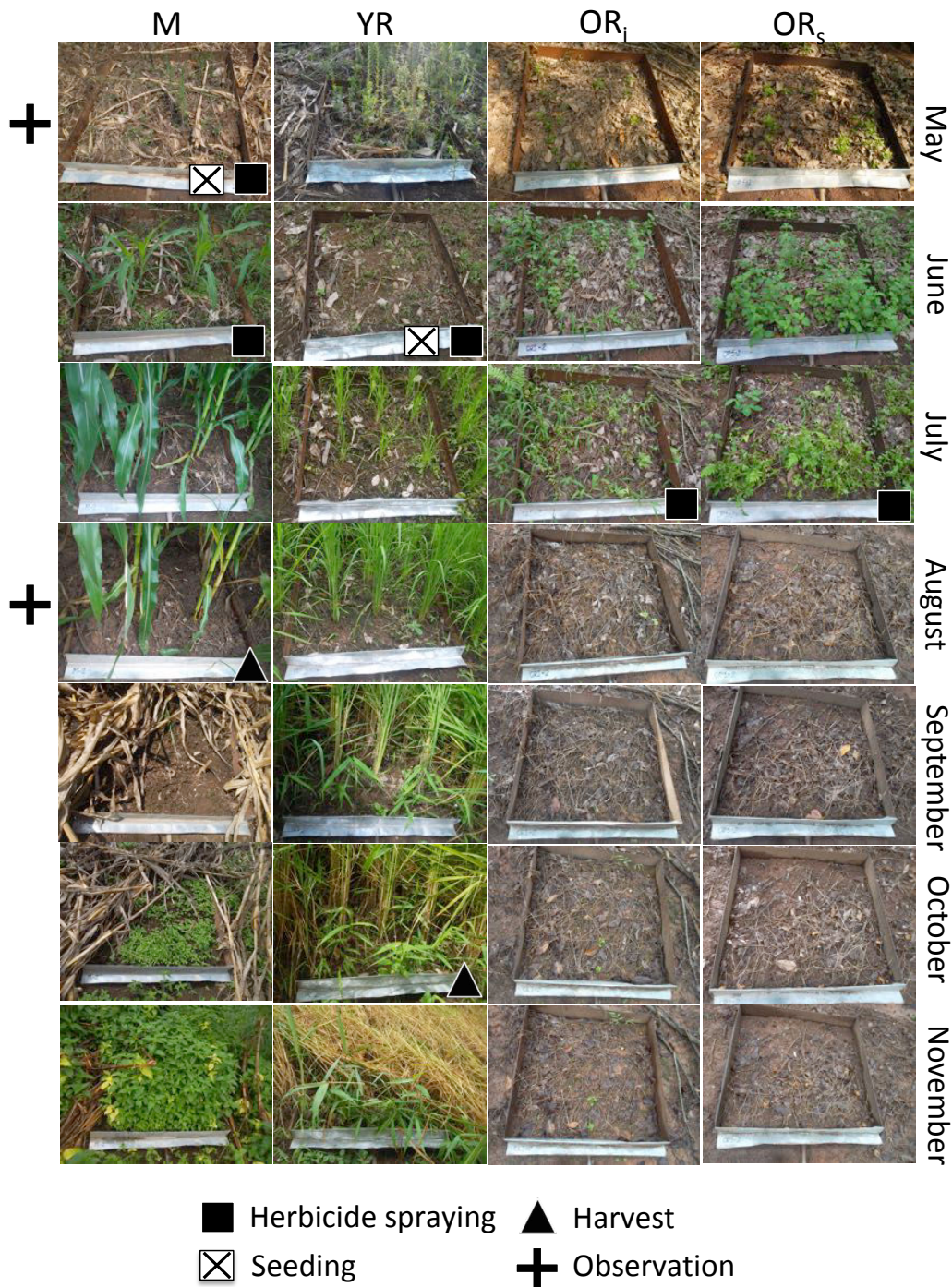


Figure 6.10: Evolution of soil cover between May and November, 2016 in maize fields (M), young rubber tree plantations with intercrop (YR), and mature rubber tree plantations inter (OR_i) and within (OR_s) tree rows. Symbols indicate actions realised during the considered month.



(1 447 mm in the weather station near OR₄, 1 631 mm in the manual rain gauge near OR₂). The monthly rainfall peaked in July 2017 and August 2018. Maximum EI₃₀ for single events (measured from the weather station) were $21.2 \cdot 10^2 \text{ kJ mm m}^{-2} \text{ h}^{-1}$ and $17.0 \cdot 10^2 \text{ kJ mm m}^{-2} \text{ h}^{-1}$ in 2017 and 2018, respectively. The monthly erosivity factor R ($10^2 \text{ kJ mm m}^{-2} \text{ h}^{-1}$, corresponding to the monthly sum of EI₃₀ divided by 100) peaked in May and July 2017, and May, August and October 2018. The total number of individual rain events higher than 0.2 mm was larger in 2017 (293) than 2018 (246), as was the number of events with cumulated rainfall height higher than 20 mm (36 in OR₂ and 34 in OR₄ in 2017, 27 in 2018).

The annual runoff coefficient was $20 \pm 7\%$ in OR₂ without herbicides and $28 \pm 4\%$ in OR₂ with herbicides. It was $35 \pm 10\%$ in OR₄ without herbicide and $44 \pm 4\%$ in OR₄ with herbicides.

6.3.2 *Plant cover dynamics under rubber tree plantations*

Measured plant cover was quite variable, as shown by the jagged aspect of the curves presented in Fig. 6.12a: using smoothed curves provided a better estimation of the cover. The success of the herbicide treatment was partial, as it resulted in significant monthly differences in plant cover between the H (with herbicide) and NH (no herbicide) treatments only in OR₂ (except before herbicide application in 2018), and at the end of 2018 in OR₄ (Fig. 6.12b). In particular, errors in the protocol led to repeated applications of herbicides in both areas of OR₄.

6.3.3 *Effect of herbicide treatment on runoff*

There was high variability in monthly runoff coefficients over the two years and among microplots. NH microplots had a slightly lower monthly runoff coefficient than H microplots (between 20% and 30% lower, Fig. 6.13, $P = 0.007$). When the model was fitted separately for OR₂ and OR₄, the treatment effect was significant only in OR₂ (not shown).

6.3.4 *Effect of plant cover on runoff*

I then investigated more precisely the effect of plant cover on surface runoff, including all rain events generating runoff and the corresponding cover estimate for each microplot. One-third of these cover estimates were between 0% and 6% (median 1.2%; low cover), one-third were between 6% and 25% (13.1%, medium cover), and one-third were between 25% and 77% (45.9%, high cover). In general runoff coefficient (square-root transformed) increased with rainfall (square-root transformed), but the slope coefficient differed depending on the soil cover class (Fig. 6.14a, model results in Table 6.6). In OR₂, the slope coefficient was significantly higher under low cover compared to high cover, and intermediate under medium cover. In OR₄, the slope coefficient was significantly higher under low or medium cover compared to high cover, where runoff coefficient did not vary significantly with rainfall height. Besides, surface runoff by soil cover decreased with soil cover mostly for large (in OR₂) or intermediate and large (OR₄) rain events (Fig. 6.14a).

Figure 6.11: Seasonal variations of rainfall height and erosivity in 2017 and 2018. 6.11a: monthly rainfall (light gray bars) and number of events > 5 mm (black dots). 6.11b: rainfall erosivity (R).

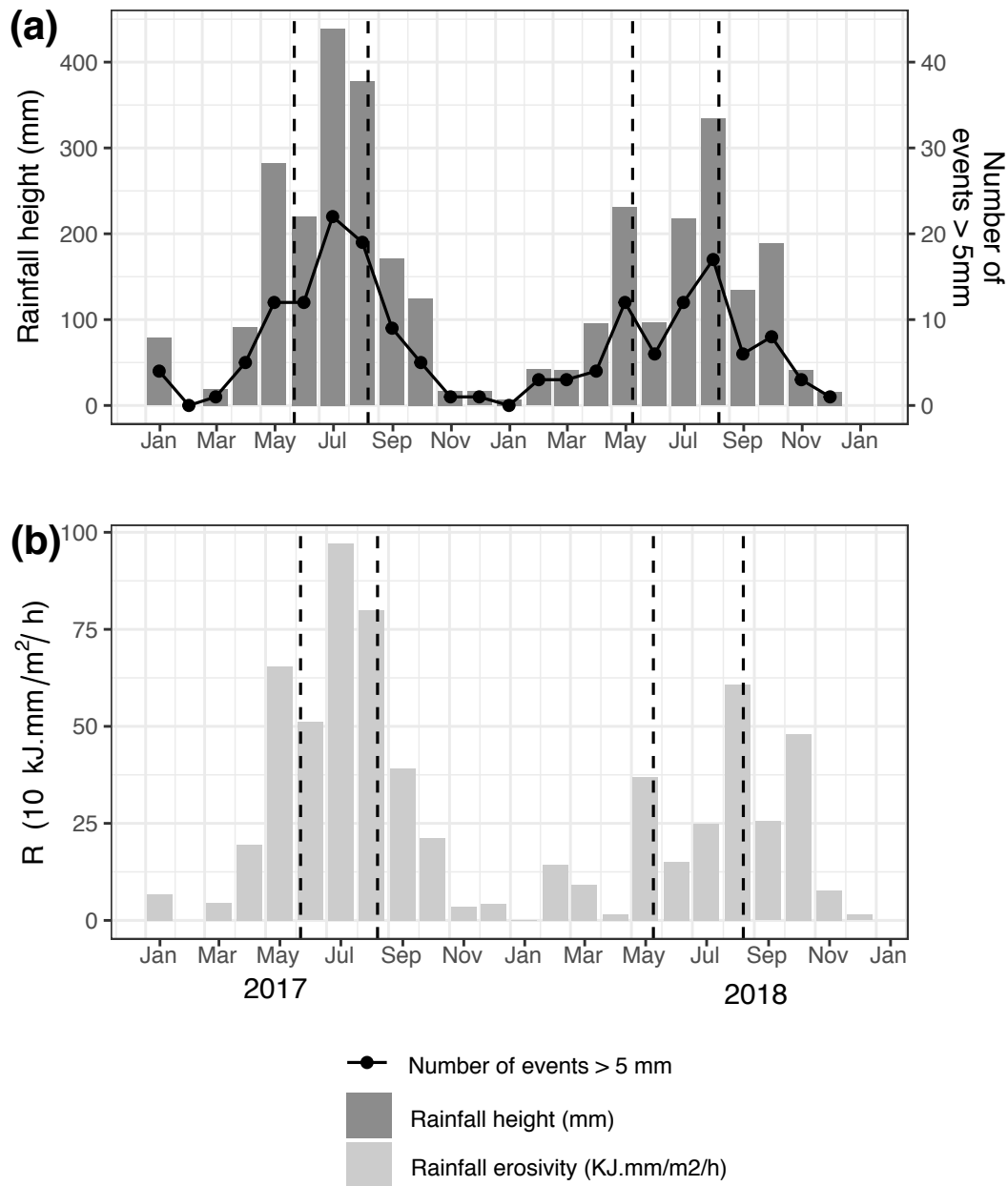
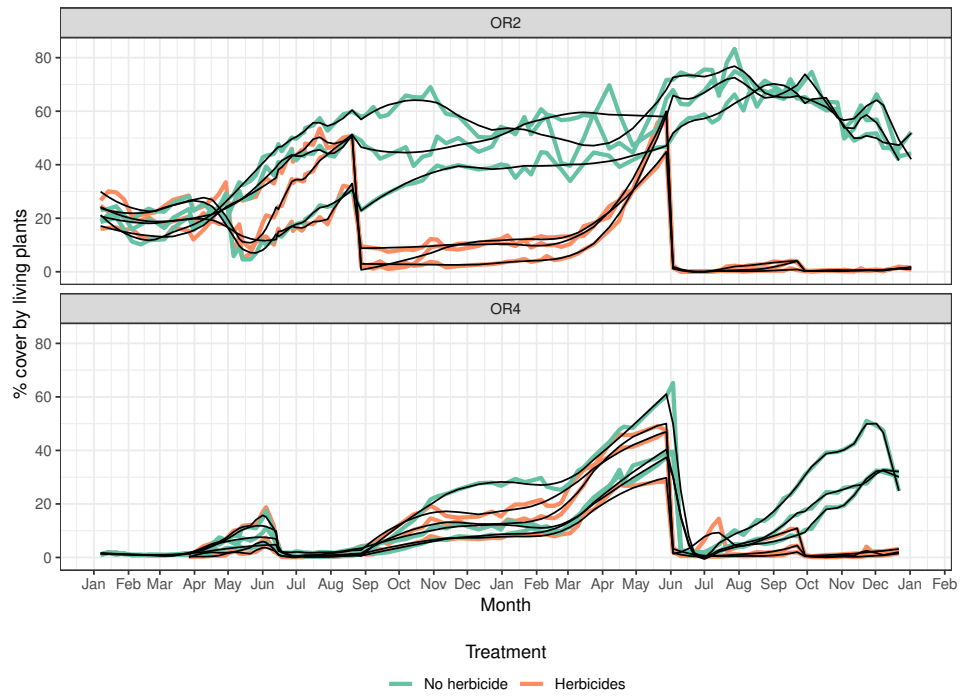


Figure 6.12: Plant cover dynamics in the two rubber tree plantations.

- (a) Fit of the plant cover dynamic model. Coloured lines represent the measures made from the weekly pictures. Black lines represent the smoothed variations (local fit with a span of 0.6), fitted separately between each herbicide application.



- (b) Effect of the treatment on monthly plant cover. Cover estimated from the smoothed curves were grouped by month: coloured boxes indicate the median and 25th and 75th percentiles for each treatment within each month.

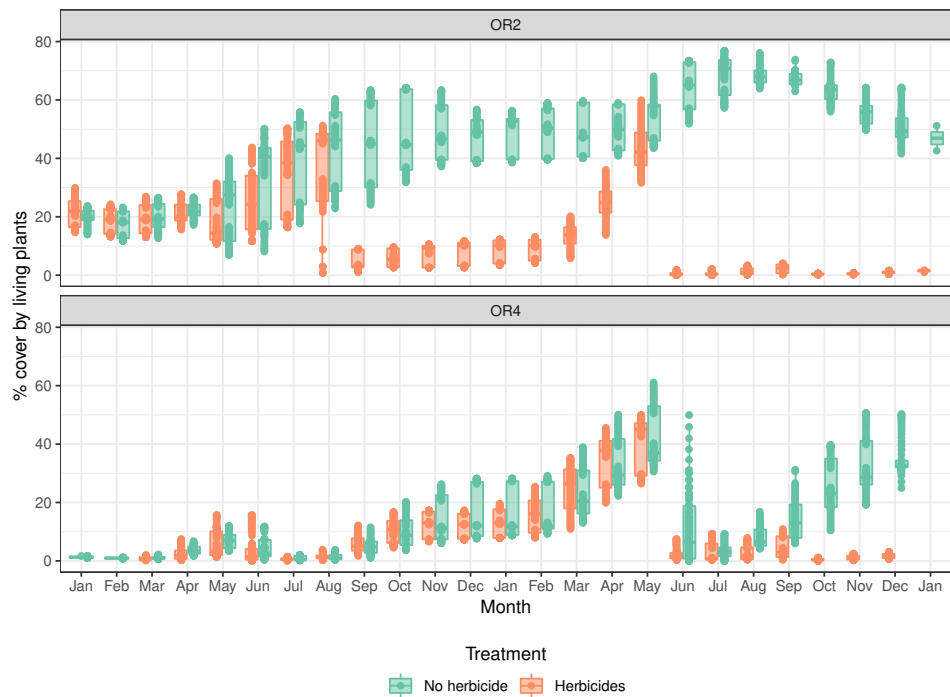


Figure 6.13: Effect of the herbicide treatment on monthly runoff coefficients. Each point represents one monthly runoff coefficient for one microplot, between January 2017 and December 2018. Microplot identity and month were included as random effects. The plantations (OR2 or OR4) were included as a fixed effect. Error bars represent the confidence intervals of the means, based on marginal effects (i.e. after controlling for the plot). Treatment effect: $P = 0.007$. Plantation effect: $P = 0.001$. R^2 (fixed effects only): 6%. R^2 (fixed and random effects): 84%. The same analysis including very intense events is presented in Fig. S6.6.

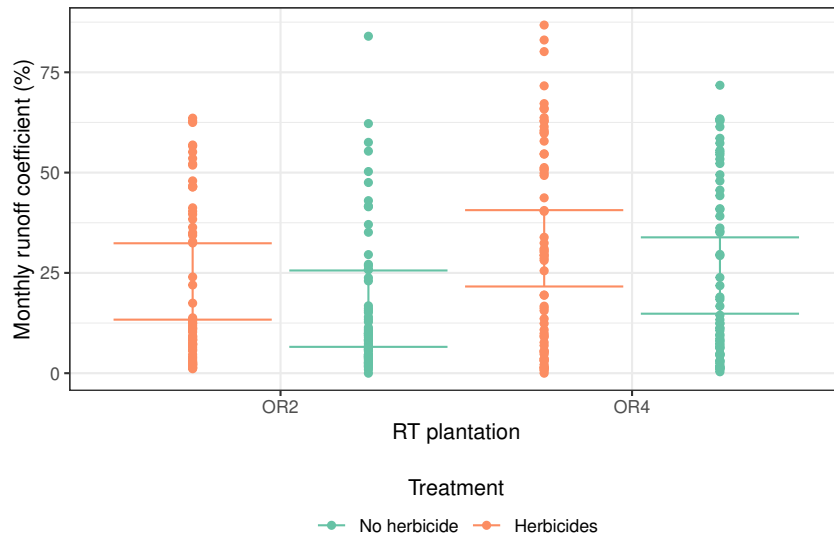


Table 6.6: Variations of runoff coefficient (square-root transformed) with rainfall height (mm, square-root transformed) depending on plant cover ("cover", proportion of living plant cover low (< 6%), medium (6% to 25%), or high (> 25%)) and the plantation (Plant.). ":" indicate interactions between the explanatory variables. Microplot identity and month were included as random factors. P-values are calculated based on Anova type-III tests. Different letters in the "Estimate" columns indicate differences significant at 5%. Results of the analysis including very intense events is presented in Table S6.5.

