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Services écosystémiques et biodiversité dans les paysages forestiers du nord de Bornéo

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Platon a dit : « L’humanité sera heureuse un jour, quand les philosophes seront rois ou quand les rois seront philosophes. »

Thomas More (1516) *Utopia*

Cela est bien dit, répondit Candide, mais il faut cultiver notre jardin.

Voltaire (1759) *Candide, ou l'Optimisme*

Remerciements

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Et enfin, à Hélène pour… tout ! Pour toi ! Mille et un mercis !

Résumé du manuscrit

D'importants changements d'occupation et d'utilisation des sols se poursuivent dans les tropiques humides, où les paysages forestiers sont particulièrement impactés. Un aménagement avisé du territoire requiert des informations sur les services écosystémiques produits dans ces paysages ainsi que sur la biodiversité qu'ils abritent. Cette thèse porte sur l'étude de la diversité d'espèces ligneuses et l'évaluation de la production de services écosystémiques (contrôle de l'érosion des sols, et atténuation du changement climatique via stockage de carbone) dans les paysages forestiers du nord de Bornéo à différentes échelles et à l'aide de données mesurées sur le terrain.

A l'échelle locale, l'étude de la distribution de la diversité d'espèces ligneuses et de la production de services écosystémiques au sein de la mosaïque paysagère entourant un village traditionnel du nord de Bornéo a souligné le rôle important des forêts naturelles, des forêts post-exploitation et des jachères liées à l'agriculture itinérante sur brûlis dans la production de services et la conservation de la diversité d'espèces ligneuses.

A l'échelle régionale, l'analyse des relations spatiales entre carbone et diversité d'espèces ligneuses sur une région du nord de Bornéo encore largement couverte de forêts a montré que le carbone de la biomasse aérienne et la diversité d'espèces ligneuse sont fortement positivement corrélés. Inversement, les corrélations entre carbone du sol et carbone de la biomasse aérienne ou diversité d'espèces ligneuses se sont révélées négatives. Des recommandations en matière de conservation et d'opportunités de développement ont été formulées.

A l'échelle globale, l'analyse quantitative de plus de 3600 mesures de pertes de sol collectées par le biais d'une revue systématique de la littérature a révélé que l'érosion des sols dans les tropiques humides est très nettement concentrée dans l'espace (au niveau des éléments de sol nu présents dans le paysage) et dans le temps (par exemple, durant la rotation des cultures). Nous avons de plus confirmé que la mise en œuvre de bonnes pratiques de gestion des sols et de la végétation pouvait permettre jusqu'à 99% de réduction des pertes de sol.

Nos travaux permettent d'avoir une meilleure compréhension de la distribution spatiale de la diversité d'espèces ligneuses et de services écosystémiques dans les paysages forestiers tropicaux encore peu étudiés, et contribueront à une approche intégrée de l'aménagement du territoire fondée sur la prise en compte des services écosystémiques, approche qui reste anecdotique dans ces régions.

Mots-clés

Services écosystémiques
Diversité d'espèces ligneuses
Stockage de carbone
Contrôle de l'érosion des sols
Utilisation des sols
Changement d'utilisation des sols
Relation spatiale
Spatialisation
Revue systématique

Thesis abstract

While substantial changes of land use and land cover are still occurring in the humid tropics, information about the amount of ecosystem services and the extent of biodiversity respectively provided by, and hosted in tropical forested landscapes is required to help decision makers achieve sound land-use planning. Working at different scales with field measurements, we focused on tree diversity, soil erosion control, and climate change mitigation through carbon storage (in both aboveground biomass and soils).

At the local scale, a study of the distribution of tree diversity and ecosystem service production over a mosaic landscape surrounding a traditional village of northern Borneo highlighted the role of natural forests, logged-over forests and land uses related to the swidden agriculture system in producing ecosystem services and hosting tree diversity.

At the regional scale, an analysis of the spatial relationships between carbon and tree diversity over a still mostly forested region of northern Borneo showed that aboveground carbon and tree diversity were strongly positively correlated. Conversely, correlations between soil carbon and either aboveground carbon or tree diversity were negative. Suggestions about conservation and development opportunities were made according to these findings.

At the global scale, the quantitative analysis of more than 3600 measurements of soil loss compiled through a systematic review of the literature revealed that soil erosion in the humid tropics is dramatically concentrated in space (over landscape elements of bare soil) and time (e.g. during crop rotation). Interestingly, the implementation of sound practices of soil and vegetation management was shown to help reduce erosion by up to 99%.

Overall, our work allows a better understanding of the spatial distribution of ecosystem services and tree diversity in tropical forested landscapes, and might prove useful for the purpose of reaching an integrated “ecosystem service based approach” for land-use planning.

Keywords

Ecosystem services
Tree diversity
Carbon storage
Soil erosion control
Land use
Land-use change
Spatial relationship
Spatialization
Systematic review

Résumé substantiel

Les services écosystémiques, qu'ils soient de production, de régulation, de soutien ou bien culturels, sont les biens et services que l'Homme retire des écosystèmes et de leur fonctionnement. L'Evaluation des écosystèmes pour le Millénaire, dont la synthèse a été publiée en 2005, a largement contribué à la généralisation de l'utilisation du concept de service écosystémique. L'estimation de la production de services écosystémiques se fait par la mesure d'indicateurs. Celle-ci étant souvent difficile, on a régulièrement recours à des substituts (« *proxies* » en anglais), mais la fiabilité de certains d'entre eux est contestée dans la mesure où ils ne présentent qu'une correspondance partielle avec les données primaires qu'ils sont censés représenter.