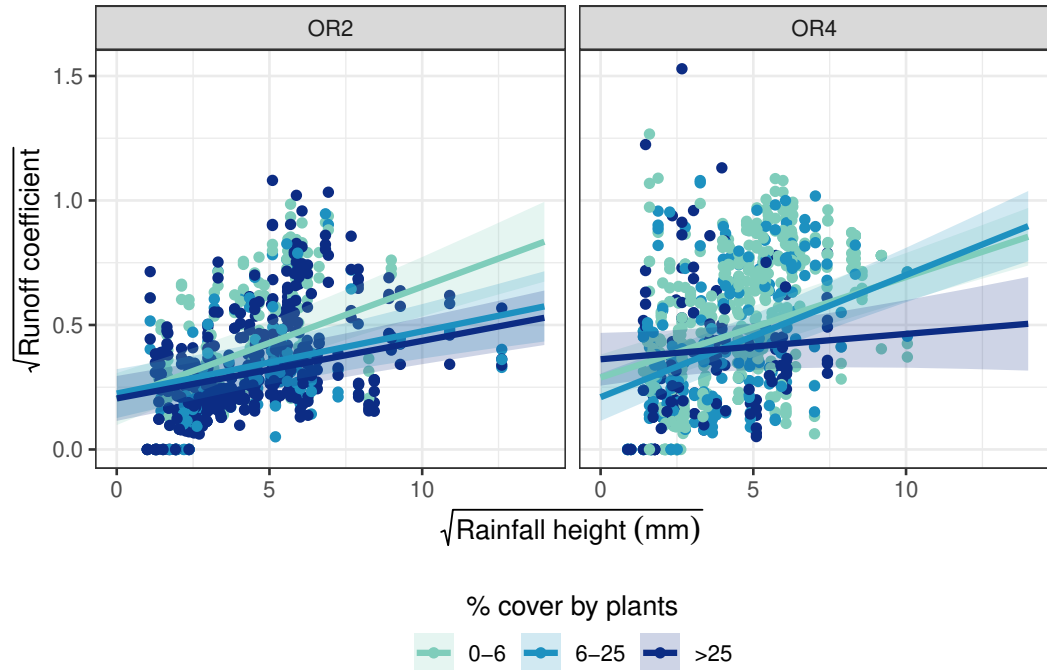
	Chisq	Df	Sum of square	Mean sum of square	P-value
(Intercept)	14.5	1			$1.4 \cdot 10^{-4}$ ***
Cover	0.4	2	0.16	0.08	$8.1 \cdot 10^{-1}$
Rainfall	43.2	1	4.21	4.21	$5.0 \cdot 10^{-11}$ ***
Plot	3.6	1	0.14	0.14	$5.8 \cdot 10^{-2}$
Cover:Rainfall	8.4	2	0.57	0.28	$1.5 \cdot 10^{-2}$ *
Cover:Plant.	11.1	2	0.30	0.15	$3.8 \cdot 10^{-3}$ **
Rainfall:Plant.	0.4	1	0.01	0.01	$5.5 \cdot 10^{-1}$
Rainfall:Plant.:Cover	11.6	2	0.31	0.16	$3.1 \cdot 10^{-3}$ **

Slope coefficient estimates

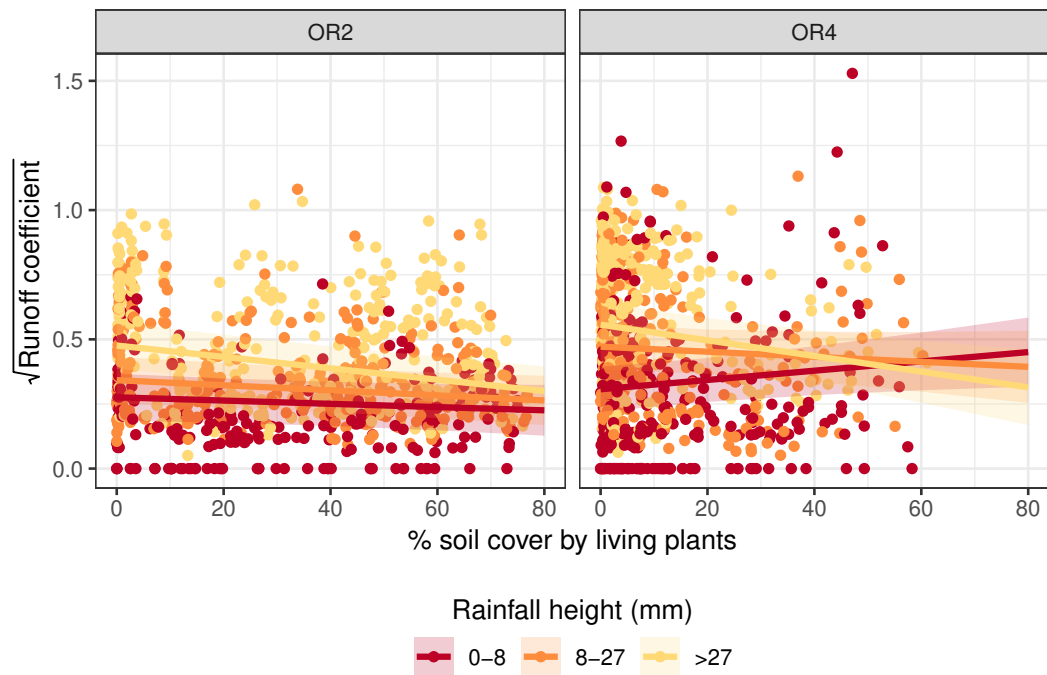
Plantation	Cover	Estimate	Plantation	Cover	Estimate
OR2	high	$2.3 \cdot 10^{-2}$ ^a	OR4	high	$1.0 \cdot 10^{-2}$ ^a
	med	$2.5 \cdot 10^{-2}$ ^{ab}		med	$4.9 \cdot 10^{-2}$ ^b
	low	$4.5 \cdot 10^{-2}$ ^b		low	$4.0 \cdot 10^{-2}$ ^b

Figure 6.14: Effect of rainfall height (square-root transformed) and soil cover on runoff coefficient (square-root transformed). Each point represents the runoff coefficient for one rain event in one microplot, between January 2017 and December 2018. Microplot identity and month were included as random effects. Coloured areas represent the confidence intervals, based on marginal effects (i.e. after controlling for the plot). The analysis including very intense events is presented in Fig. S6.7.

- (a) Effect of rainfall height on runoff coefficient, depending on soil cover. The plantations (OR2 or OR4), rainfall height, and cover class were included as a fixed effect.



- (b) Effect of soil cover on runoff coefficient, depending on rainfall height cover. The plantations (OR2 or OR4), rainfall height class, and soil cover were included as a fixed effect.



6.4 DISCUSSION

6.4.1 *Erosion monitoring in mountainous areas*

In this chapter, I investigated the variations of runoff and soil detachment with rainfall characteristics in different land uses representative of the transition currently observed in the mountainous region of Southeast Asia. I focused on fields cultivated with annual crops, fields occupied by perennial tree plantations with an early stage during which young trees are inter-cropped with annual cultivation, and a mature stage without inter-cropping.

We installed all microplots in cultivated fields or plantations, and based our measures on natural rain events (e.g. contrarily to studies involving rainfall simulations). This allowed us to measure soil erosion in "real-world" situations, but also had some shortcomings. In 2015 and 2016, we did not control (and thus could not homogenise) the management practices among the fields. In 2017 and 2018, we agreed on precise protocols with the owners (e.g. delimitation of herbicide-free areas) but they did not always transmit this information to field workers. This had minimal repercussions in OR₂, in which baseline management did not involve the use of herbicides, and where we applied herbicide ourselves in the small corresponding area. But this repeatedly disturbed our measures in OR₄, where the herbicide exclusion was not respected. Another shortcoming was the lack of precision (e.g. compared to rainfall simulations) regarding rainfall characteristics. My results showed that in mountainous areas such as the one I studied, rainfall height varies widely over a distance of a few hundred meters. This finding led us to relocate our sampling plots in 2016 and demonstrates that very local meteorological records are required to correctly analyse runoff and detachment data. As we had to move half the microplots back to OR₂ (far from the weather station) in 2017, I used only local rainfall measurements for the 2017-2018 experiment.

It is common in soil erosion studies to discard small rainy events as insignificant (generally less than half an inch, i.e. 12.5 mm, Renard et al. (1997)), and focus on medium to large events to quantify erosion. In my first experiment, I showed that indeed, medium and large events accounted for a large part of the runoff and erosion. These large events are the most visible for farmers and public authorities as they can cause floods or even landslides. Gullies, in particular, are very visible in the rubber tree plantations we studied, partly because the rubber tree lines do not follow previous terraces built on contour lines (Fig. 6.15). On the contrary, small events tend to be overlooked because they have little individual impact. Events under 25 mm, the most numerous, added up to 40%-50% of annual rainfall and 50-60% of cumulative kinetic energy. In 2016, they accounted for 10-30% of annual runoff and at least 10-25% of total soil detachment in 2016 (probably more as we did not measure detachment for events generating runoff $< 2 \text{ L m}^{-2}$). Such small events also mobilise particles which will then be more easily displaced by later events, thus contributing to high detachment during large rain events. Thus, overlooking the cumulative effect of small events could introduce significant underestimations of soil loss assessments.

Previous studies found that while rainfall height and intensity are strongly related, soil erosion was more correlated to rainfall intensity than rainfall height; while runoff was mostly correlated with rainfall height (Liu et al. 2017). In my first

Figure 6.15: Formation of a gully in OR2 plantation. The rubber tree lines do not follow contour lines, creating concentrated flows and gullies.



experiment, rainfall height was the main driver of both runoff and detachment, while maximum rainfall intensity, API and cumulative calculated kinetic energy had lower explanatory power. We did not measure kinetic energy or soil humidity directly but rather calculated these parameters using generic formulas. The poor fit of our models shows that our estimation was probably biased because it did not take into account local conditions. For API, the rate of decline of soil humidity is likely to vary according to soil contact cover and the presence of a canopy. I previously showed that in this area at the end of the dry season, soil humidity was still approximately two times higher under OR than in M or YR (see Chapter 3 and Neyret et al. (2018)). Similarly, both trees and understory generate high spatial variability of rainfall interception and throughfall, resulting in local modifications of kinetic energy and rainfall height; in particular it has been shown that throughfall under mature rubber trees has high kinetic energy (Lacombe et al. 2017). Thus, I found that when direct and local measures of kinetic energy or soil humidity are not available, rainfall height of individual rain events appears as the best predictor of surface runoff and soil detachment. This also allowed us to focus on rainfall height as the main predictor of runoff for the second experiment, in which half the microplots were far from the weather station.

6.4.2 *Afforestation by rubber tree plantations increases runoff and detachment*

I found that in both 2015 and 2016, runoff and soil detachment were much higher under OR than M or YR, with annual soil detachment rates in OR_i and OR_s on average 10 times (in 2015) and 30 times (in 2016) higher than in M and YR. Different factors varied between the two years of the experiment (soil type, meteorological conditions and microplots slopes) and might have had confounding effects on the results. First, a later monsoon in 2016 with higher rainfall and erosivity at the end of the rainy season (when rubber tree leaf litter has largely disappeared but weeds protect soil surface in M and YR) can explain the stronger effect of land use on runoff in 2016 than in 2015. Secondly, there might be an impact of soil variability: the two soil series found in the area are quite similar, both Haplustalfs characterised by moderate runoff and permeability (Moormann et al. 1966), but the Typic Haplustalfs (OR_i and OR_s in 2015; M and YR in 2016) are more gravelly, deeper, and potentially less prone to erosion than the Ultic Haplustalfs. This last hypothesis is supported by the fact that in the second experiment, I found a higher runoff in OR₄ (which corresponds to the same rubber tree plantation as used in 2016) than OR₂ (rubber tree plantation used in 2015). To make sure that this soil variability did not influence my main results about land use impact on erosion, I changed soil series-land use pairing between 2015 and 2016. I obtained similar results: the annual runoff and soil detachment per individual microplot was systematically higher in OR_i and OR_s than M or YR. Thus, while a direct comparison between 2015 and 2016 is impossible, the higher rates of runoff and detachment in OR_i and OR_s compared to M and YR are consistent; and the possible soil- or weather-related variation in sensitivity to erosion did not exceed or compensate for land use effects.

These higher rates of soil detachment and runoff in OR_i and OR_s than in M and YR were combined with notable soil surface degradation. In 2016, the slope coefficients of the linear regressions between runoff and detachment (taking into account the effect of time since the onset of the rainy season, rainfall and API) were

higher in OR_i and OR_s than in M or YR. The slope coefficients of the regression of detachment versus runoff were higher in OR_i and OR_s than M and YR. All these elements demonstrate a gradual decay of soil cohesion and infiltration capacities during the rainy season in mature rubber tree plantations, and overall a higher sensitivity of rubber tree plantations to soil degradation. It is thus important to quantify the resilience of these soil characteristics and to investigate physical (e.g. drying, cracking) or biological (earthworm activity, plant growth) factors that may contribute to the regeneration of such degraded soils.

6.4.3 *Factors affecting runoff and detachment in rubber tree plantations*

Recent studies obtained similar results in other tree plantations. Transition from open environments to teak plantations caused a large increase of overland flow and sediment yield measured at the catchment scale (Ribolzi et al. 2017), and mature rubber tree plantations are known to be quite prone to soil detachment (Lacombe et al. 2017). At least two factors can explain these results.

6.4.3.A Canopy effect

Due to their anatomy and leaf size, rubber and teak tree canopies modify throughfall and concentrate raindrops, which gain more kinetic energy (Liu et al. 2016b; Lacombe et al. 2017). Depending on their architecture, trees can also act either as umbrellas (moderately concentrating rainfall at the edges of the canopy) or as funnels (strongly concentrating rainfall near the trunk), both of which have been observed in the plantations, although not directly above the microplots. In the case of concentrated throughfall flows, the actual rain input under the canopy may be much higher than the open-field weather record. Hence, as the actual rainfall is underestimated, the runoff coefficients can locally reach values higher than 100 %. These areas are likely to act as "erosion hotspots" and to substantially increase local variation in runoff and soil detachment under trees. Tree canopy is usually dense close to the tree lines, but sparser between rows, resulting in higher rainfall interception and increased kinetic energy close to the trunks. Thus, I expected higher runoff and detachment within rubber tree rows (OR_s) than between rows (OR_i). This was not clearly observed, possibly due to high local variability in microplots' response and cover by leaf litter.

6.4.3.B Soil cover

I investigated more precisely the effects of soil cover on soil protection. Both low understory and low soil cover by residues can increase runoff and soil detachment. Soil cover by plants or leaves is known to decrease splash erosion (Liu et al. 2016b; Lacombe et al. 2017) and to increase infiltration rates (Liu et al. 2016a). In 2016, living understory in OR_i and OR_s was relatively low and quasi null from August: resilience was low and no regrowth was observed after herbicide application. Thus low living cover provided little protection, and soil was only covered by rubber tree leaf litter during most of the rainy season.

Soil cover by litter can decrease erosion in two ways. It first protects the soil surface from falling raindrops, decreasing splash erosion. It can also slow down runoff, limiting further detachment and favouring redeposition of soil particles.

However, the dynamics of litter cover under rubber trees are quite specific. While in most forests of the area, trees shed leaves continuously, ensuring permanent cover, defoliation in rubber tree occurs over a two-week period in February-March and is rapidly followed by leaf flush. On gentle slopes, Liu et al. (2015) showed that in the early rainy season, runoff and soil detachment were much lower in control rubber tree plots (>70% litter cover) than in rubber tree plots with litter removal. In our area, soil cover by leaves was high at the beginning and middle of the rainy season (>75%) but they were progressively destroyed by microorganisms, insects (termites, ants...) and abiotic processes (fragmentation, displacement...). In October, the proportion of bare soil (on average 45% of the surface) was sufficient to cause surface crusting (Fig. 6.6a) and very high detachment. Crusting generates runoff and favours detachment (Podwojewski et al. 2008a; Patin et al. 2012; Patin et al. 2018). Yet crusting cannot be considered as the sole cause of runoff production under rubber tree because rubber tree leaves are slightly waxy (Prüm et al. 2013) and form a tight tiling on the soil surface. In steep areas, they were ineffective in reducing surface runoff and might have even increased runoff in the absence of understory. While leaf litter is necessary to protect the soil from rainfall impact and therefore usually reduces runoff and soil detachment, from the results of our first study it appeared to be insufficient in mature rubber tree plantations.

This led me to quantify the effects of soil cover on soil degradation in my second experiment. I initially planned to measure simultaneously the variations of soil cover by living plants and by litter on runoff and soil detachment. I did not obtain satisfactory results for measurements of litter cover and soil detachment data for 2017 and 2018 are not available yet, so in this manuscript, I focused on the effects of soil cover by living plants on runoff. As discussed above, the protocol was only partly successful and plant cover measurements were not extremely precise. Indeed, light variability, plant drying, or plant slumping caused variability in the measurable "green" area. This was particularly true in OR2 without herbicides during the rainy season. There, large ferns covered most of the surface but were easily moved or damaged by wind or heavy rainfall, resulting in important variability of soil cover measurements. Despite the protocol discrepancies described above, I estimated that herbicide exclusion led to a decrease of about 20% to 30% of the annual runoff coefficient. I also showed that increased soil cover significantly reduced the vulnerability to large rain events. In the "high cover" class, above 25% of cover, runoff coefficient did not increase with rainfall height. This indicates that runoff volume was directly proportional to rainfall height and suggests good infiltration capacities. Plants not only slow down runoff but can also act as sediment traps, and soil detachment increases exponentially with runoff volume. It is thus likely that the effect of plant cover on soil detachment would be even stronger.

6.4.4 *Soil detachment in tree plantations of tropical mountainous regions*

While high runoff and soil detachment in mature rubber tree plantations are supported by the literature, the amount of runoff and soil detachment I found in the first study were surprisingly high. Excluding the most intense events, our estimation of total soil detachment reached $0.6 \text{ kg m}^{-2} \text{ yr}^{-1}$ in YR and M and $8.2 \text{ kg m}^{-2} \text{ yr}^{-1}$ in OR plantations. The detachment values obtained in OR plantations in 2016, in particular, were extremely high compared to previous results.

At the catchment scale, Ribolzi et al. (2017) found a raise of soil loss from 98 to 609 t km⁻² yr⁻¹ (i.e. 0.098 kg m⁻² yr⁻¹ to 0.609 kg m⁻² yr⁻¹) in a Laotian mountainous catchment, after conversion from upland rice to teak plantations. On a larger scale, and using a generic soil erosion model, Borrelli et al. (2017) calculated erosion rates ranging between 0 and 1 t ha⁻¹ yr⁻¹ (i.e. 0.1 kg m⁻² yr⁻¹) in mountainous Northern Thailand. Nevertheless, it is not possible to directly compare soil detachment measured at the 1 m² scale with sediment yields measured at the catchment or regional scale. Indeed, depending on the rainfall and topographical characteristics, a large part of the sediment is redistributed shortly after detachment. Comparing different annual crops, Podwojewski et al. (2008a) found soil detachment at the 1 m² scale ranging from 0.01 kg m⁻² yr⁻¹ to 0.40 kg m⁻² yr⁻¹ in northern Vietnam. Patin et al. (2018) measured soil detachment at the same scale under fallow land, annual crops and teaks ranging from 0.03 kg m⁻² yr⁻¹ to 3.8 kg m⁻² yr⁻¹ in northern Laos. Both studies also used 1 m² microplots and worked on similar slopes (40-55% on average) and under comparable meteorological conditions as this study.

I think that the very high soil detachment rates observed in this study result from a combination of management practices and topographical characteristics. Indeed, Liu et al. (2015) found that in rubber tree plantations of South-West China, bare soil and soil covered with leaf litter produced soil detachment of 0.47 and 0.19 kg m⁻² yr⁻¹, respectively, on gentle slopes. While a steeper slope may decrease soil detachment on bare soils (Janeau et al. 2003; Ribolzi et al. 2011), in this case I think that combined with clear-weeding it favours the exposition of bare soil by washing away rubber tree leaves; it has also been shown that the proportion of bare soil under trees increased with slope in both temperate and tropical areas (C. Valentin, *personal communication*).

I also showed that erosion models, which yield extremely variable results in Southeast Asia in particular (e.g. Gibbs and Salmon (2015)) should be complemented with field measurements to correctly estimate soil losses. In particular, most models estimating throughfall erosivity based on land uses consider tree plantations as forested areas (for example the FAO developed Gladys model, Nachtergaele et al. (2010)), and thus significantly underestimate erosion rates.

6.5 CONCLUSION

Afforestation by rubber tree is currently ongoing in various marginal areas of Southeast Asia. I showed that in mountainous areas, far from promoting soil conservation, this transition increased soil susceptibility to erosion. Particularly high soil detachment under rubber tree plantations, either intra- or inter-rows, was related to high proportions of bare soil, especially at the end of the rainy season with little or no understory and largely degraded litter. I propose two main research axes to work towards better protection of soils in mountainous areas. i., investigating farmers' motivations and practices in understory management, in order to identify new sets of agroforestry practices more favourable to soil protection and involving less intense weeding. ii., further understanding of climatic parameters influencing soil detachment and runoff is needed to identify high-risk periods and areas; in this regard, large-scale modelling should always be supported by extensive field measurements. Specifically addressing these erosion hot moments and hot spots

will reduce gross erosion rates from the most erosive events and support better protection, especially in lightly degraded areas.

Conclusion en français

L'expansion des plantations d'hévéa est actuellement en cours dans diverses zones d'Asie du Sud-Est. J'ai montré que dans les zones montagneuses, loin de favoriser la conservation des sols, cette transition augmentait la vulnérabilité des sols à l'érosion. Le détachement de sol était particulièrement élevé dans les plantations d'hévéa. Cela était lié à de fortes proportions de sol nu sous hévéas, en particulier à la fin de la saison des pluies lorsque le sous-bois est quasiment inexistant et la litière en grande partie dégradée. Je propose deux axes de recherche principaux pour faire progresser la protection des sols dans les zones montagneuses. i/ Étudier les motivations et les pratiques des agriculteurs dans la gestion du sous-bois afin d'identifier de nouveaux ensembles de pratiques agroforestières plus favorables à la protection des sols et impliquant un désherbage moins intense. ii/ Mieux comprendre les paramètres climatiques influant sur le détachement du sol et le ruissellement afin d'identifier les périodes et les zones à haut risque; à cet égard, la modélisation à grande échelle devrait toujours être étayée par des mesures de terrain approfondies. Traiter spécifiquement ces "hotspots" et "hot moments" réduira les taux d'érosion bruts dus aux événements les plus érosifs et favorisera une meilleure protection, en particulier dans les zones légèrement dégradées.

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GENERAL DISCUSSION & PERSPECTIVES

7.1 A MULTIDISCIPLINARY ON-FARM STUDY

In this thesis, I have investigated the relationships between agricultural practices, non-cultivated plants, and soil conservation in mountainous Southeast Asia. I adopted a multidisciplinary approach, drawing from plant community ecology, agronomy as well as soil sciences. I think that this project in "real-world" situations provides original and valuable data about the ecological impacts of current practices in mountainous Northern Thailand.

The study of agroecosystems can typically rely either on agronomic trials in stations or on observations of farmers' fields. On-station experiments allow to controlling soil type, fertilisers and pesticides input, as well as sowing dates (for instance) so that no external variable interferes with the effects of the treatment of interest. However, this necessarily creates conditions that are different from the real situation of farmers: for instance, the weed community found in an on-station experimental field is unlikely to be similar to those that farmers are actually confronted to. On the contrary, on-farm research aims at "understanding the farm and its environment as well as farmers' goals, constraints and opportunities" (Mutsaers et al. 1997). Weed communities depend not only on the current management (e.g. fertilising and weeding) but also on the past history and surroundings of a field. On-farm experiments are thus particularly appropriate to investigate the drivers structuring weed communities in real agro-ecosystems.

This on-farm protocol also brought challenges, both in terms of data acquisition and analysis. Firstly, as expected from an on-farm study, farmers made their own decisions regarding the planning of sowing and harvesting operations, the use of herbicides, and the crop they would plant next in the field. This led to a high number of factors varying from one field to another. The analysis of these factors was made difficult by the poor success of our interviews and the scarcity of data we could obtain regarding farmers' practices. Secondly, in the case of the herbicide exclusion experiment (Chapter 6), working in real plantations considerably complicated the study, as poor communication between field owners and field workers disturbed the established protocol. Both these issues (interview failure and communication between owners and field workers) were due to the lack of permanent field assistants and the small support we received from local organisations, both listed as key criteria for the success of on-farm studies by

Mutsaers et al. (1997). Thirdly, as we followed continuously 20 fields (initially in a balanced design with 4 land use types), other land use types were integrated into the study and led to unbalanced designs within each year of sampling. However, conducting repeated observations in farmers' fields allowed me to grasp, both by my own observations and by in-field measurements, the complexity and diversity of smallholders' practices in terms of weeding and fertilising practices, sowing and harvesting dates, or crop sequence. This variety of management practices was particularly striking in mature rubber tree plantations, in which glyphosate application - for instance - varied from zero to two applications a year. On-farm approach notably helped me characterise the socio-economic and environmental limitations constraining the observed agricultural transition (see below, part 7.2).

7.2 THE UPLANDS OF NORTHERN THAILAND, TRANSITIONING AGROECOSYSTEMS

The agricultural changes in Huai Lang, and more generally in mountainous Northern Thailand, are multifold. Huai Lang farmers are transitioning from what is generally considered "traditional" to "modern" agriculture. Upland rice is a remnant of the traditional subsistence system, with continued use of locally adapted varieties with high stature and dense leaves. The introduction and expansion of improved maize varieties, requiring higher fertiliser inputs, marked the transition towards cash cropping. This was associated with increased use of herbicides, which allows to control weeds with less labour force. However, this increasing use of herbicides is starting to raise health concerns among Thai scientists and farmers (Kongtip et al. 2017)). The resulting pressure on the government to ban the most dangerous chemicals, including paraquat (Rujivanarom 2018; Saengpassa 2018), might lead to stricter regulations in the future.

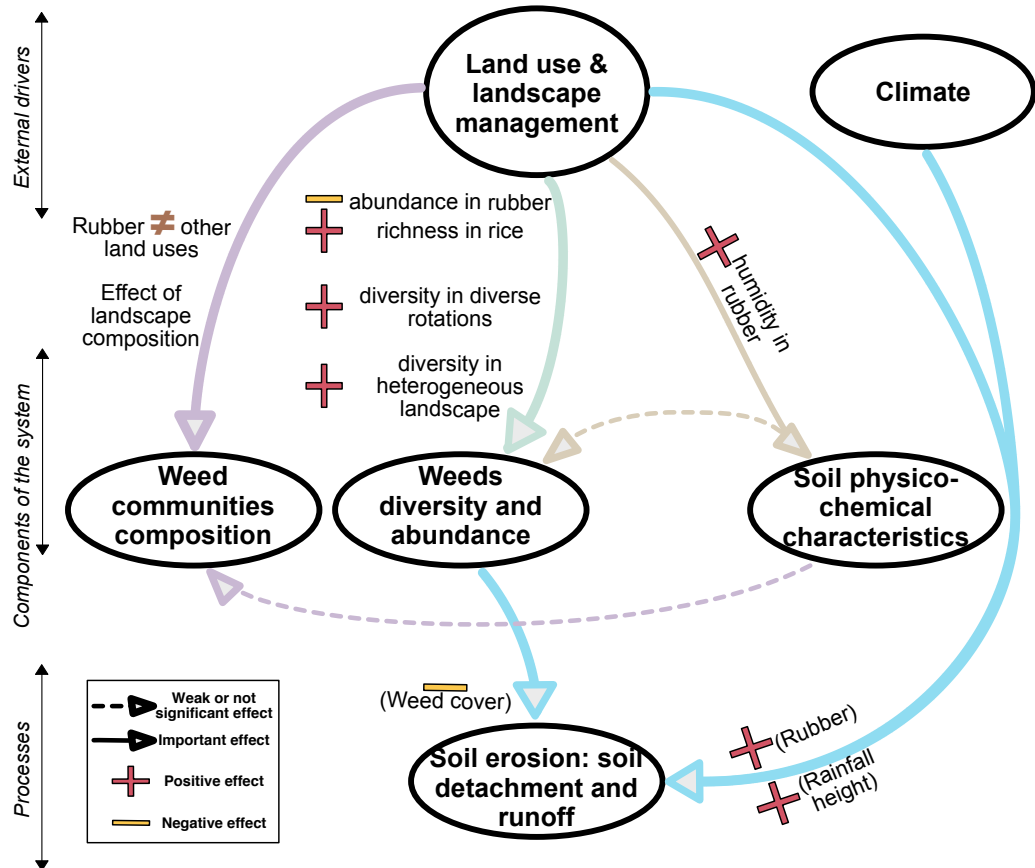
Besides, indications obtained from both field observations and farmers interviews indicate that this current situation is transitory. Growing constraints in terms of labour shortage, environmental degradation, and impossibility to further modernise the farming practices (e.g. no possible mechanisation on steep slopes) indicate that the system is likely to rapidly evolve, either by the abandonment of the most remote and degraded lands or by the replacement of annual crops by other land use types (Bae et al. 2012). This can explain the increasing expansion of tree plantations in these environments and suggests that they are likely to continue expanding, despite their low environmental and socio-economic sustainability (Manivong and Cramb 2008). However, rubber tree cultivation in the area is still relatively recent, which might explain the high variability of weeding and fertilising practices we observed. As farmers do not have well-established management practices for rubber trees yet, encouraging a switch towards less intensive weeding in rubber trees might be easier than under other crops.

7.3 LAND USE INTENSIFICATION AND LAND USE CHANGE EFFECT ON WEED BIODIVERSITY

Most studies investigating the effects of land use intensification or land use change on weed communities were conducted in temperate areas (e.g. Fried et al. (2008), Hyvönen et al. (2011) and de Mol et al. (2015), but see also Hosseini et al. (2014) and Nam-Matra (2017)). The agro-ecosystem that I observed in Huai Lang has similarities with these systems, as it presented, for instance, intense use of herbicides and a shortening of crop rotations. However, besides soil, climate and crop type differences, the structure of the landscape is very different because Huai Lang uplands are farmed by smallholders, resulting in much smaller fields and a mosaic landscape. They are also on steep slopes that constrain field size and create more heterogeneity due to the presence of numerous gullies and streams. I showed in Chapter 3 that **rubber tree plantations thoroughly changed weed communities composition**. Upland rice, which requires relatively low inputs, had a positive effect on weed richness compared to maize: this is consistent with results in temperate areas that showed that species richness is higher in low-input compared to conventional systems (Hyvönen and Salonen 2002; Edesi et al. 2012) (Fig. 7.1). **However, the effect of land use identity (e.g. rice v. maize) was exceeded by the impact of both temporal (Chapter 4) and spatial (Chapter 5) land use diversity**. I found that landscape heterogeneity increased species richness, supporting previous results in European agricultural landscapes (Gaba et al. 2010; Petit et al. 2016). In particular, natural habitats such as forests or riparian areas seemed to affect shrub and tree communities composition, consistently with previous results that semi-natural habitats can act as reservoirs for biodiversity (Fried et al. 2009), while herbaceous species richness decreased with field size (also consistent with Gabriel et al. (2005) and Gaba et al. (2010)). However, the landscape elements usually considered in studies of temperate agroecosystems (field margins, hedges, ponds) are quite different from those present in Huai Lang (banana groves, roadsides, neglected gullies) and further characterisation of the flora in these habitats would be needed to confirm my results. Besides, combining agronomical studies with ecological concepts, for instance by identifying meta-community processes as was proposed in Chapter 5, could increase our understanding of the functioning of communities in agricultural contexts.

Regarding the temporal land use variability, most existing studies found a positive impact of diversified rotations on weeds richness or diversity (Cardina et al. 2002; Ulber et al. 2009), but without clearly separating the effects from each crop from that of the number of crops or the frequency of change (but see Doucet et al. (1999) for a comparison of the effects of weeding and rotation on weeds). The crop sequences observed in Huai Lang were extremely variable and depended on socio-economic factors - such as market prices, labour availability, or need for subsistence crops - as well as weed management factors. I showed that even on a short-term (3 years) basis, not only the number of land use types, but also the number of land use changes in a given field, significantly affected the richness and diversity of herbaceous weeds (Fig. 7.1). These results can be explained by i/ the diversification of growing conditions (light, planting date, soil resource availability) that allows the germination and growth of more diverse species (Smith et al. 2008; de Rouw et al. 2013; Colbach et al. n.d.). For instance, increased shade from rice leaves is likely

Figure 7.1: Take-home message: summary of the main results of this thesis. Rubber tree plantations strongly increase soil detachment and runoff, which can be attenuated by an abundant plant cover, although it is usually low in mature plantations. They also significantly increase soil humidity and harbour very specific weed communities compared to other land uses. Rice fields increase species richness. The temporal and spatial diversity of land uses increase plant diversity, and landscape composition also modifies weed communities.



to impede the germination of some of the most common weeds such as the shade-intolerant species *A. conyzoides*. And ii/ the frequency of disturbance, thought to temporarily disrupt the reproduction of the dominant species (Martin and Fetton 1993), should lead to more diverse communities. While few dominant species in a field often mimic the crop, have similar requirements and thus high competitiveness towards the crop (Colbach et al. 2010; Borgy et al. 2012), high weed diversity is on the contrary expected to result in the use of a wider range of resources and in lower competitiveness towards the crop (Storkey and Neve 2018). Thus, maintaining spatial and temporal land use heterogeneity is important not only in terms of biodiversity conservation, but might also have direct and positive impacts on farmers' ability to manage weeds.

However, the introduction of rubber trees, perennial crop often grown in very large plantations, diminishes both the temporal and spatial heterogeneity of the landscape. The expansion of rubber trees into the uplands could have not only direct (due to the specific growing conditions under rubber trees), but also indirect (through spatial and temporal homogenisation) effects on plant communities. I have investigated in Chapter 3 the direct effects of mature rubber tree plantations

on weed communities. Due to low light availability and humid conditions, they harboured weed communities very different from that of other land uses (Fig. 7.1). However, these communities were quite variable, as was their species richness. This high variability was probably related to large variations in the management of the plantations. This differed from the more homogeneous practices observed in maize or rice fields.

In addition, the expansion of rubber tree plantations is likely to have indirect effects on the environment. The temporal land use variability in rubber tree plantations is null, as in any perennial plantation with no intercrop. Although the study presented in Chapter 4 did not include mature rubber tree plantations, it showed that in human-disturbed agricultural landscapes, the maintenance of biodiversity can critically depend on the temporal diversity of land uses. Secondly, rubber tree plantations are usually larger than annual crop fields and two neighbour mature rubber tree plantations are likely to present very homogeneous growing conditions, leading to more homogeneous landscapes than in an annual crops' landscape. This is also valid at a smaller scale, as growing conditions within one plantation are also very homogeneous. Yet, as shown in Chapter 5, landscape heterogeneity supports the maintenance of plant diversity, for instance through regular re-establishment of agro-intolerant species from field borders. Thus, should rubber tree plantations become dominant in Huai Lang, **the temporal and spatial homogenisation related to their expansion could reinforce the direct, and potentially negative, effect of rubber plantations on plant diversity**, and by extension to invertebrate, reptile, bird and mammal diversity.

7.4 THE EFFECTS OF AFFORESTATION BY RUBBER TREES ON SOIL CONSERVATION

The above-mentioned changes in weed communities and weed abundance, combined with land use changes, were expected to impact soil characteristics and erosion processes. Previous investigations suggested that afforestation by tree plantations (e.g. teak or rubber trees) could significantly increase erosion processes, especially when soil cover is low (Lacombe et al. 2016; Ribolzi et al. 2017; Patin et al. 2018). In the present work, **I confirmed that afforestation by rubber trees, at least under current weeding practices, critically increases soil degradation**. Soil detachment rates were 10 to 30 fold more important under rubber trees than under annuals crops, and often exceeded $10 \text{ kg m}^{-2} \text{ yr}^{-1}$. Such results, at the 1 m^2 scale, cannot be easily extended to catchment-scale or regional erosion rates. Indeed, at the field level, detached particles are likely to sediment downslope, to their initial place. Rill and gully erosion can also substantially participate to overall soil losses but was not quantified in this study. At the catchment level, the presence of vegetation strips (either planted or semi-natural) can trap sediments. Runoff can also be redistributed and re-infiltrated by terraces, resulting in a lower overall erosion rate, although our observations of terraces in Huai Lang show that they were often ineffective in this regard, especially when tree lines crossed the terraces and created areas of preferential flows and gullies (Chapter 6). **My findings at small scale will be complemented by studies of catchment-level stream monitoring data conducted since 2015 in Huai Lang catchments. This will enable us to**

assess the sediment delivery ratio at the outlet of the catchment, i. e. the ratio between the potential erosion assessed from the small plots extrapolated to the whole catchment and the really measured soil losses.

Different parameters determine the severity of erosion in a given area, affecting soil particles detachment, transport and redeposition. One of these determinants is the resistance to erosion, which includes, for instance, the cohesion, structural stability, and infiltration capacities of a soil. In Chapter 3, I have shown that except for soil humidity, **afforestation by rubber trees in Huai Lang had little impact, at least at small scale, on topsoil characteristics**: carbon content, bulk density, or infiltration rates, which could have been indicators of soil degradation or vulnerability to erosion, were similar under all land uses. These weak relationships between soil and weeds could be due to the scale at which we measured the different parameters. Weed characteristics were measured at the 1 m² scale, while soil characteristics were measured from 100 cm³ cylinders (20 cm² area), except soil humidity for which more data were available. Besides, my data showed a high level of spatial (both intra- and inter-field) and temporal variability. This was not surprising in an on-farm study of complex, rarely straightforward processes. However, by using adapted statistical methods (such as mixed models, to take into account the nestedness of the data) on a sizeable dataset, I showed that **land use identity impacted some of the interactions between weeds and soil characteristics**. For instance, plant density in the rainy season was anti-correlated to soil humidity, which was likely to prevent runoff by drying the soil through evapotranspiration; and plant biomass was correlated to soil carbon content, indicating better structural integrity. These results were a first indication that weed cover could participate in improving soil resistance to erosion. I also expected that higher plant abundance (biomass or density) would enhance erosion-related soil characteristics, such as infiltration rates or the structural stability of aggregates; however, this was not observed. A finer above-ground and below-ground description of weed communities, realised at the same scale as soil characterisation (i. e. 10 cm² to 50 cm² area), would be necessary to complement these results.

In addition to the inherent resistance capacities of soil, erosion rates are also massively driven by the erosivity of the rainfall reaching the ground, which determines the strength of splash erosion. I showed that consistently with the literature, **rainfall height was among the best predictors of runoff and detachment**. Besides, the kinetic energy of raindrops is largely determined by vegetation and soil cover. A high canopy, such as the one of rubber trees, concentrates raindrops (Lacombe et al. 2017). Falling raindrops can reach their maximum speed in approximately 7 m to 10 m (Morgan 2005), and are thus very erosive; they can then be slowed down by the presence of contact cover. I did not detect any difference in runoff or soil detachment between the position of the microplots (within tree rows: expecting high rainfall interception, or between the row: expecting lower interception), possibly due to the high heterogeneity of the throughfall within each of these classes. However, I demonstrated that one of the main factors explaining the higher runoff and soil detachment rates under mature tree plantations, compared to maize or young rubber tree plantations with intercrop, was the lack of soil cover during the second part of the rainy season. This is consistent with early studies in Indonesia, which showed that clean-weeded under rubber tree plantations caused to massive soil degradations even on flatlands. This led to the dismissal of such weeding

practices in Indonesian plantations (Swart 1921). Indeed, while our study plots under maize or young rubber tree with intercrop were covered by weeds, crop or crop residues throughout the rainy season, there was a low resilience of weed communities and thus high proportions of bare soil under rubber tree plantations after herbicide application. However, **herbicide exclusion under mature rubber trees decreased runoff by up to 30 % within two years**. This could be due both to direct protection from plant cover and to an indirect effect through a better stabilisation of rubber leaves litter cover by living plants and indicates that changes in weeding practices could significantly improve soil conservation in the area. This effect was mostly due to the reduction of runoff for the largest rain events: as soil detachment normally increases exponentially with runoff volume, this mitigation of runoff could significantly decrease soil degradation during large rain events.

These results addressed the quantitative effect of weed cover under mature rubber trees, which could simply be summarised as: the more weed biomass and the more weed cover, the less runoff. An important perspective to this work is to address more qualitatively the effect of plant communities on erosion under rubber trees. Indeed, different species might provide different protection against erosion, depending on their root and stem architecture, height, and leaf size (Burylo et al. 2012a; Burylo et al. 2012b; Seitz et al. 2016). Thus, measuring erosion rates under plant communities of varying specific and functional richness could provide additional insights in the possibility to combine biodiversity and soil conservation under rubber tree plantations.

7.5 STEPS TOWARDS PLANT AND SOIL CONSERVATION IN MOUNTAINOUS NORTHERN THAILAND

Southeast Asia is a hotspot of plant, mammals, and insects diversity. Yet, due to rapid agricultural changes and intensification, it has also become a hotspot of environmental degradations, both in terms of biodiversity and soil conservation. Restoring these ecosystems, while maintaining current levels of agricultural production, is not realistic. In a land-sparing (v. land-sharing) perspective, concentrating cultivation in a few very intensive areas, while reforesting others, would probably result in locally sharp increases of environmental degradation in the cultivated lands and pose problems of land tenure and farmers' subsistence. Besides, Ghimire et al. (2014), for instance, showed that reforestation actions on degraded grasslands in Nepal failed to restore favourable soil conditions, even after 25 years. On the other hand, drastically reducing herbicide inputs in annual crops, such as maize or rice, is not a viable option for farmers, who lack the labour force and economic incentives to return to traditional hand-weeding methods. However, **the present work shows that it might be possible to sustain high levels of plant diversity at the field level, by maintaining temporal and spatial land use heterogeneity**. This is also likely to promote not only field-level but also landscape-level diversity by preserving species that are not adapted to agricultural fields.

The question of the management of rubber tree plantations is slightly different. The major, and maybe most urgent environmental issue in rubber tree plantations is soil degradation. Contrarily to rice and maize fields, there is little scientific support for the existence of competition between weeds and latex production. Abraham

Figure 7.2: Agroforestry practices for enhanced biodiversity and soil conservation under rubber trees. "Jungle rubber" tree plantation (left) and rubber tree plantation intercropped with tea (right) in Xishuangbanna Botanical Garden, Yunnan, China.



and Joseph (2016) found that in India, no-weeding practices under rubber trees significantly enhanced soil quality, without any effect on latex yield. In Indonesia and Malaysia, clean weeding has long been abandoned due to intense soil erosion (Gelder 1950). Various alternatives exist to increase soil cover under rubber trees. *Mucuna bracteata* and *Pueraria phaseoloides*, for instance, are used in flatlands of central and Southern Thailand under young rubber trees to improve soil fertility (Thoumazeau et al. 2019). However, they do not provide additional income for farmers during the unproductive phase of rubber tree cultivation (contrarily to maize or rice) and do not survive in closed canopy conditions once the trees are mature. In the Yunnan (Southern China), rubber tree plantations have also been expanding rapidly. There, various agroforestry experiments are currently ongoing that aim at combining soil conservation and increased income by planting cocoa, coffee or tea trees under rubber trees. Such practices have the benefit to increase both farmers' income and soil protection (Fig. 7.2). Cultivation of fruit or timber trees in rubber tree plantations in Southern Thailand is rarer but has been reported as the only sustainable system on the long-term for smallholders, because they decrease farmers' dependence on natural rubber price fluctuations (Stroesser et al. 2018). However, such practices also require large financial investments and labour force to maintain, both of which are limiting factors among Huai Lang smallholders. For this reason, I think that limiting weeding under rubber tree plantations would be a more easily acceptable compromise, at least in the short term, to support soil conservation and lower farmers' labour costs. Various obstacles, however, might prevent this transition, including farmers' willingness to have "clean plantations" to

improve the safety of tapping operations at night (easier circulation, avoidance of snake bites) and prevent fires.

While the area was traditionally a mosaic landscape of diverse crops cultivated in small fields, the large-scale introduction of rubber trees participates to the homogenisation of the landscape. The management of these plantations, both in terms of fertilisation, weeding and tapping calendar is still very diverse, probably due to the relatively recent history of rubber trees in the area. A regional homogenisation of these practices towards the most degrading could be a disaster in terms of soil conservation, but this situation also constitutes a unique opportunity to orient these practices towards more environmentally friendly practices. This would require conducting, on the one hand, in-depth interdisciplinary studies to investigate the drivers, motivations, and paths for changes in local farmers practices, for instance by extending sustainability analyses led by colleagues in Southern Thailand (Biret et al. 2019) to plantations in mountainous areas. On the other hand, larger-scale on-farm experiments really involving farmers in the design and trial of diverse weeding methods could also lead to easier innovation and distribution of more sustainable practices.