Cette thèse porte sur l'évaluation de la production de services écosystémiques à différentes échelles, à l'aide de données mesurées sur le terrain afin d'éviter les écueils inhérents à l'utilisation de certains substituts. Nous avons choisi d'étudier le contrôle de l'érosion des sols, l'atténuation du changement climatique via stockage de carbone dans les sols et la biomasse aérienne, et enfin la diversité d'espèces ligneuses (qui n'est pas un service écosystémique en soi, mais est intrinsèquement lié à la production de biens et services multiples). Ces deux services et l'une des composantes de la biodiversité ont été choisis pour la complémentarité des échelles à laquelle ils interviennent (locale, régionale et globale) et leur importance pour les populations qui en dépendent.

A l'échelle du paysage, nous avons mesuré les stocks de carbone, la diversité d'espèces ligneuses et les pertes de sol dans différents types d'occupation ou d'utilisation des sols aux environs d'un village du nord de Bornéo dont les moyens de subsistance sont liés à l'agriculture sur brûlis et la culture de l'hévéa. La production de services et la diversité d'espèces ligneuses sont maximales en forêt naturelle. Les forêts post-exploitation produisent des services similaires à ceux des forêts naturelles (bien qu'en quantité moindre du fait de l'exploitation) et abritent de même une importante diversité d'espèces ligneuses. Les types d'utilisation des sols liés à l'agriculture sur brûlis fournissent plus de services et abritent une diversité d'espèces ligneuses plus importante que les plantations industrielles de palmiers à huile ou d'hévéas qui se développent dans ces régions. Ces résultats plaident pour la protection inconditionnelle des forêts naturelles restantes, une gestion pertinente des forêts post-exploitation afin d'éviter qu'elles ne soient converties en plantations, et un soutien pour le maintien de systèmes d'agriculture et d'agroforesterie traditionnels.

A l'échelle de la région, nous avons réalisé des inventaires botaniques et pédologiques dans différents types de végétation (forêts de plaine, forêts sur tourbe, forêts sur sable blanc, etc.). Ces inventaires nous ont permis d'élaborer des modèles régionaux de distribution de carbone (à la fois dans la biomasse aérienne et le sol) et de diversité d'espèces ligneuses. Nous avons trouvé une corrélation positive entre carbone dans la biomasse aérienne et diversité d'espèces ligneuses. La corrélation devient négative lorsque l'on considère le carbone du sol car ce dernier est particulièrement élevé dans les tourbières où la diversité est faible. Si nous avons

mis en évidence une importante congruence spatiale entre les zones présentant les plus hautes valeurs (« *hotspots* ») de carbone dans la biomasse aérienne et de diversité d'espèces ligneuses, celle-ci est nulle dès lors que l'on s'intéresse au carbone du sol. Ceci souligne à quel point il est nécessaire de considérer la répartition spatiale de services écosystémiques multiples lors de l'aménagement du territoire. Car dans le cas contraire, des politiques choisies pour améliorer ou protéger la production d'un SE pourraient s'avérer nettement préjudiciables à ceux qui n'auront pas reçu une attention suffisante.

Enfin, à l'échelle des tropiques humides, nous nous sommes concentrés sur le service de contrôle de l'érosion des sols, par le biais d'une revue systématique des données de pertes de sol disponibles dans la littérature. Il s'agissait de combler un vide existant car, s'il existe plusieurs études sur la biodiversité ou les stocks de carbone au niveau des tropiques humides, aucune ne traitait jusqu'alors du service de contrôle de l'érosion des sols. Cette revue a permis de synthétiser quantitativement l'influence du couvert végétal dans le contrôle de l'érosion des sols. Elle a pu confirmer que l'érosion des sols se concentre dans l'espace (au niveau des éléments nus d'un paysage) et dans le temps (entre deux rotations de cultures). Le service de contrôle de l'érosion des sols étant fourni dès lors que le couvert végétal est suffisamment développé, des pratiques simples de conservation des sols (mise en place de haies, paillage des zones cultivées, etc.) permettent d'obtenir des diminutions de pertes de sol drastiques.

Nos travaux permettent d'avoir une meilleure compréhension de la distribution spatiale de la diversité d'espèces ligneuses et de services écosystémiques dans les paysages forestiers tropicaux, et contribueront à une approche intégrée de l'aménagement du territoire fondée sur la prise en compte des services écosystémiques, encore anecdotique dans ces régions.

Sommaire

Liste des abréviations

ABIES	: Agriculture alimentation Biologie Environnement Santé
CGIAR	: « *Consultative Group for International Agricultural Research* »
CIRAD	: Centre de coopération Internationale en Recherche Agronomique pour le Développement
CoLUPSIA	: « *Collaborative Land-Use Planning and Sustainable Institutional Arrangements* »
DEL	: Diversité d'Espèces Ligneuses
EM	: Evaluation des écosystèmes pour le Millénaire
GIEC	: Groupe d'experts Intergouvernemental sur l'Evolution du Climat
IPCC	: « *Intergovernmental Panel on Climate Change* »
MODIS	: « *Moderate Resolution Imaging Spectroradiometer* »
PSE	: Paiements pour Services Environnementaux
REDD	: « *Reducing Emissions for Deforestation and forest Degradation* »
SE	: Services Ecosystémiques
SPOT	: Satellite Pour l'Observation de la Terre