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Appendix



ADDITIONAL INVESTIGATIONS

S1.1 FUNCTIONAL TRAITS ANALYSIS

The objective of the analysis of functional traits was to identify relationships between traits and some environmental variables, such as land use or soil characteristics. For instance, some traits might be strongly associated with very poor soils, high infiltration capacities, or rubber tree plantations. In the following paragraphs, I detailed the approach I took to describe weed traits from the species identified in Huai Lang, the preliminary results I obtained and the reasons why the study was not completed.

S1.1.1 *Building a plant trait dataset*

Some traits among the weed species found in Huai Lang could be directly observed or obtained from expert knowledge, such as the plant's life form (herbaceous, shrub or trees). However, I also wanted to obtain other trait data related to plant strategies (e.g. Surface Leaf Area, seed production and dissemination, growth rate, photosynthetic pathway) and traits that could be related to erosion control (e.g. leaf size, canopy height, fine root density, root architecture and rooting depth). These we were unable to measure directly in the field, even if we had restricted the analysis to one or two traits, due to time constraints.

I thus opted to use published trait data. I first looked in major scientific databases, such as the TRY database or published datasets (e.g. Osborne et al. (2014)). However, most of the species found in Huai Lang, including many of the relatively abundant ones, were absent or poorly described in these databases. I extended the search to multiple other databases, including the following (in bold, the major data sources):

- **the Flora of China** (<http://www.efloras.org/>);
- the WIKWIO Project (Weed Identification and Knowledge in the Western Indian Ocean) ([WIKWIOProjectWeedIdentificationandKnowledgeintheWesternIndianOcean](http://wikwio.org/));
- **the Invasive Species compendium** (<https://www.cabi.org/isc/>);
- the Plantnet riceweeds project (http://publish.plantnet-project.org/project/riceweeds_en/);

- the **Seed information database** at Kew (<http://data.kew.org/sid/>);
- the Useful Tropical Plants database (<http://tropical.theferns.info/>);
- the Global Invasive Species Database (<http://http://issg.org/database/>);
- the India biodiversity portal (<https://indiabiodiversity.org/species/>);
- the Phytotaxa database (<https://biotaxa.org/Phytotaxa/>);
- Medicinal plants in Viet Nam (Institute of Materia Medica - HANOI - WHO/WPRO, 1990, 444 p.) (<http://www.nzdl.org/gsdImod?e=d-00000-00---off-owhoedm--00-0----0-10-0-a=d&c=whoedm&cl=CL1.1&d=HASH16e13d8f98944d7e8576f3.3.59>);
- the Bhutan Biodiversity portal ();
- the Global database of plants with root-symbiotic nitrogen fixation: NodDB (Tedersoo et al. 2018).

This approach only gave passable results. Firstly, the different databases were not normalised and sometimes gave contradictory results. Besides, the data depends entirely on the correct species identification: yet most species in tropical areas are not well described, and could have been split into different species with slightly different traits. Besides, I was only able to obtain trait data on a small number of species (Table S1.1).

S1.1.2 Preliminary results

I nevertheless conducted a few analyses to investigate the relationships between plant traits and environmental variables. I conducted RLQ and fourth corner analyses. These are two methods that aim at testing associations between a set of traits and a set of environmental conditions based on the species abundance. The analysis was conducted only on species and traits for which I had enough data. Figure S1.1 shows the results of the fourth corner analysis (without p-value correction for multiple testing). It suggests that annual plants were more associated with soils with high N content and low humidity and to maize fields than perennials. It also shows that environmental conditions have an effect on weeds' reproductive strategy, as fallow was associated with higher seed mass, while humid soils hosted fewer plants reproducing only by seeds. However, this method involves multiple testing and should be corrected to limit the risk α , i.e. to consider that a test is significant when it is due only to chance. None of the relationships described above remained significant after p-value correction. This lack of significant results could be due either to the absence of any relationship between plant traits and environmental variables in the considered system or to the limited number of species included in the study, which might limit the detection of any important trend.

Lacking the possibility to obtain a complete trait database, I thus did not pursue this analysis.

S1.2 GLYPHOSATE MEASUREMENT IN SOILS

Weeding practices, and in particular the type and dose of herbicides, are likely to strongly affect weed communities. The objective of this experiment was to provide additional information on the intensity of herbicide application in Huai Lang. It was prompted by the apparent vagueness of the information provided by farmers during interviews. From these interviews, I determined that glyphosate, atrazine and gramoxone were the main herbicides used in the fields, sometimes in combination. Glyphosate was used in almost all fields, and for simplicity, I focused only on this herbicide.

Various methods exist that allow the quantification of herbicide residues in liquids or soils, such as chromatography or the use of radioisotopes. These methods are precise but very expensive, and I thus looked for another method to obtain at least rough estimates of herbicides content in our soil samples. A new methodology, developed by the firm Abraxis, proposes to use immunoassays (ELISA) to quantify glyphosate residues in liquids (Fig. S1.2). This technique has also been used in sediments (McMurry et al. 2016), but never in agricultural soils, although the firm proposes a method for extraction.

In this experiment, I aimed i/ to test the feasibility of glyphosate measurement in agricultural soils with the immunoassay method; ii/ to determine the amount of glyphosate present in soils sampled in two sampling seasons (rainy season 2017, dry season 2018); and iii/ follow the glyphosate degradation in the samples with time, with the hypothesis that based on these decay curves we would be able to estimate the initial doses of application.

S1.2.1 *Immunoassay protocol*

The first step of this experiment was to extract glyphosate from soils. We used the protocol indicated by the firm. I first mixed 10 g of soil with 12.5 mL of 1 N Na-OH and put the vials for 30 min in an automatic shaker. We did not have the equipment required to properly centrifuge the samples, so instead, I vacuum filtered each sample using GF/F filters (diameter 25 mm). Each extract was then stored at -80°C until analysis. After de-freezing the samples, I diluted the samples to 1/100 using the glyphosate diluent provided in the kit. The general principle of the assay is presented in Fig. S1.2 and the precise protocol can be found online: https://www.abraxiskits.com/wp-content/uploads/2016/07/Glyphosate_PN500086_PL.pdf. In each assay, a calibration curve is created from standards of known glyphosate concentration. Each control and sample is replicated three times.

S1.2.2 *Preliminary tests*

I conducted preliminary tests in October 2017 to check whether the method was applicable in soils and to estimate its sensitivity and saturation rates. The samples used for this preliminary assay, along with the expected outcome of the test, and the actual results are presented in Table S1.2. In particular, I used a soil sampled in March 2016, with or without added glyphosate, to determine whether the sensibility of the test was sufficient.

Figure S1.2: Immunoassay for glyphosate detection. 1: the plate is coated with anti-glyphosate antibodies (Ab1). 2: The sample is added, and glyphosate binds to the antibodies. 3: a second antibody (Ab2) is added, and binds to the glyphosate. 4: a secondary antibody (Ab3), which also acts as an enzyme, binds to Ab2. 5: the enzyme substrate is added and converted to a coloured form. The absorbance of the final solution depends on the initial amount of glyphosate in the sample.

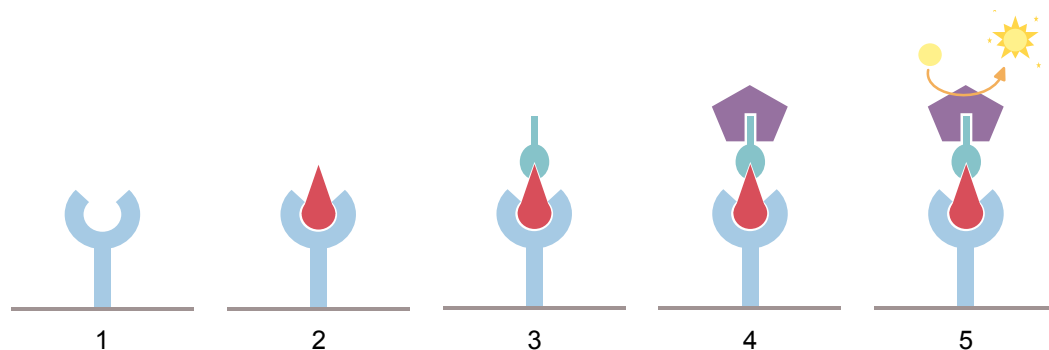


Table S1.2: Expected and actual results of the preliminary tests.

	Description	Expected result	Result
Controls			
c1	No soil	-	- (under detection threshold)
c2	No enzyme	-	+ (probably experimental mistake)
c+	Positive control (from the kit)	+ (0.75ppm in liquid)	+ (0.99 - 1.03 ppm in liquid)
Samples			
em_nb	soil sample from field M1	+	0.7- 1 ppm (liquid) i.e. 175-250ppm (soil)
e1	soil sample from field M1, + 1mL glyphosate (1/1000 dilution)	+	>4ppm (liquid), i.e. >1000ppm (soil), over saturation threshold
e2	soil sample from field M1, + 2mL glyphosate (1/1000 dilution)	+	>4ppm (liquid), i.e. >1000ppm (soil), over saturation threshold

As shown in Table S1.2, the controls - save one, in which there was an error during the experiment - gave positive or negative (i.e. under the detection threshold) responses corresponding to my expectations. However, the concentration obtained for the positive control was higher than expected, suggesting that the precision of the analysis was limited. Both samples with added glyphosate had concentrations much higher than the assay's saturation rate. However, I detected glyphosate in Huai Lang soil sample (without glyphosate addition) six months after sampling and approximately one year after the herbicide was applied, which suggests that glyphosate has a long residence time in these soils. I conducted other preliminary experiments (not shown), including tests with soils which I knew had not been exposed to glyphosate, and - as expected - did not detect any.

This shows that the immunoassay method was sensitive enough to detect glyphosate at the doses similar to what was found in Huai Lang. However, these preliminary experiments also showed that the method's precision would only allow a semi-quantitative ranking of the soils glyphosate content.

S1.2.3 First results on Huai Lang samples

In November 2017 and March 2018, one composite sample of approximately 200 g was taken from each study field. All fields were sampled on the same day and the samples were kept refrigerated until brought back to the lab. There, an aliquot of each sample was immediately taken to extract glyphosate. The rest of the samples were left at 25 °C and ambient humidity. I then repeated the protocol (aliquot, extraction) every 5 weeks for a total of 5 extracts per sample. I was able to analyse only the first sample series (i.e. November 2017, first extraction).

This series was analysed on the same day, but in two separate plates (96 wells each). Some samples were analysed twice to compare between filtered or centrifuged samples. Each plate included its own calibration standards. The results of

the two plates are presented in Fig. S1.3. The first part of the experiment worked (Fig. S1.3a): the calibration curve had the expected shape. The samples in which we expected no glyphosate (soil sampled in a forest and in a Laotian agricultural soil with no use of herbicides) were under the detection rate. This allowed us to detect that in 2017, little herbicide was used in YR4, OR5, and M5; this corresponded to my expectations, as YR4 and M5 were left as fallows (or young rubber with fallow) and that owners in OR5 reported no use of glyphosate. On the contrary, OR1, OR2, ULR5 and M1 had high rates of glyphosate. However, there were relatively high variations among replicates within each sample (not shown), and a precise extrapolation of the glyphosate concentration was not always possible.

The second part of the experiment did not succeed: as can be seen in Fig. S1.3b the calibration curve was incorrect. There was probably an experimental issue, or the plate might have been defective; it was thus impossible to assess the glyphosate concentration.

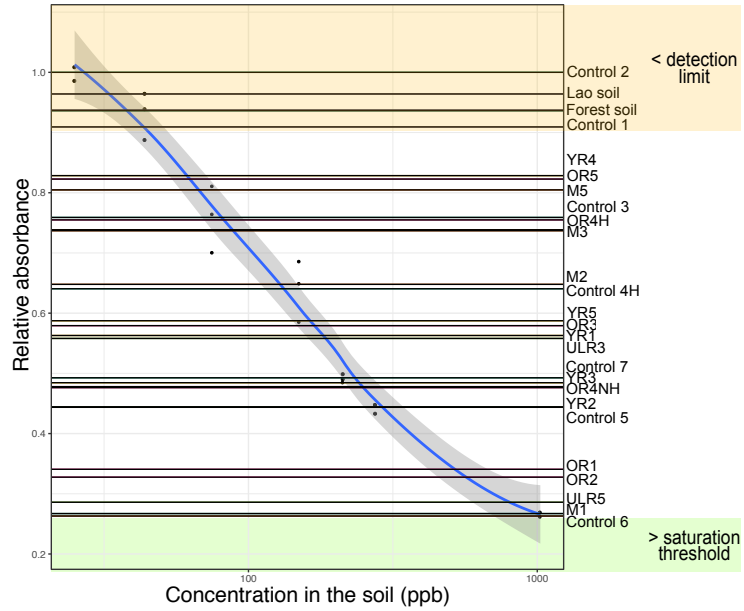
I had planned to conduct the analyses again on the samples, which had not been properly analysed at first, and then to conduct similar analyses on each point of the time series. The other samples for November 2017, and all samples for March 2018, were properly extracted but could not be analysed with the immunoassay method due to funding constraints, and the experiment had to be delayed.

S1.2.4 *Perspective*

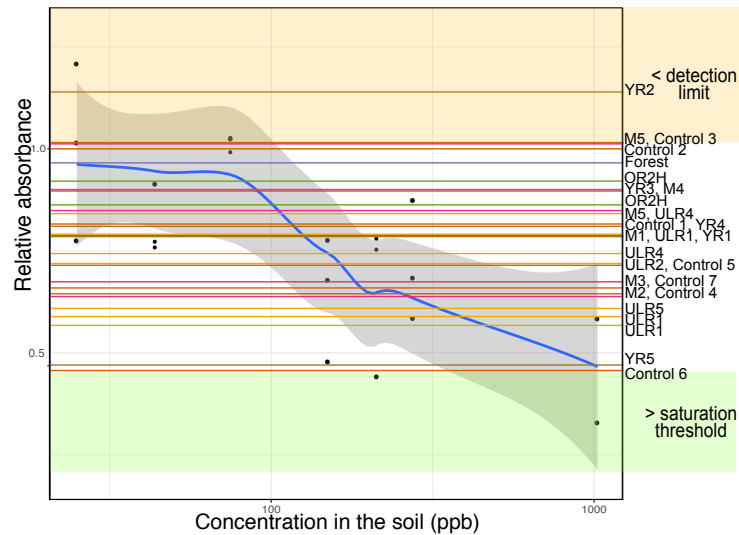
A semi-quantitative measure of glyphosate in soils could provide insightful information about the actual weeding practices conducted in Huai Lang. Besides, following the dynamics of glyphosate degradation in such soils would indicate the strength of its persistence in soils and an idea about the length of its environmental impact. To this day, all the samples are frozen and ready to be analysed in a future research project.

Figure S1.3: Results of the Glyphosate immunoassays. Black dots represent the values of the three replicates per standard solution. The blue line represents the calibration curve calculated from the standards. The horizontal black lines represent the mean absorbance value for each sample (three replicates).

(a) Plate 1



(b) Plate 2



APPENDIX FOR CHAPTER 2

S2.1 PLANT COMMUNITIES CHARACTERISATION

Table S2.1: List of EPPO codes, plant species, and relative importance index (RI). RI was calculated as the mean of the frequency and relative abundance of the species, all plots included, multiplied by 100. EPPO codes in uppercase are official codes as per the EPPO database. Lowercase codes are custom codes for species absent from the database. Species labeled as "unidentified" correspond to species clearly different from the other species, but which we were unable to identify. Species labeled as "unsure" correspond to plants which might belong to one or the other of the identified species, but could not be identified with certainty (they were not included in the analysis).

EPPO code	Species	Family	RI
<i>Herbaceous species</i>			
SPLPA	<i>Acmella paniculata</i> (Wall. ex DC.) R.K.Jansen.	Compositae	17.6
adizo	<i>Adiantum zollingeri</i> Mett. ex Kuhn (unresolved)	Pteridaceae	1.4
AGECO	<i>Ageratum conyzoides</i> (L.) L.	Asteraceae	79.9
AIIGA	<i>Alpinia galanga</i> (L.) Willd.	Zingiberaceae	0.9
BQGEV	<i>Angiopteris evecta</i> (G. Forst.) Hoffm.	Marattiaceae	5
AXOCO	<i>Axonopus compressus</i> (Sw.) P.Beauv.	Poaceae	0.5
BIDPI	<i>Bidens pilosa</i> L.	Asteraceae	25.5
BLUSO	<i>Blumea lacera</i> (Burm.f.) DC.	Asteraceae	19
BOEER	<i>Boerhavia erecta</i> L.	Nyctaginaceae	0.5
CLLAS	<i>Centella asiatica</i> (L.) Urb.	Apiaceae	2.3
chesp	<i>Cheilocostus speciosus</i> (J.Koenig) C.D.Specht	Costaceae	0.9
EUPOD	<i>Chromolaena odorata</i> (L.) R.M.King & H.Rob.	Asteraceae	18.5
COMBE	<i>Commelina benghalensis</i> L.	Commelinaceae	0.5
ERISU	<i>Conyza sumatrensis</i> (S.F.Blake) Pruski & G.Sancho	Asteraceae	53.6
CRSCR	<i>Crassocephalum crepidioides</i> (Benth.) S.Moore	Asteraceae	28
CYBCR	<i>Cyanotis cristata</i> (L.) D.Don	Poaceae	0.5
ckssu	<i>Cyclosorus subelatus</i> (Baker) Ching subelata	Thelypteridaceae	34.9
CYNDA	<i>Cynodon dactylon</i> (L.) Pers.	Poaceae	4.2
CYPIR	<i>Cyperus iria</i> L.	Cyperaceae	7.7
CYPLX	<i>Cyperus laxus</i> Lam.	Cyperaceae	2.3
CZTPA	<i>Cyrtococcum patens</i> var. <i>latifolium</i> (Honda) Ohwi	Poaceae	4.1
DIGTI	<i>Digitaria radicata</i> (J.Presl) Miq.	Poaceae	6.4
DIGMB	<i>Digitaria setigera</i> Roth	Poaceae	0.5
DIUAL	<i>Dioscorea alata</i> L.	Dioscoreaceae	8.6

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EPPO code	Species	Family	RI
ELEIN	<i>Eleusine indica</i> (L.) Gaertn.	Poaceae	10.2
EPHHL	<i>Euphorbia heterophylla</i> L.	Euphorbiaceae	0.5
EPHHI	<i>Euphorbia hirta</i> L.	Euphorbiaceae	22.3
FIMAE	<i>Fimbristylis aestivalis</i> Vahl	Cyperaceae	0.9
gigab	<i>Gigantochloa albociliata</i> (Munro) Kurz	Poaceae	0.9
gptch	<i>Gymnopetalum chinense</i> (Lour.) Merr.	Cucurbitaceae	0.5
IMPCY	<i>Imperata cylindrica</i> (L.) Raeusch.	Poaceae	4.5
IMPSS	<i>Imperata</i> sp. 2	Poaceae	4.1
CYPKH	<i>Kyllinga nemoralis</i> (J.R.Forst. & G.Forst.) Dandy ex Hutch. & Dalziel	Cyperaceae	0.5
	<i>Lepistemon binectariferum</i> (Wall.) Kuntze	Convolvulaceae	2.3
LEFCH	<i>Leptochloa chinensis</i> (L.) Nees	Poaceae	8.2
lidlt	<i>Lindernia latifolia</i> (unresolved)	Linderniaceae	5.9
lidsp	<i>Lindernia</i> sp1	Linderniaceae	2.7
RHYRE	<i>Melinis repens</i>	Poaceae	1.8
MTCVI	<i>Mitracarpus hirtus</i> (L.) DC.	Rubiaceae	43.5
MOLST	<i>Mollugo pentaphylla</i> L.	Molluginaceae	1.8
MUBSS	<i>Musa</i> sp.	Musaceae	0.9
HYOAU	<i>Oldenlandia auricularia</i> (L.) K.Schum.	Rubiaceae	9.1
OXACO	<i>Oxalis corniculata</i> L.	Oxalidaceae	18.6
PANBR	<i>Panicum brevifolium</i> L.	Poaceae	6.3
PANNT	<i>Panicum notatum</i> Retz.	Poaceae	7.3
PANRE	<i>Panicum repens</i> L.	Poaceae	0.5
PASCO	<i>Paspalum conjugatum</i> P.J.Bergius	Poaceae	16.2
PESPO	<i>Pennisetum polystachion</i> (L.) Schult.	Poaceae	26.4
PHRKA	<i>Phragmites karka</i> (Retz.) Trin. ex Steud..	Lauraceae	6.8
PYLAM	<i>Phyllanthus amarus</i> Schumach. & Thonn.	Phyllanthaceae	6.8
PHYMI	<i>Physalis angulata</i> L.	Solanaceae	0.5
PUEPH	<i>Pueraria phaseoloides</i> (Roxb.) Benth.	Leguminosae	4.1
SALSS	<i>Salvia</i> sp.	Lamiaceae	5.9
SCFDU	<i>Scoparia dulcis</i> L.	Plantaginaceae	1.4
selhl	<i>Selaginella helferi</i> Warb.	Selaginellaceae	22.3
SETPA	<i>Setaria palmifolia</i> (J.Koenig) Stapf	Poaceae	0.5
SIDAC	<i>Sida acuta</i> Burm.f.	Malvaceae	0.5
SIDRH	<i>Sida rhombifolia</i> L. ssp. <i>rhombifolia</i>	Malvaceae	1.4
SOLAM	<i>Solanum americanum</i> Mill..	Solanaceae	6.8
stjcr	<i>Stephania crebra</i> Forman	Menispermaceae	0.5
tcxim	<i>tectaria impressa</i> (Fée) Holttum <i>impressa</i>	Tectariaceae	2.3
thsla	<i>Thysanolaena latifolia</i>	Poaceae	17.6
UK1	Unidentified (other species)		2.7
UK2	Unidentified (other species)		0.5
UK3	Unidentified (other species)		1.8
US1	Unsure		0.5
US2	Unsure		0.9
US3	Unsure		0.5
US4	Unsure		0.5
US5	Unsure	Poaceae	0.9
US6	Unsure		0.5
US7	Unsure	Poaceae	0.9
US8	Unsure		0.5
US9	Unsure		0.5
US10	Unsure		0.9

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EPPO code	Species	Family	RI
US11	Unsure		0.5
US12	Unsure		0.9
US13	Unsure		0.5
URNLO	<i>Urena lobata</i> L.	Malvaceae	0.5
VENSS	<i>Vernonia</i> sp.	Compositae	3.6
ZINOF	<i>Zingiber officinale</i> Roscoe	Zingiberaceae	0.5
zysspe	<i>Zygostema</i> sp.		0.9
<i>Shrub species</i>			
ABMMO	<i>Abelmoschus moschatus</i> Medik.	Malvaceae	0.5
Abelmosks	<i>Acacia concinna</i> (Willd.) DC.	Fabaceae	2.3
amlmi	<i>Amalocalyx microlobus</i> Pierre ex Spire	Apocynaceae	1.4
ZNODU	<i>Anomianthus dulcis</i> (Dunal) J.Sinclair	Annonaceae	2.7
adapo	<i>Ardisia polycephala</i> Wall. ex A.DC.	Primulaceae	3.2
bwuso	<i>Baliospermum solanifolium</i> (Burm.) Suresh	Euphorbiaceae	0.5
cajcr	<i>Cajanus crassus</i> (King) Maesen	Leguminosae	0.5
cwsgr	<i>Casearia grewiifolia</i> Vent.	Salicaceae	0.5
celpa	<i>Celastrus paniculatus</i> Willd.	Celastraceae	2.7
VITRE	<i>Cissus repens</i> Lam.	Vitaceae	1.4
cogpi	<i>Combretum pilosum</i> Roxb. ex G.Don	Combretaceae	0.5
KXLFO	<i>Cratoxylum formosum</i> (Jacq.) Benth. & Hook.f. ex Dyer	Hypericaceae	0.9
cklba	<i>Cyclea barbata</i> Miers	Menispermaceae	8.6
dagov	<i>Dalbergia ovata</i> Benth.	Fabaceae	6.8
dagri	<i>Dalbergia rimosa</i> Roxb.	Fabaceae	2.3
DEDGA	<i>Desmodium gangeticum</i> (L.) DC.	Fabaceae	2.3
DEDVE	<i>Desmodium velutinum</i> (Willd.) DC.	Fabaceae	0.9
DIUNU	<i>Dioscorea glabra</i> Roxb.	Dioscoreaceae	0.5
elgcf	<i>Elaeagnus conferta</i> Roxb.	Elaeagnaceae	0.5
euocc	<i>Euonymus cochinchinensis</i> Pierre	Celastraceae	5.4
FLCJA	<i>Flacourtia jangomas</i> (Lour.) Raeusch.	Salicaceae	0.5
fleso	<i>Flemingia sootepensis</i> Craib	Leguminosae	3.6
hrspe	<i>Harrisonia perforata</i> (Blanco) Merr.	Rutaceae	0.5
ixrja	<i>Ixora javanica</i> (Blume) DC.	Rubiaceae	0.9
mbeto	<i>Maesa ramentacea</i> (Roxb.) A. DC.	Primulaceae	0.5
MLLPA	<i>Mallotus paniculatus</i> (Lam.) Müll.Arg.	Euphorbiaceae	0.5
MANES	<i>Manihot esculenta</i> Crantz	Euphorbiaceae	0.5
MIKMI	<i>Mikania micrantha</i> Kunth	Compositae	4.6
mijpc	<i>Millettia pachycarpa</i> Benth.	Leguminosae	14
MIMIN	<i>Mimosa diplotricha</i> Sauvalle	Fabaceae	23.7
MOMCH	<i>Momordica charantia</i> L.	Cucurbitaceae	2.7
MUCPR	<i>Mucuna pruriens</i> (L.) DC.	Leguminosae	1.4
paepi	<i>Paederia pilifera</i> Hook.f.	Rubiaceae	19.9
srpqu	<i>Sauropus quadrangularis</i> (Willd.) Müll.Arg.	Phyllanthaceae	0.5
smiln	<i>Smilax lanceifolia</i> Roxb.	Smilacaceae	1.4
smiov	<i>Smilax ovalifolia</i> Roxb. ex D.Don	Smilacaceae	0.9
SOLVE	<i>Solanum verbascifolium</i> L. (unresolved)	Solanaceae	2.3
TTSSS	<i>Tetrastigma</i>	Vitaceae	0.5
tssla	<i>Thespesia lampas</i> (Cav.) Dalzell	Malvaceae	0.5
THNGR	<i>Thunbergia grandiflora</i>	Acanthaceae	8.2
TOUSS	<i>Tournefortia</i> sp.	Boraginaceae	1.4
tvepa	<i>Trevesia palmata</i> (Roxb. ex Lindl.) Vis.	Araliaceae	2.3

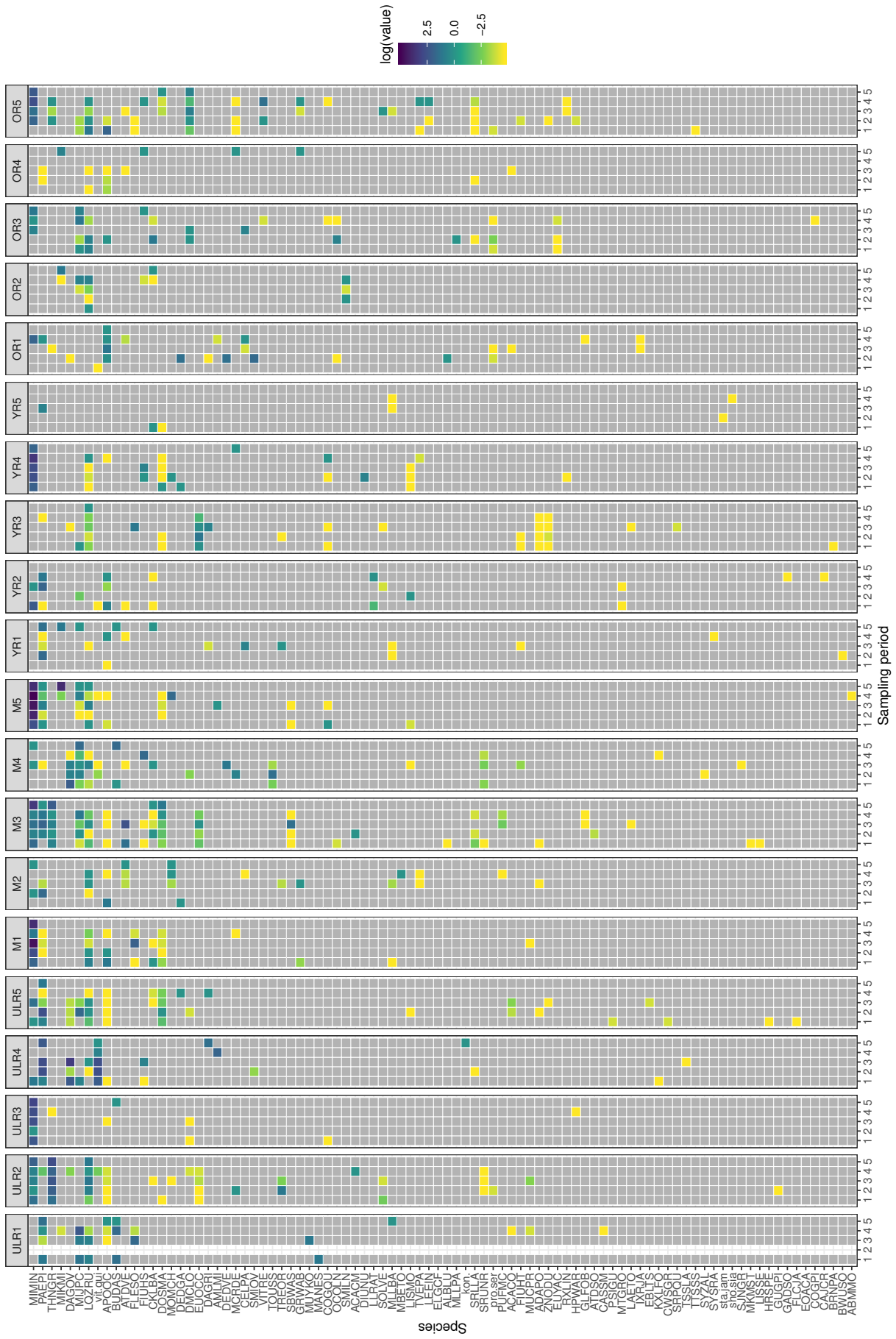
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EPPO code	Species	Family	RI
US14	Unsure		0.9
US15	Unsure		0.5
US16	Unsure		0.5
<i>Tree species</i>			
acacm	Acacia megaladena Desv.	Fabaceae	0.9
alblu	Albizia lucidior (Steud.) I.C.Nielsen	Fabaceae	0.9
atdso	Antidesma sootepense Craib	Phyllanthaceae	0.5
atdve	Antidesma velutinosum Blume	Phyllanthaceae	5.4
apococ	Aporosa octandra (Buch.-Ham. ex D.Don) Vickery	Phyllanthaceae	19.4
BRNPA	Broussonetia papyrifera (L.) L'Hér. ex Vent.	Moraceae	0.5
BUDAS	Buddleja asiatica Lour.	Scrophulariaceae	3.2
llrat	Callerya atropurpurea (Wall.) Schot	Fabaceae	0.9
cogqu	Combretum quadrangulare Kurz	Combretaceae	4.1
DMCLO	Dimocarpus longan Lour.	Sapindaceae	5.4
DOSMA	Diospyros malabarica (Desr.) Kostel.	Ebenaceae	12.2
eblts	Embelia tsjeriam-cottam (Roem. & Schult.) A.DC.	Primulaceae	0.5
eoaca	Eriolaena candollei Wall.	Malvaceae	0.5
euyac	Eurya acuminata DC.	Pentaphylacaceae	1.4
FIUHT	Ficus hirta Vahl	Moraceae	2.3
FIUHS	Ficus hispida L.f.	Moraceae	5.4
gadso	Gardenia sootepensis Hutch.	Rubiaceae	0.5
GUGPI	Garuga pinnata Roxb.	Burseraceae	0.5
glfob	Gluta obovata Craib	Anacardiaceae	1.4
grwab	Grewia abutilifolia Vent. ex Juss.	Malvaceae	2.3
HPWAR	Harpullia arborea (Blanco) Radlk.	Sapindaceae	0.9
laeto	Lagerstroemia tomentosa C. Presl	Lythraceae	0.9
leein	Leea indica (Burm. f.) Merr.	Vitaceae	0.9
lqzru	Lepisanthes rubiginosa (Roxb.) Leenh.	Sapindaceae	26.6
LISMO	Litsea monopetala (Roxb.) Pers.	Lauraceae	3.2
lisse	Litsea semecarpifolia (Wall. ex Nees) Hook.f.	Lauraceae	0.5
MCRDE	Macaranga denticulata (Blume) Müll.Arg.	Euphorbiaceae	4.1
MLLBA	Mallotus barbatus Müll.Arg	Euphorbiaceae	3.6
mkmst	Markhamia stipulata (Wall.) Seem	Bignoniaceae	0.5
mtgro	Mitragyna rotundifolia (Roxb.) Kuntze	Rubiaceae	0.9
MUYKO	Murraya koenigii (L.) Spreng.	Rutaceae	0.9
ocoln	Ocotea lancifolia (Schott) Mez	Lauraceae	1.8
rxlin	Oroxylum indicum (L.) Kurz	Bignoniaceae	1.4
pnfsp	Paranephelium sp	Sapindaceae	0.5
	Pentacme siamensis (Miq.) Kurz shorea siamensis	Dipterocarpaceae	0.5
PSIGU	Psidium guajava L.	Myrtaceae	0.5
pufmc	Pterospermum macrocarpum Hochr. (unresolved)	Malvaceae	1.4
sjngr	Senna garrettiana (Craib) H.S.Irwin & Barneby	Fabaceae	0.5
CASSM	Senna siamea (Lmk.) Irwin & Barneby	Fabaceae	0.9
	Stachycarpa jamaicensis		0.5
srlla	Sterculia lanceolata Cav.	Sterculiaceae	4.5
srunr	Stereospermum neuranthum Kurz	Bignoniaceae	3.2
SBWAS	Streblus asper Lour.	Moraceae	2.7
sysra	Symplocos racemosa Roxb.	Symplocaceae	0.5
syzal	Syzygium albiflorum (Duthie ex Kurz) Bahadur & R.C.Gaur	Myrtaceae	0.5
TREOR	Trema orientalis (L.) Blume i	Cannabaceae	2.3

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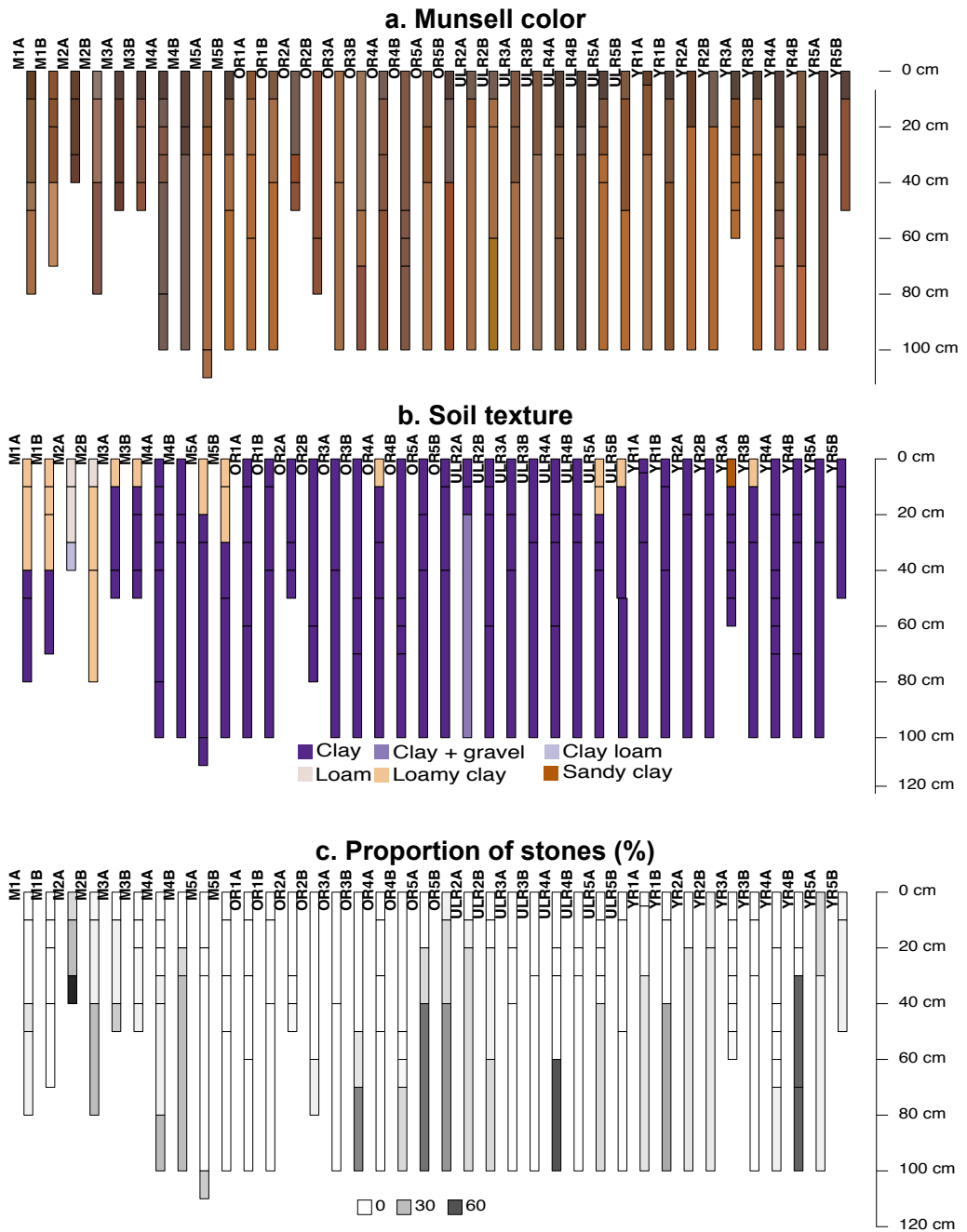
EPPO code	Species	Family	RI
	unidentified (other species)		0.5
VIXQU	Vitex quinata (Lour.) F.N.Williams	Lamiaceae	5
prdse	Protium serratum (Wall. ex Colebr.) Engl.	Burseraceae	3.2

Figure S2.2: Distribution of shrub and tree species in the plots throughout the sampling periods. Corresponding codes can be found in Table S2.1. A grey box indicates that the species is absent. The x-axis (1 to 5) designates the five sampling periods (March 2016, November, March 2017, November 2017, March 2018).



S2.2 SOIL PROFILES

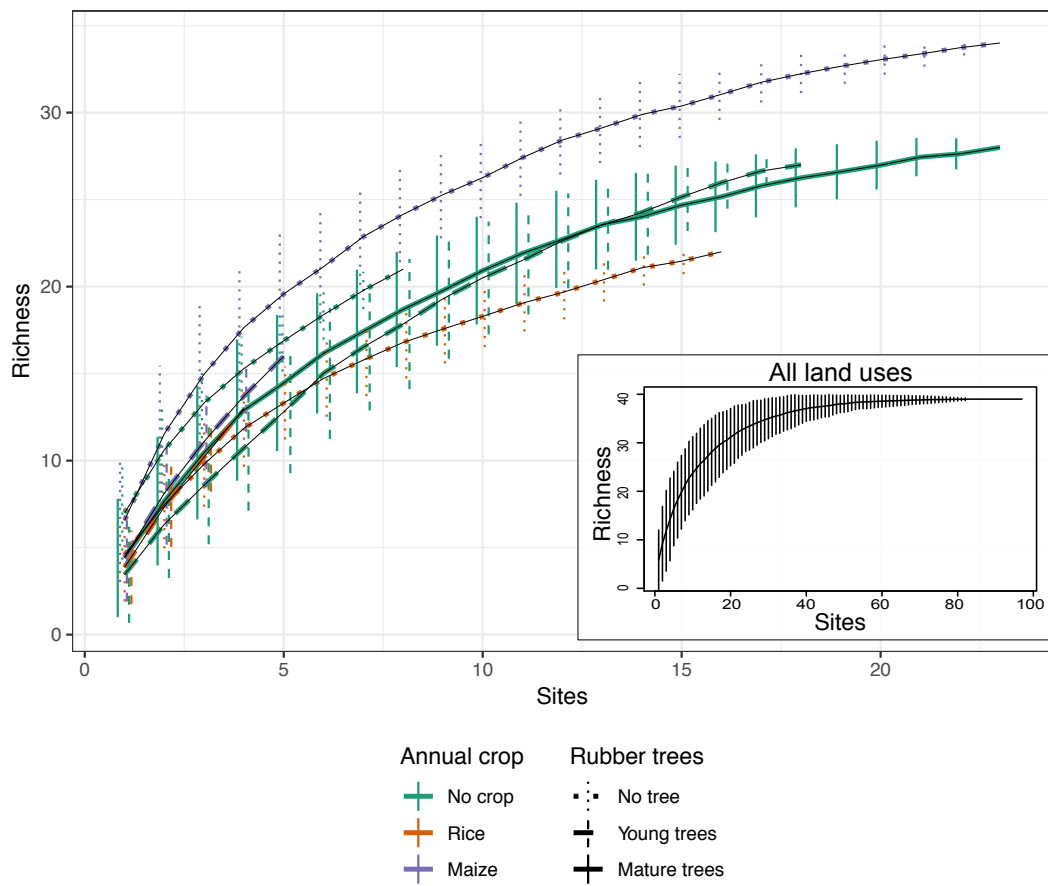
Figure S2.3: Soil profiles description for all studied fields. a. Munsell color; b. Soil texture; c. percentage of stones depending on depth. A and B correspond to profiles realised at the top and bottom, of each field, respectively.