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Chapitre 1

Introduction générale, objectifs et plan du manuscrit

1.1 Les services écosystémiques

1.1.1 Contexte et définitions

Les conclusions de l'Evaluation des écosystèmes pour le Millénaire (EM), entamée en 2001 suite à une commande des Nations Unies et qui aura duré quatre ans, insistent sur le rôle crucial des écosystèmes dans le bien-être humain (Millennium Ecosystem Assessment, 2005). Le lien entre les écosystèmes et les populations se fait notamment, selon l'EM, par le biais de « services écosystémiques » (SE), définis comme étant les bénéfices que l'Homme obtient des écosystèmes. Un SE n'existe à proprement parler que s'il est fourni par un écosystème (composante « fourniture » du SE) et qu'il y a une demande de la part des populations (composante « demande » du SE), que celles-ci soient situées à proximité de l'endroit où le SE est fourni (SE local), ou plus éloignées (SE régional ou global). Selon le cadre conceptuel proposé par l'EM (Figure 1.1), il existe quatre types de SE : les services d'approvisionnement (nourriture et bois d'œuvre entre autres; également appelés « biens écosystémiques »), les services de régulation (par exemple la purification de l'eau ou le contrôle des nuisibles), les services culturels (notamment ceux liés à l'esthétique ou la spiritualité), et les services de soutien (services sous-jacents qui permettent aux écosystèmes de fonctionner, parmi lesquels figurent la formation des sols ou le recyclage des nutriments).

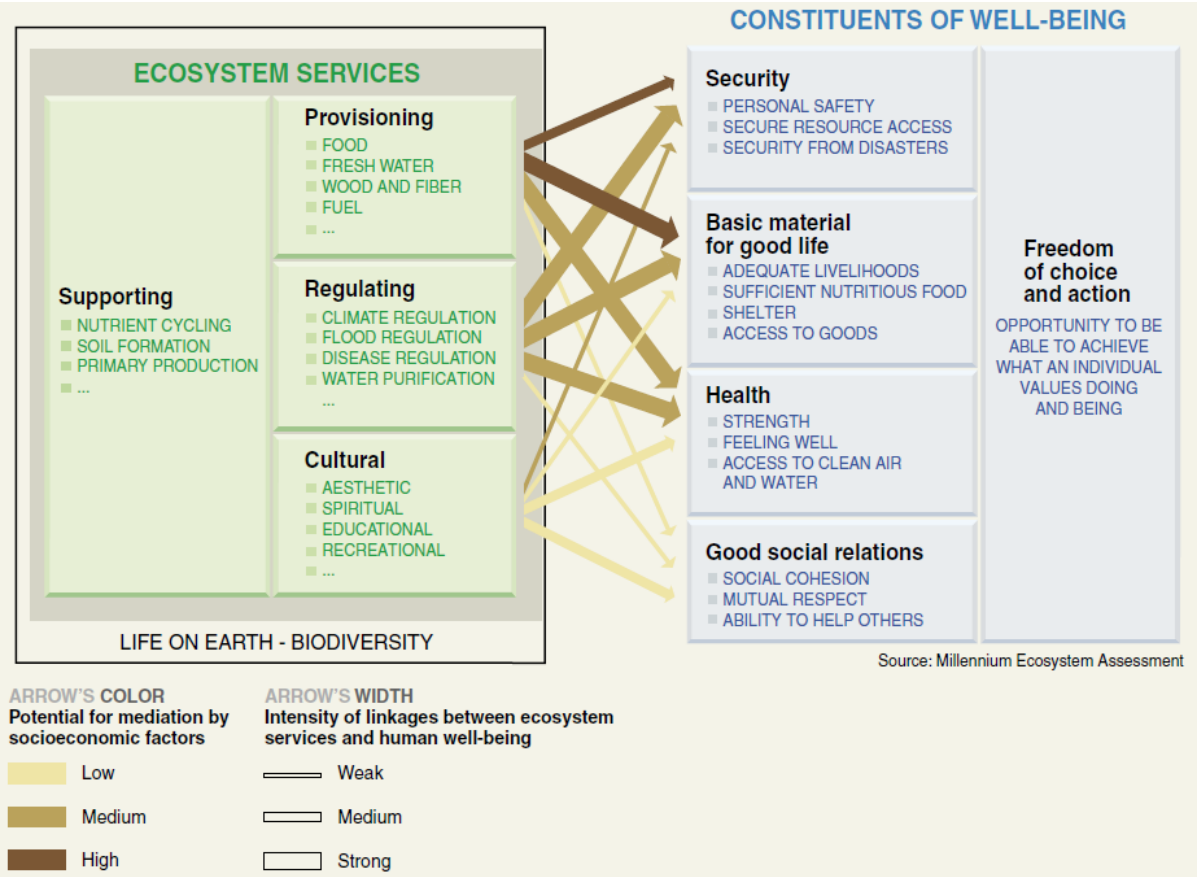

Figure 1.1. Cadre conceptuel de l'EM (Millennium Ecosystem Assessment, 2005)

Après la publication de l'EM, de nombreux autres cadres conceptuels ont émergé (Boyd & Banzhaf, 2007; Wallace, 2007; Fisher & Turner, 2008), arguant notamment du fait que l'EM confondrait les SE avec les bénéfices qu'en tirent les populations, et rappelant la nécessité de différencier processus biophysiques, fonctions et services écosystémiques (Figure 1.2). Si ces cadres conceptuels divergent toujours entre eux, c'est notamment dû à des différences dans la finalité de l'utilisation du concept de SE, qui peut aller par exemple de l'évaluation économique des bénéfices qui découlent des SE (Fisher & Turner, 2008) à la gestion des ressources naturelles d'un territoire (Wallace, 2007).