APPENDIX FOR CHAPTER 3

s3.1 SPECIES ACCUMULATION CURVES FOR SHRUBS AND TREES

Figure S3.1: Species accumulation curves for shrub and tree species, depending of the land use. Bottom right: global species accumulation curve, all land uses considered.



s3.2 ARTICLE 1.

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

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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

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 (EI_{30} /monthly rainfall, with EI_{30} 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, Jumba (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

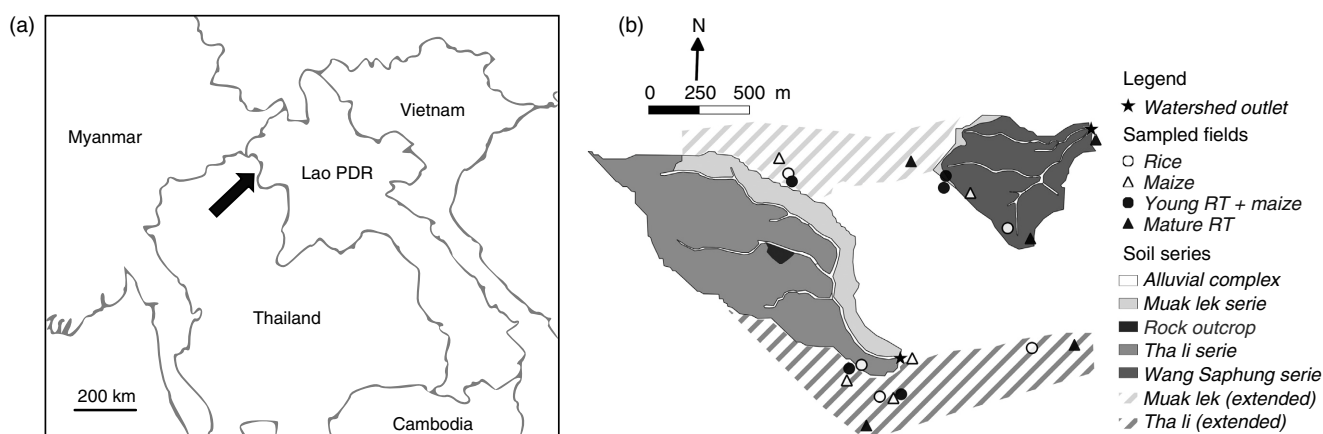


Figure 1 Situation of the study area. (a) Location of Huai Lang study site. (b) Plots location in the study area. Right: catchment dominated by mature RT plantations. Left: catchment dominated by annual crops. Soil series were taken adapted from Jumpa (2012), and hatched areas represent areas where soil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

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

Series name (abbrev.)	USDA classification	Texture	Soil depth	Soil pH
Muak Lek Series (Ml)	Ultic Haplustalfs	Clayey-skeletal	Shallow	5.5–6
Tha Li Series (Tl)	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

Table 2 Summary of farming practices reported by field owners for the crop preceding sampling. This information is given as an indication: it has not been directly verified on the field. Gly = Glyphosate (L/ha), Gra = Gramoxone (L/ha), Met = Metsulfuron-methyl (g/ha), All = Allmix (Metsulfuron-methyl + Chlorimuron-ethyl, g/ha), At = Atrazine (kg/ha). All fertilizer amounts are given in kg/ha.

Field	Crop	Planting	Harvest	Crop density (m ⁻²)	Average distance between rows × trees (m) ^a	Fire	Herbicide			Fertilizer		
							Type	Date	Total amount	Type	Date	Total amount
ULR1	Rice	Late May	Oct	11.6 ± 3.0		Y	Gra	May	15.6	46-00	Aug	95
ULR2	Rice	Late May	Oct	13.6 ± 4.0		Y	Gly	May	7.5	46-00	June, Aug	125
ULR3	Rice	June	Nov	12.8 ± 3.0		Y	Met	May, August	90			
ULR4	Rice	Late June	Late Nov	15.8 ± 2.7		Y	Gly	May, June	25	21-00	July	125
ULR5	Rice	July	Nov	12.8 ± 2.3		Y	Gly	July	15	46-00	Aug	65
M1	Maize			3.4 ± 0.9		N	All	August	45			
M2	Maize	May	Sept-Oct	3.4 ± 1.3		Y	Gly	July	0.7	46-00	June	125
						N	Gly	April	10	46-00	May	130
						Y	Gra	May	3.6			
						Y	Gly	Late May	1.8	46-00	July	13
							At	Late May	0.4	15-15-15	Late July	95
							Gra	Late July	2.7			
M3	Maize	May	Sept	2.8 ± 1.9		N	Gly	April, May	12.5	46-00	July	95
						Y	At	April, May, July	3.5	15-15-15	July	95
						Y	Gra	July	3.8			
M4	Maize	May	Aug	4.8 ± 1.5		Y	Gly	July	10	46-00	July	125
							At	July	0.9			
M5	Maize	July	Sept	1 ± 1.2		N	Gly	June, August	1.7	46-00	August	95
YR1	RT + Maize			2.4 ± 0.5	6.4 ± 0.7/2.9 ± 0.3	N	Gly	Avril	2.1	46-00	June	85
YR2	RT + Maize			1.2 ± 1.3	7.1 ± 0.5/3.8 ± 1.0	N	Gly	Avril	2.1	46-00	June	85
YR3	RT + Maize	July	Sept	3 ± 0.7	7.1 ± 0.3/3.7 ± 0.5	N	Gly	June, July	1.7	46-00	July	60
YR4	RT + Maize			2.6 ± 2.1	6.4 ± 0.5/3.5 ± 0.2	N	Gly	June	18.8	46-00	July	80
							At	Late June	2.8			
YR5	RT + Maize	July	Sept	1.6 ± 1.3	6.2 ± 0.5/3.0 ± 0.2	N	Gra	Late June	15.6		June	125
						N	Gly	June	25	46-00		
OR1	RT				4.7 ± 0.9/4.1 ± 0.5	N	Gra	May, Oct	5.2		May, July, Sept	1250 ^b
OR2	RT				7.7 ± 0.6/3.1 ± 0.1	N	Unable to contact					
OR3	RT				7.6 ± 1.3/4.6 ± 0.4	N						
OR4	RT				7.3 ± 0.9/3.5 ± 0.4	N						
OR5	RT				6.4 ± 0.3/3.1 ± 0.1	N	Gly	June, Aug, Sept	7.5	15-15-15	May, August	85
						N				15-15-15	June, October	80

^aIrregular planting patterns can be explained by steep slopes that make the following of contour lines more difficult. ^bThe owner reported that he used 1 kg of fertilizer per tree, three times a year.

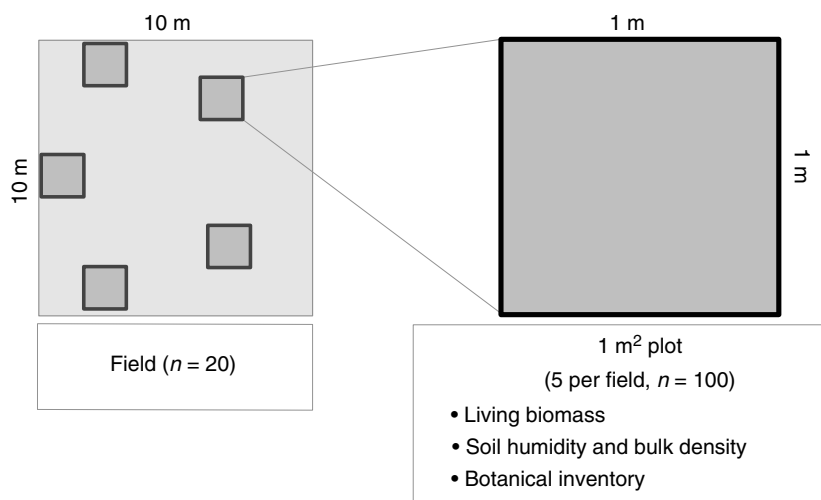


Figure 2 Sampling protocol.

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%,

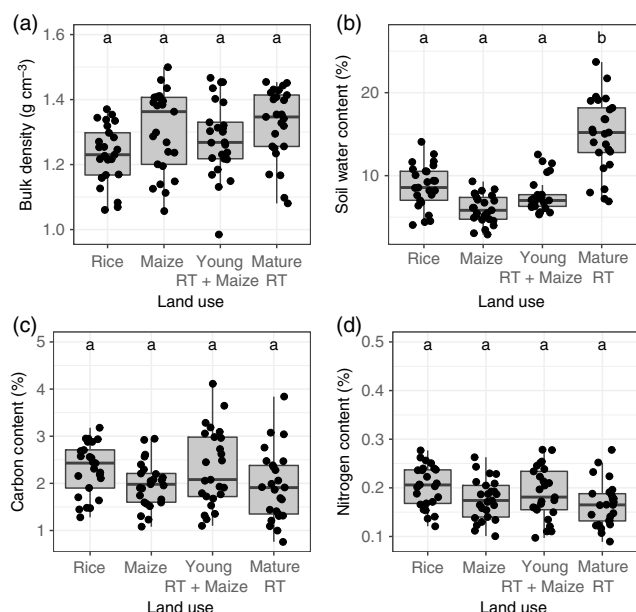


Figure 3 Variations of soil properties with land uses. Soil bulk density (a), soil water (b), carbon (c) and nitrogen (d) contents per square metre in each land use at the end of the dry season, that is 4–5 months after harvesting. Each dot represents one sampling plot. Different letters indicate significant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

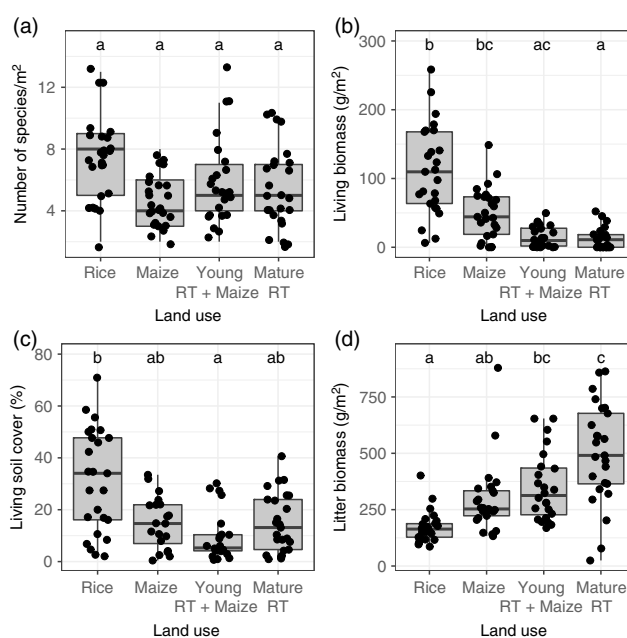


Figure 4 Variations of weed richness and abundance with land uses. Number of species per m² (a), living weed biomass (b), proportion of soil covered with living plants after litter removal (c) and litter biomass (d) in each land use at the end of the dry season, that is 4–5 months after harvesting. Each 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

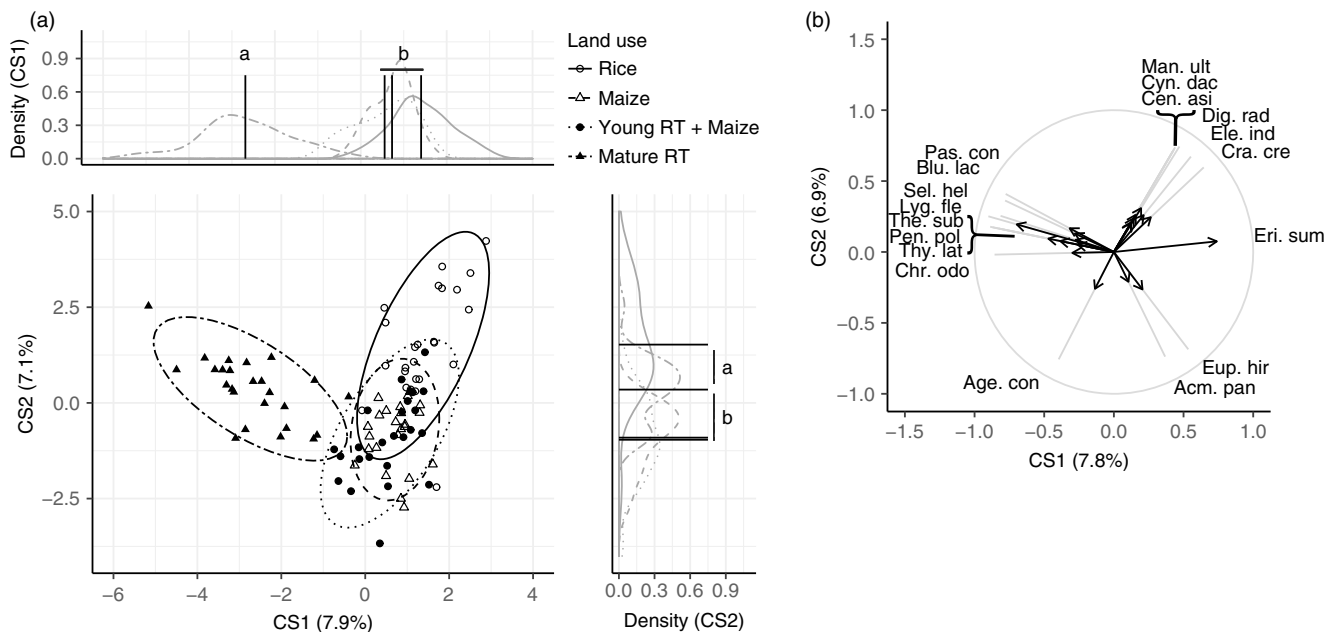


Figure 5 Variation of weed assemblages with land uses. (a) Position of the different land uses on the first two axes of the BCA (third axis not shown). Density curves indicate the smoothed kernel density of coordinates of each crop along axes, with the density on the y-axis (equivalent to smoothed histograms). 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/m²), species richness (m²) or living soil cover (%)) on a soil property (Y: soil bulk density (g/cm³), 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 $Y \sim LU$. * 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/m²) in our study were much higher than those recorded under similar crops in eastern Thailand (0.18 kg/m² in mature RT plantations, 0.08 kg/m² 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 (%)): $Y \sim X \times \text{LU}$. * 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 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 ^{a,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 ($1.3 \pm 0.1 \text{ g/cm}^3$) was higher than reported in RT monoculture in lowland Acrisols of Sumatra (Indonesia) (0.93–0.98 g/cm^3 , 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/cm^3 , 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

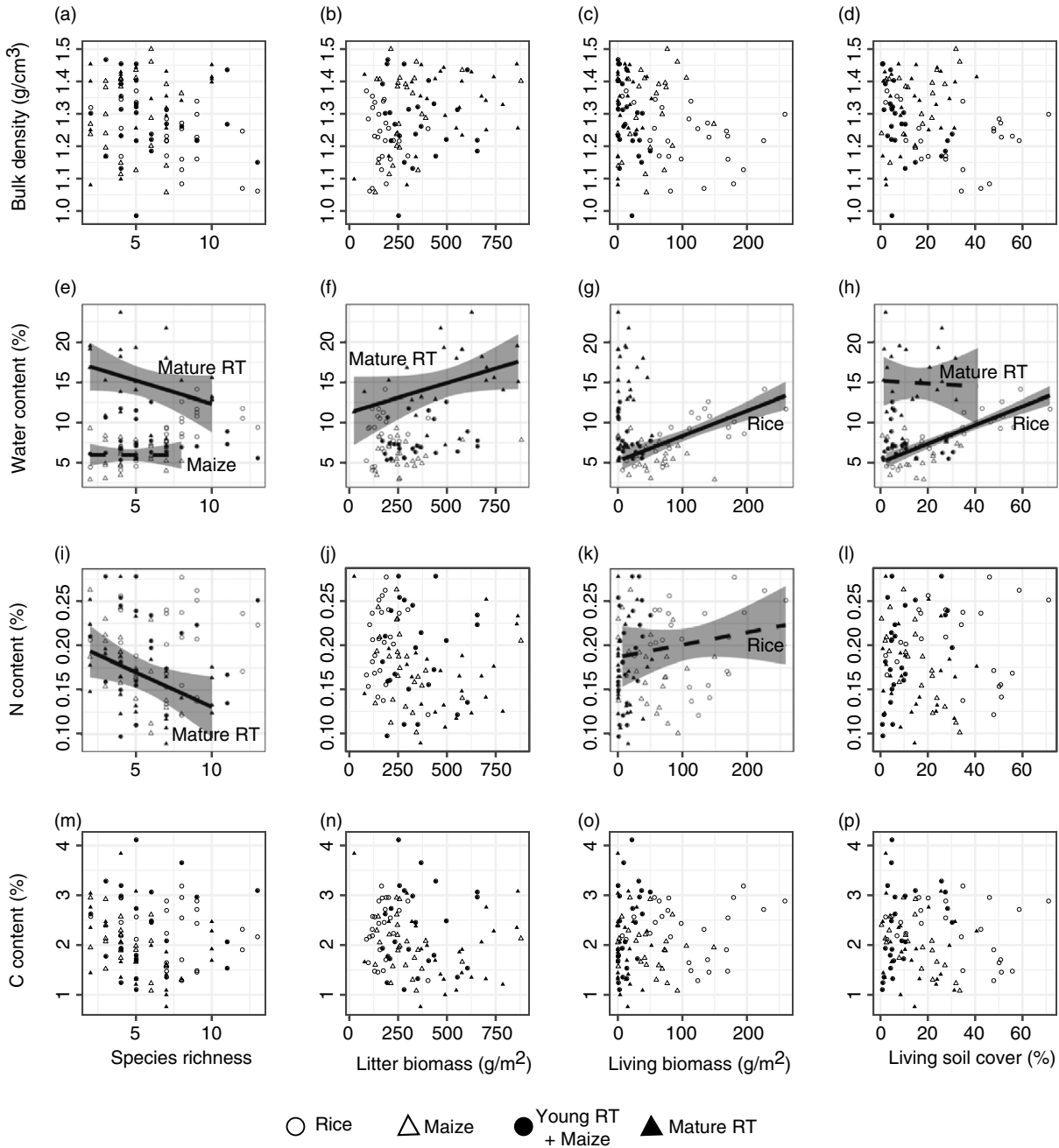


Figure 6 Interactions of weed richness and abundance with soil properties. Solid and dashed lines indicate, respectively, trends significant at 5% and 10%.

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.

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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.

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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.

APPENDIX FOR CHAPTER 4

Figure S4.1: Variation of species richness per field with the number of land use shifts for fields whose current annual crop is maize. Bars represent the mean \pm standard deviation. Different letters indicate significant differences within each group ($P < 0.05$).

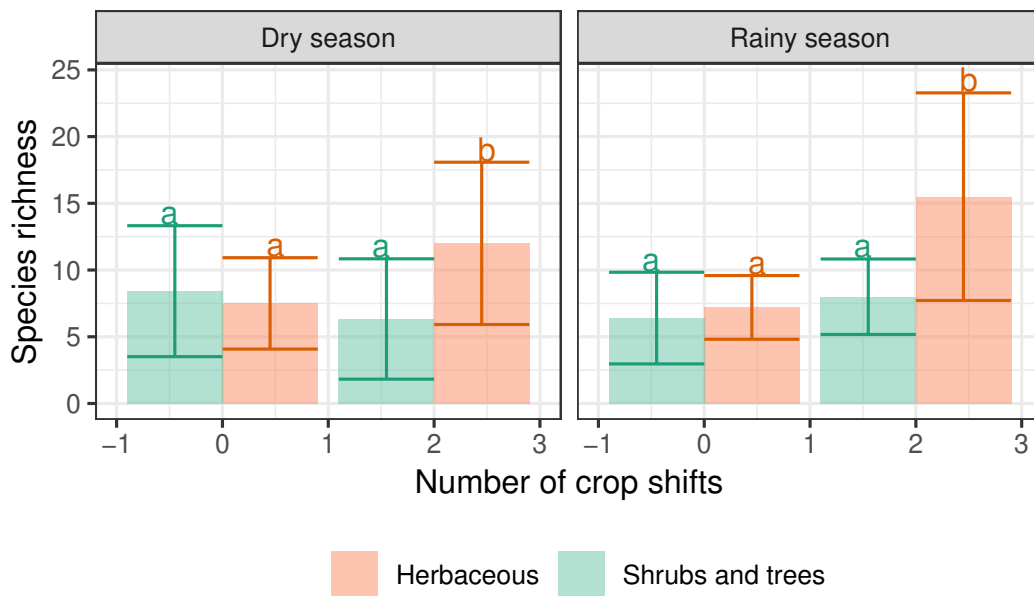


Table S4.1: Effects of crop type and crop variability on plant richness, diversity and abundance. R²: Likelihood-ratio based pseudo-R-squared. *: P < 0.05. **: P < 0.01. ***: P < 0.001. Significance letters are defined based on a p-value threshold of 0.05.