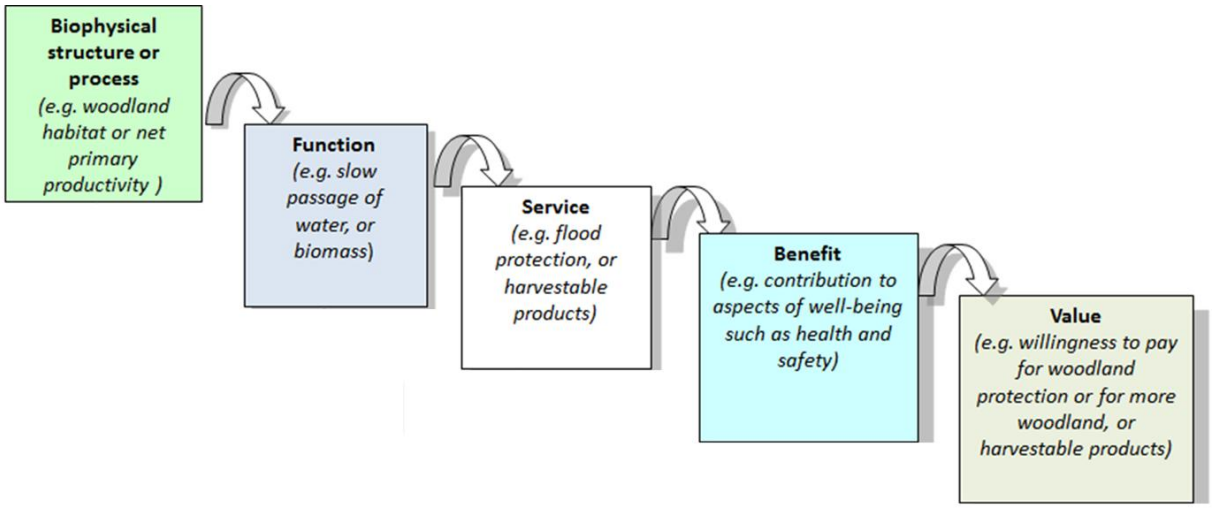

Figure 1.2. Relations entre processus biophysiques, fonctions et services écosystémiques, bénéfices retirés par l'Homme et valeurs associées (d'après Haines-Young & Potschin, 2010)

1.1.2 Mesure des SE

Dans la suite de l'exposé, toute mention du terme SE fera référence à la composante « fourniture » de celui-lui. C'est en effet cette composante que nous avons choisi d'étudier au cours de nos travaux. Il en va de même de la majorité des études traitant des SE, la composante « demande » n'étant abordée que plus rarement (mais voir par exemple Locatelli *et al.* (2014), où les deux composantes sont prises en compte).

Avant de chercher à quantifier les bénéfices issus des SE (éventuellement en termes monétaires), il s'agit de mesurer les SE en termes biophysiques. Des indicateurs de la production de SE sont utilisés à cette fin. La pertinence du choix des indicateurs est conditionnée par une compréhension fine des SE, une étude de ceux-ci étant de fait nécessaire préalablement à leur mesure. Le cadre conceptuel de cette étude a été dessiné par Kremen (2005) qui propose de (1) identifier les fournisseurs (espèces, entités, etc.) de SE, (2) déterminer l'influence de la structure des communautés sur le fonctionnement des écosystèmes, (3) étudier les facteurs environnementaux qui ont une influence majeure sur la production de SE, et (4) mesurer l'échelle spatio-temporelle à laquelle les SE, ainsi que leurs fournisseurs, agissent.

Ainsi, des quantifications de SE ont régulièrement été réalisées, à une échelle pouvant être locale comme globale (voir par exemple Kremen *et al.*, 2002; Naidoo *et al.*, 2008). De même, la valeur économique des bénéfices que l'Homme retire des SE a également pu été estimée pour divers SE et à des échelles variées (voir par exemple Costanza *et al.*, 1997; Barbier *et al.*, 2011).

Parce que les indicateurs les plus pertinents de production des SE ne sont pas toujours facilement mesurables, des substituts (« *proxies* » en anglais) sont régulièrement employés. Les types d'occupation ou d'utilisation des sols sont par exemple souvent utilisés pour rendre compte de la production de certains SE, chaque type se voyant attribuer une valeur moyenne de production du SE en question (cas du stockage de carbone; voir Naidoo *et al.*, 2008). Or, certains substituts ne présentent qu'une correspondance partielle, tant d'un point de vue qualitatif (patrons de répartition) que quantitatif (ordre de grandeur et variabilité) avec les données primaires qu'ils sont censés représenter (Figure 1.3). Ceci peut avoir des répercussions importantes, notamment dans le cadre de l'étude des relations entre SE multiples (Eigenbrod *et al.*, 2010).

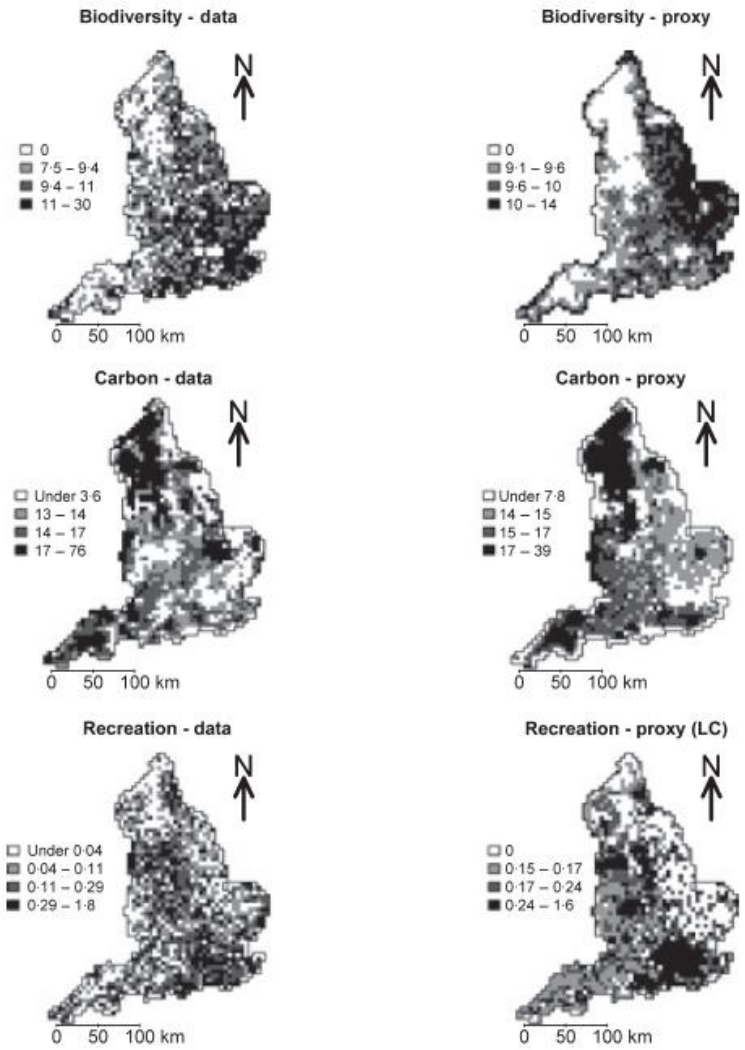

Figure 1.3. Distribution de SE en Angleterre à partir de données primaires ou de substituts (d'après Eigenbrod *et al.*, 2010)

1.1.3 Etude des relations entre SE

Dès lors qu'au moins deux SE ont été mesurés par le biais d'indicateurs ou de substituts, il est possible d'en étudier les relations. La nature de ces relations, si tant est qu'il y en ait, diffère selon la dimension spatiale (ponctuelle vs. étendue, autrement dit au niveau de parcelles de mesure vs. sur des zones plus étendues) et temporelle (statique vs. dynamique) de l'étude. Selon les cas, ces relations peuvent être alternativement des corrélations, congruences/divergences ou synergies/trade-offs (Figure 1.4).

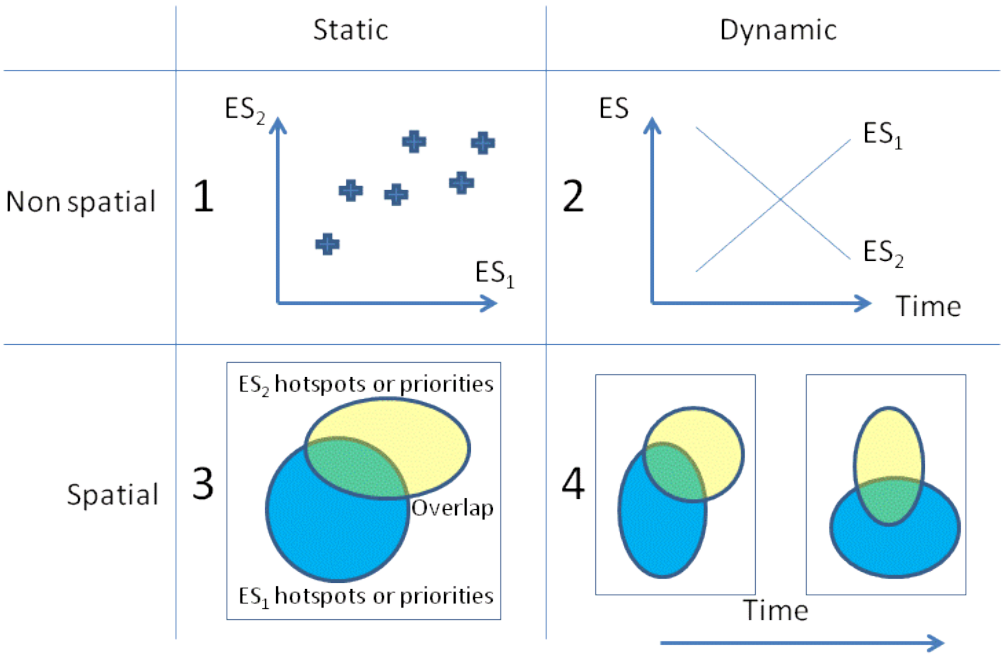

Figure 1.4. Quatre approches pour l'étude des relations entre services : (1) Corrélation entre services; (2) Synergies et trade-offs entre services dans le temps; (3) Congruence ou divergence spatiale entre service; (4) Synergies et trade-offs entre services dans le temps et l'espace (Locatelli, 2013)

L'étude des congruences/divergences spatiales entre SE se fait souvent en examinant le chevauchement (« *overlap* ») des zones présentant, pour les distributions respectives, les plus hautes valeurs de production de SE (« *hotspots* »). On parlera de congruence (divergence) spatiale entre les SE X et Y quand le chevauchement des zones à la fois « *hotspots* » de X et de Y sera supérieur (inférieur) au chevauchement attendu, c'est-à-dire celui de « *hotspots* » de SE aux distributions spatiales aléatoires.