	Number of land use types	Season	Number of land use types*Season	Spatial	Annual crop	Presence of trees	Annual crop * Presence of trees	Number of shifts	Estimate (dry season)	Estimate (rainy season)	R ² (%)
	Partial R ²	Partial R ²	Partial R ²	Partial R ²	Partial R ²	Partial R ²	Partial R ²				
Richness (all species)	3 ns	0 ns	7 ns	1 ns	1 ns	1 ns	1 ns	1	15.8 (11.6 - 20.1) ^a	13.1 (7.8 - 18.5) ^a	36
								2	16.3 (13.6 - 19) ^a	18.9 (16.2 - 21.7) ^a	
								3	17.3 (11.4 - 23.2) ^a	18 (11.2 - 24.8) ^a	
Richness (herbaceous species)	11 *	0 ns	0 ns	7 ns	1 ns	6 ns	0 ns	1	8.1 (5.2 - 11) ^a	8.5 (4.9 - 12.1) ^a	55
								2	12 (10.2 - 13.9) ^a	12.9 (11 - 14.8) ^a	
								3	12 (8 - 16.1) ^a	11.8 (7.2 - 16.4) ^a	
Richness (tree/shrub species)	0 ns	0 ns	12 *	23 *	0 ns	20.	2 ns	1	7.4 (4.6 - 10.2) ^a	4.3 (0.7 - 7.8) ^a	47
								2	4.3 (2.5 - 6) ^a	6.1 (4.3 - 7.8) ^a	
								3	5.3 (1.4 - 9.2) ^a	6.2 (1.7 - 10.7) ^a	
Dominance (all species)	11 *	12 ***	0 ns	0 ns	2 ns	8 ns	4 ns	1	0.7 (0.6 - 0.9) ^a	0.9 (0.7 - 1) ^a	41
								2	0.6 (0.5 - 0.7) ^a	0.7 (0.6 - 0.8) ^a	
								3	0.4 (0.2 - 0.6) ^a	0.5 (0.3 - 0.8) ^a	
Dominance (herbaceous species)	13 **	8 **	0 ns	4 ns	3 *	3 ns	4 ns	1	0.8 (0.7 - 0.9) ^a	0.9 (0.7 - 1) ^a	51
								2	0.6 (0.5 - 0.7) ^{ab}	0.7 (0.6 - 0.8) ^a	
								3	0.5 (0.3 - 0.7) ^b	0.6 (0.4 - 0.8) ^a	
Shannon (all species)	11 *	8 ***	0 ns	1 ns	1 ns	2 ns	6 ns	1	1 (0.7 - 1.4) ^a	0.8 (0.4 - 1.2) ^a	23
								2	1.2 (1 - 1.4) ^a	0.9 (0.7 - 1.1) ^a	
								3	1.7 (1.2 - 2.2) ^a	1.4 (0.8 - 1.9) ^a	
Shannon (herbaceous species)	10 **	6 *	2 ns	6 ns	1 ns	0 ns	4 ns	1	0.7 (0.4 - 1) ^a	0.7 (0.3 - 1.1) ^a	44
								2	1.1 (0.9 - 1.3) ^{ab}	0.9 (0.7 - 1.1) ^a	
								3	1.5 (1 - 1.9) ^b	1.1 (0.6 - 1.6) ^a	
Shannon (tree/shrub species)	0 ns	0 ns	0 ns	1 ns	2 ns	17.	0 ns	1	0.7 (0.2 - 1.1) ^a	0.7 (0.1 - 1.2) ^a	48
								2	0.6 (0.3 - 0.9) ^a	0.6 (0.3 - 0.9) ^a	
								3	0.6 (0 - 1.2) ^a	0.5 (-0.1 - 1.2) ^a	
Biomass*	3 ns	4.	4 ns	0 ns	9.	8 ns	3 ns	1	8.6 (4.6 - 12.5) ^a	3.5 (-1.5 - 8.5) ^a	34
								2	8.3 (5.9 - 10.7) ^a	7.1 (4.6 - 9.6) ^a	
								3	4.6 (-0.9 - 10.2) ^a	4.3 (-2.1 - 10.8) ^a	
Abundance**	4 ns	5 *	0 ns	1 ns	4 ns	0 ns	6 ns	1	5.2 (4.3 - 6) ^a	5.8 (4.7 - 6.9) ^a	26
								2	5.5 (5 - 6) ^a	6 (5.5 - 6.5) ^a	
								3	4.6 (3.4 - 5.8) ^a	5.2 (3.7 - 6.6) ^a	

* gm⁻², square root-transformed
 ** plant m⁻², log-transformed

Table S4.2: Effects of crop type and number of land use shifts on plant richness, diversity and abundance in maize fields only. R²: Likelihood-ratio based pseudo-R-squared. *: P < 0.05. **: P < 0.01. ***: P < 0.001. Significance letters are defined based on a p-value threshold of 0.05.

	Number of land use types	Season	Number of land use types*Season	Spatial	Presence of trees	Number of shifts	Estimate (dry season)	Estimate (rainy season)	R ² (%)
Richness (all species)	21 n.s	1 n.s	18 n.s	9 n.s	5 n.s	15.3 (10.9 - 19.7) ^a	12.5 (6.6 - 18.4) ^a	60	
Richness (herbaceous species)	77 ***	13 n.s	11 n.s	72 ***	4 n.s	17.5 (9.6 - 25.5) ^a	22 (12.7 - 31.3) ^a	61	
Richness (tree/shrub species)	0 n.s	11 .	11 n.s	29 .	39 **	7.1 (5.1 - 9) ^a	7.3 (3.9 - 10.6) ^a		
Dominance (all species)	18 .	76 ***	28 .	0 n.s	21 n.s	14.2 (10.4 - 18.1) ^b	18.2 (13.3 - 23.2) ^b	76	
Dominance (herbaceous species)	25 .	71 ***	27 .	1 n.s	2 n.s	7.1 (4.5 - 9.7) ^a	3.9 (0.4 - 7.4) ^a	63	
Shannon (all species)	33 *	58 **	25 .	9 n.s	4 n.s	5.6 (1 - 10.2) ^a	5.7 (0.2 - 11.1) ^a		
Shannon (herbaceous species)	71 ***	44 *	25 .	66 ***	12 n.s	0.6 (0.5 - 0.7) ^a	0.8 (0.7 - 0.9) ^a		
Shannon (tree/shrub species)	3 n.s	0 n.s	1 n.s	22 n.s	18 n.s	0.4 (0.2 - 0.6) ^b	0.8 (0.6 - 1) ^a		
Biomass*	32 .	30 **	11 n.s	7 n.s	46 ***	0.7 (0.6 - 0.9) ^a	0.7 (0.5 - 0.9) ^a	89	
						1.1 (0.8 - 1.3) ^a	0.8 (0.5 - 1.1) ^a	60	
						1.7 (1.3 - 2.1) ^b	0.9 (0.4 - 1.4) ^a		
						0.7 (0.3 - 1.1) ^a	0.7 (0.5 - 0.9) ^a		
						0.7 (0.6 - 0.9) ^a	0.7 (0.5 - 0.9) ^a		
						1.6 (1.3 - 1.9) ^b	1.3 (0.9 - 1.6) ^b		
						0.7 (0.3 - 1.1) ^a	0.7 (0.1 - 1.2) ^a	50	
						0.5 (-0.3 - 1.2) ^a	0.6 (-0.3 - 1.5) ^a		
						6 (4.1 - 7.9) ^a	0.7 (-2.6 - 4) ^a	49	
						7.3 (3.7 - 10.9) ^a	5.7 (1 - 10.4) ^a		

Table S4.3: Results of the redundancy analyses conducted separately for herbaceous and tree-shrubs communities for maize fields only. The number of land use shifts, the season, and the presence of trees are used as explanatory variables for the Hellinger-transformed abundance matrix. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Explanatory variable	Df	Herbs	Shrubs
		% of total explained variance	% of total explained variance
N land use types	2	9.8	11.6
Season	1	2.4	1.5
Presence of trees	1	4.7	3.3
Residuals (%)		83	86

 APPENDIX FOR CHAPTER 5

Table S5.1: Pearson correlation coefficients within the local environment dataset

	N content	C content	C:N ratio	Humidity	pH	Bulk density	% coarse elements	% sand	% clay	% silt
C content	93									
C:N ratio	0	35								
Humidity	2	-10	-34							
pH	31	26	-10	-27						
Bulk density	-62	-60	-8	-12	-15					
% coarse elements	4	11	18	-22	40	-29				
% sand	-52	-31	53	-40	4	25	38			
% clay	32	15	-41	42	-25	-12	-66	-86		
% silt	49	34	-34	8	35	-29	38	-51	0	
Slope	13	-2	-37	17	46	-23	51	-20	-10	56

APPENDIX FOR CHAPTER 6

Figure S6.1: Comparison of weather station and rain gauges data for daily rainfall height. Lines represent rainfall height as measured in the weather station. Circles represent local rainfall height as measured by rain gauges close to M (maize fields) and YR (young RT plantations) (open circles) or to OR_i (mature RT plantations, inter rows) and OR_s (mature RT plantations, within rows) (full circles). When the differences between the manual rain gauges and the station was under 30%, the circles were not drawn for clarity.

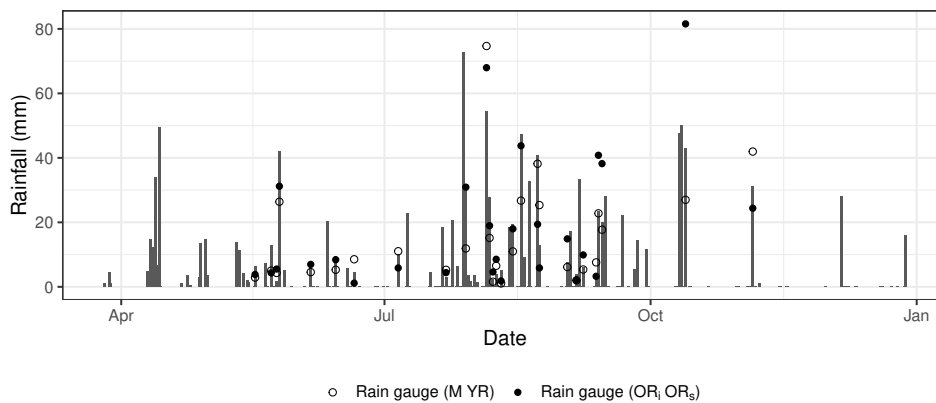


Table S6.1: Cumulative rainfall height and kinetic energy separated by rainfall height in 2015 and 2016, from May onwards, in maize fields (M), young rubber tree plantations with intercrop (YR), and mature rubber tree plantations inter (OR_i) and within (OR_s) tree rows, including very intense events. In 2015, results are presented separately for M/YR and OR_i/OR_s because of rainfall spatial variability.

	2015				2016			
	(M YR OR _i OR _s)		Total	Total	< 25 mm	25-50 mm	>50 mm	Total
Rainfall (mm)	409 440	389 407			214 221	1011 1069	530	499
Kinetic energy* (kJ m ⁻²)	976 996	444 425	151 150	1570 1570	1095	549	253	1897
n events	50 51	12 11	3 3		47	14	6	

* Calculated from the weather station.

Table S6.2: Annual runoff and soil detachment (from May onwards, including very intense events) per microplot and per rainfall height (mm) in maize fields (M), young rubber tree plantations with intercrop (YR), and mature rubber tree plantations inter (ORi) and within (ORs) tree rows.

	Runoff (L m ⁻²)				Detachment (g m ⁻²)				
	<25	25-50	>50	Total	<25	25-50	>50	Total	
2015	M	5	24	13	42	1	47	87	136
		10	60	26	95	5	735	143	883
		17	65	40	122	8	250	173	431
	YR	27	57	38	122	58	249	157	465
		25	55	20	101	105	149	51	305
		12	32	13	58	9	89	9	107
	ORI	59	251	62	371	209	2230	367	2807
		89	283	43	415	709	4819	365	5894
		55	266	24	345	181	2348	569	3098
	ORS	67	170	86	323	625	2973	902	4500
		73	165	81	319	409	3137	1799	5344
		53	115	62	230	268	1846	1236	3350
2016	M	18	19	28	65	17	79	267	364
		20	24	31	75	48	125	189	362
		38	42	36	116	92	134	137	363
	YR	24	31	41	97	41	86	202	330
		26	33	40	99	50	103	102	255
		26	30	27	83	57	125	81	263
	ORI	122	163	269	554	606	1029	6087	7722
		226	237	276	738	1827	3615	11335	16777
		165	205	262	631	1487	2771	11244	15502
	ORS	135	152	260	547	975	1746	8094	10815
		101	119	224	444	743	1311	6255	8309
		139	167	253	558	1024	1858	8077	10959

Figure S6.2: Monthly runoff coefficient (a) and soil detachment (b) in maize fields (M), young rubber tree plantations with intercrop (YR), and mature rubber tree plantations inter (OR_i) and within (OR_s) tree rows in 2015. Monthly runoff coefficient was calculated as the cumulative runoff (L m⁻²) divided by cumulative rainfall height mm for each month, including very intense events. Different letters indicate significant variations within each month.

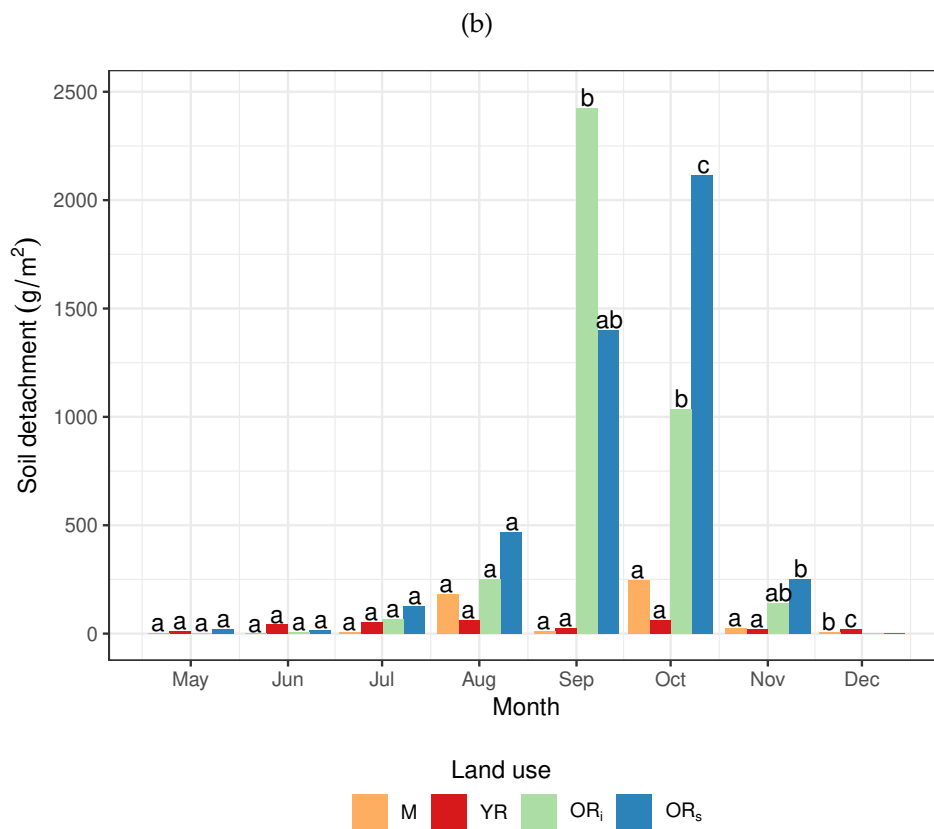
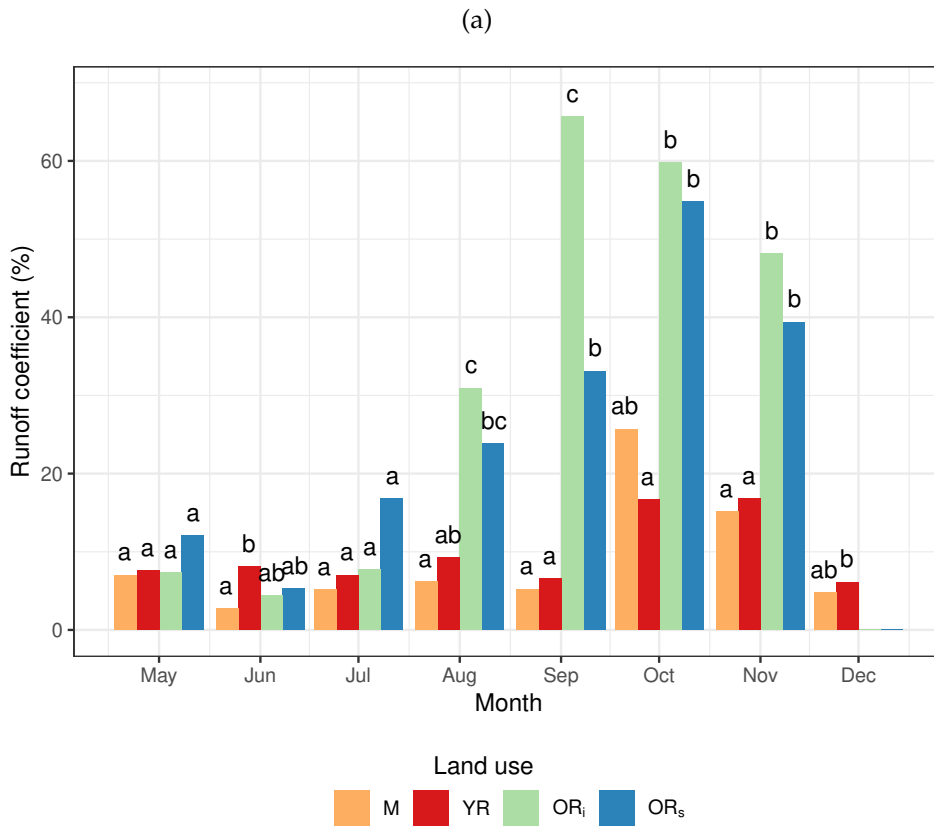


Figure S6.3: Monthly variations of surface runoff coefficient in 2016 in maize fields (M), young rubber tree plantations with intercrop (YR), and mature rubber tree plantations inter (OR_i) and within (OR_s) tree rows, including very intense events. Different letters indicate differences significant at 5% within each month.

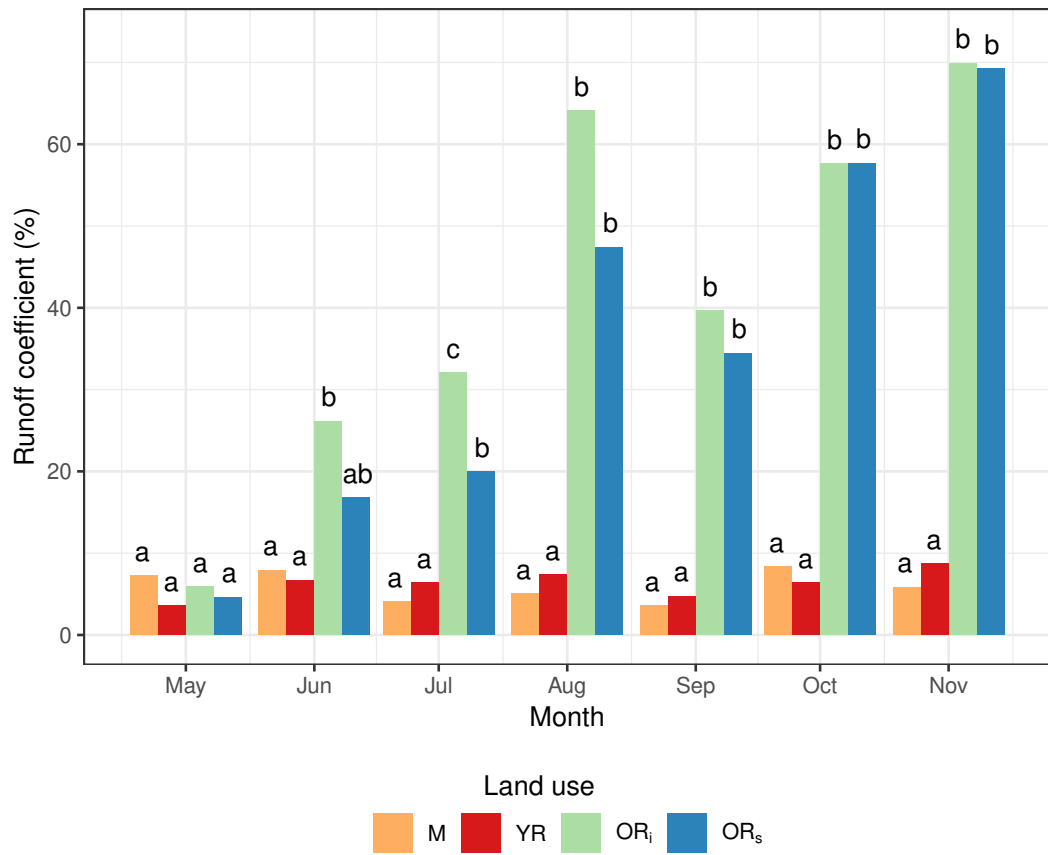


Figure S6.4: Runoff and soil detachment variations with land use, rainfall characteristics and time since the onset of the rainy season in 2016 in maize fields (M), young rubber tree plantations with intercrop (YR), and mature rubber tree plantations inter (OR_i) and within (OR_s) tree rows, including very intense events. Runoff and detachment were transformed using model-specific box-cox transformations, which λ parameter is indicated in each subfigure.