Il y a interaction entre SE lorsque plusieurs SE sont sensibles aux variations d'un même paramètre extérieur (par exemple, une augmentation de la température), ou bien que des changements dans la production d'un SE modifient celle de SE tiers. Ces interactions sont appelées synergies si les productions de SE augmentent conjointement, et trade-offs si elles évoluent en sens contraire (Raudsepp-Hearne *et al.*, 2010). Si la présence (ou absence) de corrélations et congruences n'implique pas qu'il y ait interaction entre les SE concernés, des synergies/trade-offs entre SE témoignent *a contrario* d'une interaction entre ceux-ci.

Le type de relation entre SE (l'absence de relation en faisant partie) dépend bien évidemment des services étudiés. Ainsi, il existe souvent des trade-offs entre les services d'approvisionnement et ceux de régulation ou culturels (Raudsepp-Hearne *et al.*, 2010). Mais alors, comment expliquer que pour une même paire de SE, les relations puissent être différentes ? Cela peut notamment provenir du fait, comme expliqué précédemment, que les SE sont mesurés par le biais d'indicateurs ou de « *proxies* ». La congruence entre SE peut ainsi être différente selon que l'on a utilisé, pour les mesurer, des données primaires ou des « *proxies* » (Eigenbrod *et al.*, 2010). De même, les dimensions spatiales et temporelles ont une influence prépondérante dans la nature de la relation entre SE (Figure 1.5), et des conclusions différentes peuvent par exemple être tirées en fonction du site d'étude (par exemple, Sud-Est vs. Nord-Ouest du Royaume-Uni; Anderson *et al.*, 2009), de l'échelle de travail (par exemple, Bornéo vs. toute l'Indonésie; Murray *et al.*, 2015) ou encore de la résolution temporelle de l'étude (par exemple, un mois ou un an pour l'étude du service de protection du littoral; Koch *et al.*, 2009).

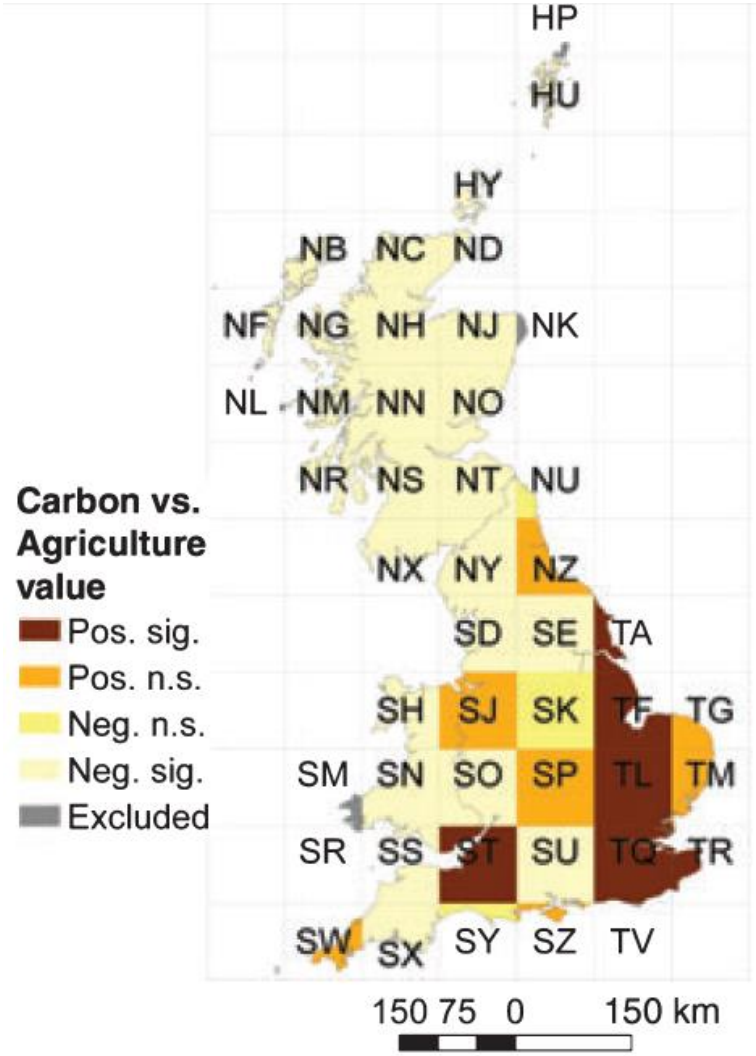

Figure 1.5. Relation entre stockage de carbone et valeur des produits agricoles en fonction de la région (d'après Anderson *et al.*, 2009). L'étude de cette relation dans deux régions pourtant voisines (par exemple « SU » et « TQ ») peut conduire à des conclusions opposées.

La nature des relations entre des SE multiples peut influencer la teneur de politiques de gestion des ressources naturelles ou encore l'aménagement du territoire. On comprend dès lors les conséquences potentiellement délétères qu'une quantification erronée des SE pourrait avoir sur les ressources naturelles.

1.1.4 Biodiversité et SE

Si la biodiversité ne peut être considérée comme un SE en soi, ses diverses composantes influencent la production de SE de façon complexe et variée (Figure 1.2, Tableau 1.1). Ainsi, certaines composantes de la biodiversité peuvent directement être utilisées comme « biens écosystémiques » (par exemple, fruits et bois d'œuvre) alors que d'autres influencent des services tels que la régulation des régimes hydriques (Diaz *et al.*, 2006). La perte de biodiversité constatée actuellement aura des répercussions sur le fonctionnement des écosystèmes (Cardinale *et al.*, 2012), et par voie de conséquence sur le bien-être des populations qui en dépendent (Diaz *et al.*, 2006).

Tableau 1.1. Exemple de SE dont la production est influencée de façon complexe et variée par des composantes de la biodiversité (d'après Diaz *et al.*, 2006)

Ecosystem Services	Main Components of Diversity Involved and Mechanisms That Produce the Effect
Regulation through carbon sequestration in the biosphere of climatic conditions suitable to humans and the animals and plants they consider important	*** Arrangement and size of landscape units—Carbon loss is higher at forest edges, therefore as forest fragments decline in size or area/perimeter ratio, a larger proportion of the total landscape is losing carbon.
	** Functional composition—Small, fast-growing, fast-decomposing, short-lived plants retain less carbon in their biomass than large, slow-growing, slow-decomposing, long-lived plants.
	* Number of species—High number of species can slow down the spread of pests and pathogens, which are important agents of carbon loss from ecosystems.

Asterisks indicate importance and/or degree or certainty (*** > ** > *) of the link between the ecosystem service in question and different components of biodiversity. Biodiversity components refer to plant assemblages unless otherwise specified. The putative mechanisms have been empirically tested in some cases, but remain speculative in others (modified from [3]). The list of ecosystem services is illustrative, rather than exhaustive.
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1.2 Les forêts tropicales et les services écosystémiques associés

1.2.1 Les forêts tropicales : contexte et enjeux

Les forêts tropicales, qui couvrent moins de 10% de la surface des terres émergées (Lewis, 2006), ne forment pas un ensemble homogène. Il existe plusieurs types de forêts tropicales : les forêts tropicales humides, les forêts tropicales de mousson, et enfin les forêts tropicales sèches (Figure 1.6). Aux forêts tropicales s'ajoutent, dans la zone intertropicale (c'est-à-dire entre les tropiques du Cancer et Capricorne situés à environ 23° de latitude Nord et Sud, respectivement), d'autres types de végétation naturelle, tels les savanes herbeuses ou arborées. Au sein de la zone intertropicale, la discrimination entre les différents types de végétation naturelle est en grande partie liée aux différences de conditions climatiques (température et précipitations, tant leurs valeurs annuelles que leurs variations au cours de l'année, mais aussi durée/intensité de la saison sèche).

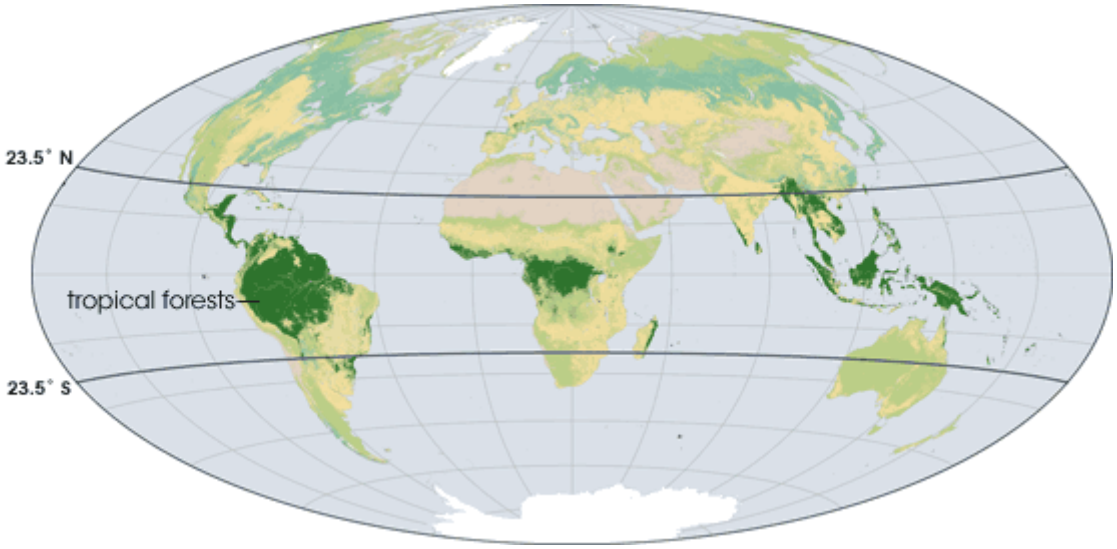

Figure 1.6. Répartition spatiale des forêts tropicales. L'image provient d'une classification de l'occupation des sols réalisée à partir d'images MODIS
(Source : http://earthobservatory.nasa.gov/Features/Deforestation/)

Les recherches se sont en premier lieu concentrées sur les forêts tropicales du fait de la biodiversité importante et originale qu'elles renferment. Une étude récente estime que les forêts tropicales comptent entre 40 000 et 53 000 espèces d'arbres (Slik *et al.*, 2015). En comparaison, il n'y a que 124 espèces d'arbres dans l'ensemble des forêts tempérées d'Europe (Latham & Ricklefs, 1993).