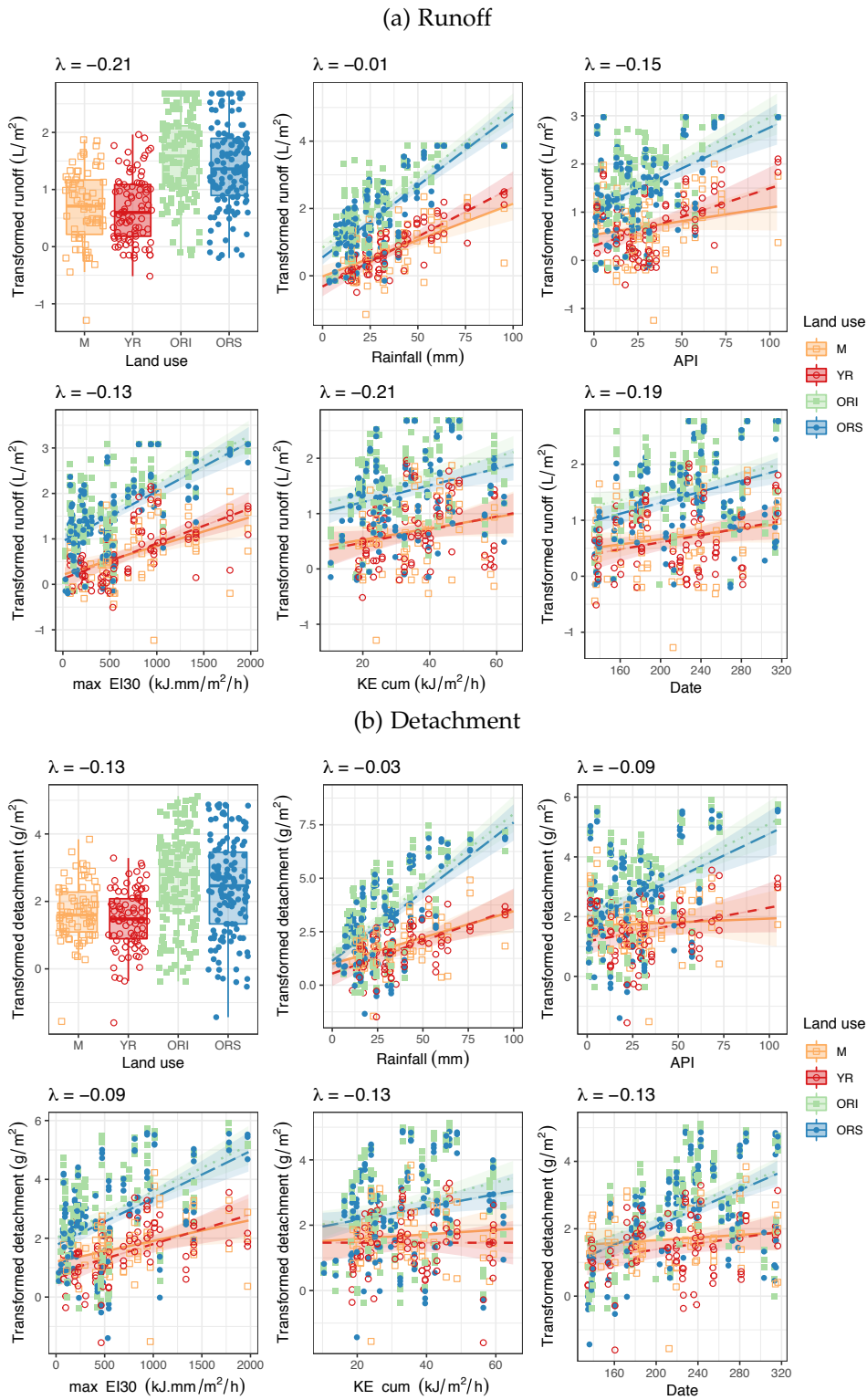


Table S6.3: Model selection for A. runoff and B. soil detachment, all land uses combined, and including the most intense events. y is A. transformed runoff or B. transformed detachment. x is the considered explanatory variable. a and b are the model coefficients. λ is the box-cox transformation with negatives allowed parameter (see 2 for details). Full models including interactions with land use were fitted and then simplified using AIC-based stepwise regression. We further removed terms whose type III anova test were insignificant (except when higher order terms, e.g. interactions, were significant). In the final model, indexed coefficients denote significant differences between land uses (a_i : significant interaction between x and land use; b_i : significant differences of land use intercepts). R^2 indicates conditional R^2 (i.e. including both fixed and random effects) of the final model. AIC is the Akaike Information Criteria of the final model. API: Antecedent Precipitation Indec. EI_{30} : rainfall intensity. EC: rainfall kinetic energy.

A. $Y = \text{Runoff (3.1 L m}^{-2}\text{)}$

X	Model type	R^2 (%)	AIC	λ (conf. int)
Rainfall (mm)	$y = a_i x + b_i$	67	849	-0.01 (-0.09 0.05)
API	$y = ax + b_i$	39	916	-0.15 (-0.23 - -0.09)
Max EI_{30} (3.1 kJ mm m ⁻² h ⁻¹)	$y = ax + b_i$	50	850	-0.13 (-0.19 -0.07)
Cumulative KE (3.1 kJ m ⁻²)	$y = ax + b_i$	32	881	-0.21 (-0.27 - -0.15)
Date	$y = ax + b_i$	32	907	-0.19 (-0.27 - -0.13)

B. $Y = \text{Detachment (3.1 g m}^{-2}\text{)}$

X	Model type	R^2 (%)	AIC	λ (conf. int)
Rainfall (mm)	$y = a_i x + b_i$	48	1459	-0.03 (-0.07 0.01)
API	$y = a_i x + b_i$	26	1451	-0.09 (-0.13 -0.07)
Max EI_{30} (3.1 kJ mm m ⁻² h ⁻¹)	$y = ax + b_i$	31	1412	-0.09 (-0.11 - -0.05)
Cumulative KE (3.1 kJ m ⁻²)	$y = ax + b_i$	15	1400	-0.13 (-0.15 -0.09)
Date	$y = a_i x + b_i$	29	1332	-0.13 (-0.15 -0.09)

Table S6.4: Model selection for A. runoff and B. soil detachment, all land uses combined. y is A. transformed runoff or B. transformed detachment. x is the considered explanatory variable. a and b are the model coefficients. λ is the box-cox transformation with negatives allowed parameter (see 2 for details). Full models including interactions with land use were fitted and then simplified using AIC-based stepwise regression. We further removed terms whose type III anova test were insignificant (except when higher order terms, e.g. x^2 or interactions, were significant). In the final model, indexed coefficient denote significant differences between land uses (a_i : significant interaction between x and land use; b_i : significant differences of land use intercepts). R^2 indicates conditional R^2 (i.e. including both fixed and random effects) of the final model.

A. $Y = \text{Runoff (3.1 L m}^{-2}\text{)}$			
M YR			
	Model	R^2 (%)	λ (conf. int.)
Rainfall (mm)	$y = ax + b$	65	0.25 (0.21 0.31)
API	$y = ax + b$	25	0.15 (0.07 0.21)
Max EI ₃₀	$y = ax + b$	54	0.17 (0.11 0.23)
Cumulative KE	$y = ax + b$	15	0.09 (0.03 0.15)
Date	$y = b$	1	0.09 (0.03 0.17)
OR _i OR _s			
Rainfall (mm)	$y = ax + b_i$	67	0.29 (0.25 0.35)
API	$y = ax + b$	31	0.17 (0.13 0.23)
Max EI ₃₀	$y = ax + b$	46	0.21 (0.15 0.25)
Cumulative KE	$y = ax + b$	13	0.15 (0.09 0.19)
Date	$y = ax + b$	12	0.15 (0.11 0.21)
B. $Y = \text{Detachment (3.1 g m}^{-2}\text{)}$			
M YR			
	Model	R^2 (%)	λ (conf. inf.)
Rainfall (mm)	$y = ax + b$	30	0.01 (-0.09 0.09)
API	$y = ax + b$	4	-0.03 (-0.13 0.07)
Max EI ₃₀	$y = ax + b$	21	-0.03 (-0.11 0.05)
Cumulative KE	$y = b$	0	-0.05 (-0.13 0.05)
Date	$y = ax + b$	4	-0.03 (-0.13 0.05)
OR _i OR _s			
Rainfall (mm)	$y = ax + b$	47	0.05 (-0.01 0.09)
API	$y = ax + b$	18	-0.03 (-0.07 0.01)
Max EI ₃₀	$y = ax + b$	25	-0.03 (-0.07 0.03)
Cumulative KE	$y = ax + b$	5	-0.07 (-0.11 -0.03)
Date	$y = ax + b$	21	-0.07 (-0.11 -0.03)

Table S6.5: Model results: variation of the runoff coefficient (square-root transformed) with rainfall height ("rainfall", mm, square-root transformed) depending on plant cover ("cover", proportion of living plant cover low (< 6%), medium (6% to 25%), or high (> 25%)) and the plantation (Plant.). ":" indicate interactions between the explanatory variables. Microplot identity and month were included as random factors. P-values are calculated based on Anova type III tests. Different letters in the "Estimate" columns indicate differences significant at 5%.

	Chisq	Df	Sum of square	Mean sum of square	P-value
(Intercept)	15.7	1			$7.3 \cdot 10^{-5}$ ***
Cover	0.2	2	0.23	0.12	$9.2 \cdot 10^{-1}$
Rainfall	45.6	1	4.72	4.72	$1.4 \cdot 10^{-11}$ ***
Plot	3.9	1	0.14	0.14	$4.9 \cdot 10^{-2}$ *
Cover:Rainfall	6.8	2	0.56	0.28	$3.4 \cdot 10^{-2}$ *
Cover:Plant.	12.6	2	0.34	0.17	$1.8 \cdot 10^{-3}$ **
Rainfall:Plant.	0.3	1	0.01	0.01	$5.7 \cdot 10^{-1}$
Rainfall:Plant.:Cover	14.3	2	0.38	0.19	$7.9 \cdot 10^{-4}$ ***

Slope coefficient estimates

Plantation	Cover	Estimate
OR2	high	$2.4 \cdot 10^{-2}$ <i>a</i>
	med	$2.7 \cdot 10^{-2}$ <i>ab</i>
	low	$4.2 \cdot 10^{-2}$ <i>b</i>
OR4	high	$1.0 \cdot 10^{-2}$ <i>a</i>
	med	$4.3 \cdot 10^{-2}$ <i>b</i>
	low	$3.9 \cdot 10^{-2}$ <i>b</i>

Figure S6.5: Increase of log-transformed soil detachment with log-transformed surface runoff for all individual events (including very intense events) causing detachment in 2016 in maize fields (M), young rubber tree plantations with intercrop (YR), and mature rubber tree plantations inter (OR_i) and within (OR_s) tree rows. The effects of log-transformed runoff ($P < 10^{-12}$, of land use ($P < 10^{-12}$ were significant. The slope coefficient in OR_i and OR_s (confidence interval: 4.1 g L^{-1} to 4.5 g L^{-1}) was significantly higher than in YR and M (confidence interval: 2.4 g L^{-1} to 3.15 g L^{-1} ; interaction: $P < 10^{-7}$). R^2 for fixed and random effects was 86 %.

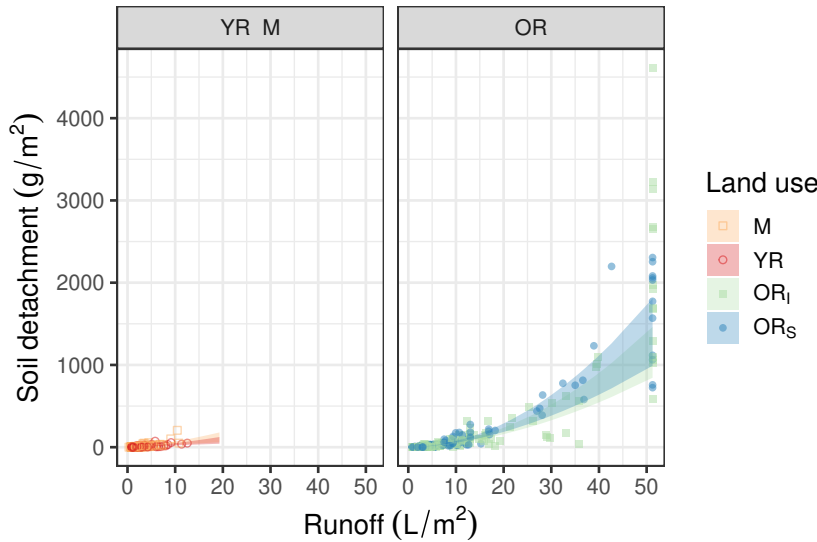


Figure S6.6: Effect of the herbicide treatment on monthly runoff coefficients, including very intense events. Each point represents one monthly runoff coefficient for one microplot, between January 2017 and December 2018. Microplot identity and month were included as random effects. The plantations (OR₂ or OR₄) were included as a fixed effect. Error bars represent the confidence intervals of the means, based on marginal effects (i.e. after controlling for the plot). Treatment effect: $P = 0.01$. Plantation effect: $P = 0.002$. R^2 (fixed effects only): 5%. R^2 (fixed and random effects): 85 %.

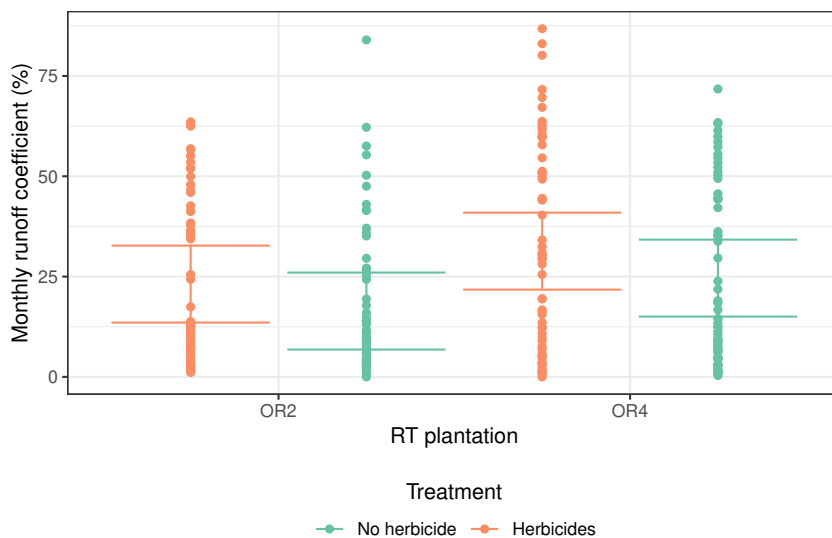
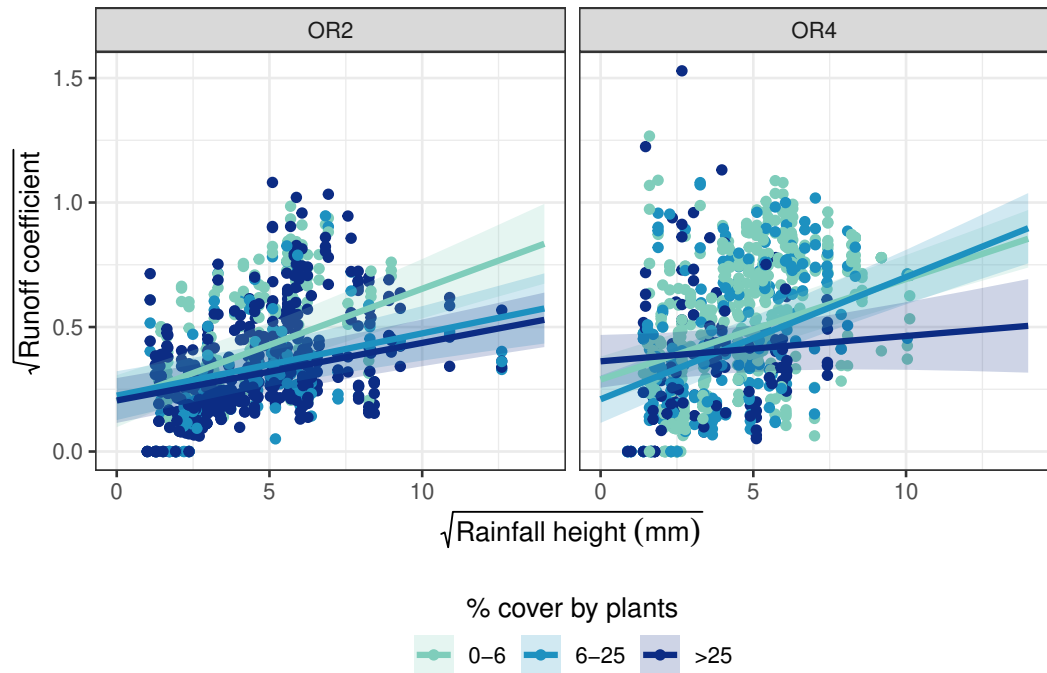


Figure S6.7: Effect of rainfall height (square-root transformed) on runoff coefficient (square-root transformed) depending on the soil cover, including very intense events. Each point represents the runoff coefficient for one rain event in one microplot, between January 2017 and December 2018. Low, medium and high soil cover correspond to cover under 6 %, between 6 % and 25 %, and over 25 %, respectively. The plantations (OR2 or OR4), rainfall height, and cover class were included as a fixed effect. Microplot identity and month were included as random effects. Coloured areas represent the confidence intervals, based on marginal effects (i.e. after controlling for the plot).



Adventices et érosion du sol dans un agroécosystème montagneux en transition du Nord de la Thaïlande : une analyse multidisciplinaire

L'intensification et l'expansion rapide des plantations d'*Hevea brasiliensis* dans les régions montagneuses d'Asie du sud-est ont conduit à d'importantes dégradations de la biodiversité et des sols. Les adventices remplissent de nombreux services écosystémiques, par exemple en favorisant la protection du sol. Toutefois, les facteurs déterminants les communautés adventices et les interactions entre ces communautés et les processus d'érosion du sol sont mal connus. Deux fois par an entre 2016 et 2018, nous avons réalisé des inventaires botaniques et des caractérisations de sol à Huai Lang, au nord de la Thaïlande, dans 20 champs appartenant à plusieurs types d'usage du sol correspondant à la transition entre les cultures annuelles et les plantations d'hévéa. Nous avons également mesuré l'effet du type d'usage du sol et des pratiques de désherbage sur le ruissellement et le détachement de sol dans des plots d'érosion de 1m². Les résultats montrent que la composition des communautés végétales est principalement déterminée par le type d'usage du sol et les caractéristiques paysagères, tandis que la variabilité temporelle des cultures dans un champ favorise la diversité végétale. Les plantations d'hévéa matures supportent des communautés végétales très spécifiques et favorisent des ruissellements et détachements de sol très élevés, qui peuvent être atténués par la présence d'un couvert végétal. Cette étude suggère que la conservation du sol et de la biodiversité en Asie du sud-est devrait être fondée à la fois sur une évolution des pratiques à l'échelle du champ (par ex. désherbage moins intense) et sur un maintien de la diversité spatiale des agroécosystèmes.

Mots-clés: adventices, agroécosystème, érosion du sol, Asie du sud-est, communautés végétales

Weeds and soil erosion in a changing mountainous agro-ecosystem of north Thailand - A multidisciplinary analysis

In Mountainous South-East Asia, rapid agricultural intensification and the expansion of rubber tree plantations in the past decades led to drastic biodiversity losses and intense soil degradation. Weeds provide diverse ecosystem services, including soil protection and support for biodiversity at higher levels. However, the determinants of weed communities in mountainous areas of Southeast Asia, and the interactions of these communities with soil characteristics and erosion processes, are still largely unknown. We conducted soil characterisation and botanical inventories in Huai Lang, Northern Thailand, in 20 fields from different land uses along the transition from annual crops to mature rubber tree plantations twice a year from 2016 to 2018. Using 1m² erosion microplots, we also measured runoff and soil erosion in different land uses, and in rubber tree plantations under different weeding practices. We show that weed communities composition was mostly determined by land use and landscape characteristics, while crop temporal variability was an important determinant of plant diversity. Rubber tree plantations had specific weed communities and had exceptionally high soil detachment rates compared to maize or young plantations, but weed cover was effective in decreasing these erosion rates. Altogether, our results suggest that soil and plant biodiversity conservation in mountainous Southeast Asia should involve both on-field adaptations (e.g. less intense weeding practices, especially under rubber tree plantations) and landscape-scale management programs, with a focus on maintaining landscape diversity.

Keywords: weeds, agro-ecosystem, soil erosion, Southeast Asia, plant communities