Depuis 10 ans, la nécessité de préserver les forêts tropicales a pris un nouveau tournant. En effet, les importants stocks de carbone qu'elles renferment, tant dans leurs sols (Lal, 2005) que dans la biomasse aérienne (Pan *et al.*, 2011), font des forêts tropicales l'une des composantes clé des stratégies d'atténuation du changement climatique. Afin de réduire les

émissions de gaz à effet de serre liées à la déforestation qui touche les forêts tropicales, les Nations-Unies ont créé en 2005 le programme REDD (devenu depuis REDD+), qui vise à « Réduire les Emissions liées à la Déforestation et à la Dégradation de la forêt ». Preuve de l'effort investi dans l'estimation des stocks de carbone contenus dans les forêts tropicales, plusieurs cartes pantropicales de biomasse – le carbone représentant environ 47% de la masse sèche de biomasse (McGroddy *et al.*, 2004) – sont à présent disponibles (Saatchi *et al.*, 2011; Baccini *et al.*, 2012).

Si les forêts tropicales sont intrinsèquement des puits de carbone (Lugo & Brown, 1992; Lewis *et al.*, 2009), on envisage désormais le biome « forêt tropicale » comme une source de carbone, dès lors que l'on tient compte des émissions brutes liées à la déforestation (Pan *et al.*, 2011). Ainsi, la déforestation qui touche les forêts tropicales (Figure 1.7) et parmi les multiples causes de laquelle figurent notamment l'expansion de l'agriculture et l'extraction non-encadrée de bois (Vitousek, 1994; Geist & Lambin, 2002), est une menace tant pour la conservation de la biodiversité que la protection des stocks de carbone.

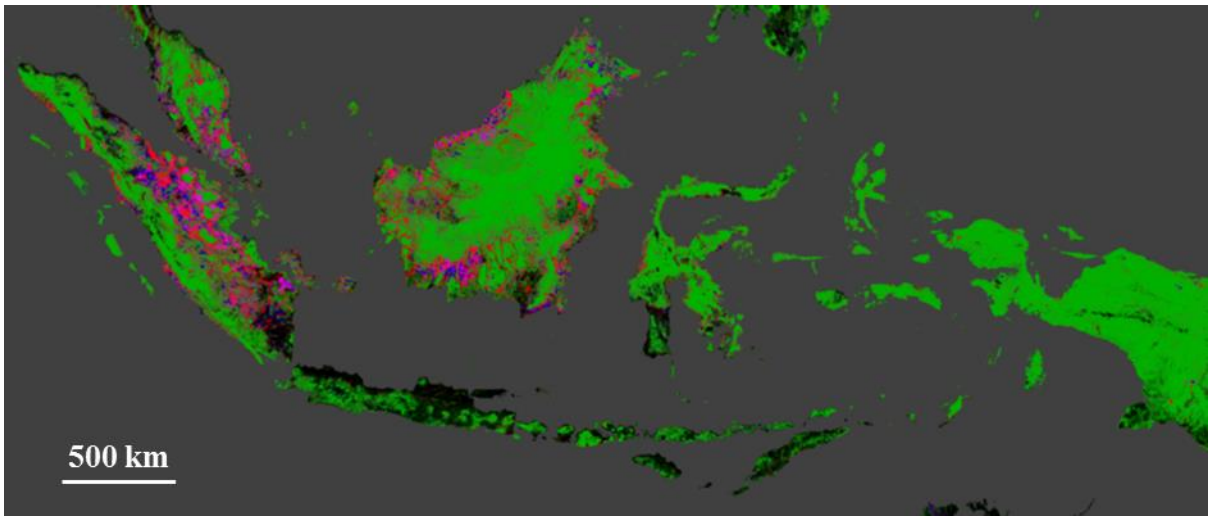

Figure 1.7. Evolution du couvert forestier entre 2000 et 2013 ; cas de l'Indonésie (d'après Hansen *et al.*, 2013). Les étendues de forêt qui n'ont pas été modifiées durant la période sont en vert, celles perdues en rouge, celles gagnées en bleu, et celles où il y a eu à la fois perte et gain durant la période en mauve.

1.2.2 Autres SE fournis par les forêts tropicales

Outre l'atténuation du changement climatique, SE à l'échelle d'action globale, les forêts tropicales jouent également un rôle crucial à l'échelle régionale dans la régulation des régimes hydriques, par la prévention des crues en saison humide ou le soutien des débits d'étiage en saison sèche (Myers, 1997).

Parmi les autres SE d'importance fournis par les forêts tropicales figure notamment le contrôle de l'érosion des sols. Les conséquences de l'érosion des sols sont multiples, tant localement que de façon plus diffuse dans l'espace, et incluent par exemple la hausse des

rejets de CO_2 dans l'atmosphère, la baisse de la qualité de l'eau ou la sédimentation des réservoirs (Lal, 2003; Millennium Ecosystem Assessment, 2005; Morgan, 2005).

Les SE dont peuvent bénéficier les populations vivant à la périphérie ou dans les forêts tropicales (ce que l'on considère comme des services « locaux ») comprennent par exemple l'approvisionnement en produits forestiers ligneux (bois d'œuvre, bois de chauffage, etc.) et non ligneux (champignons, baies, graines, etc.), en viande de brousse, la lutte contre les pestes biologiques ou encore la beauté des paysages (Myers, 1997; Locatelli *et al.*, 2014).

1.3 Caractéristiques de la zone d'étude

1.3.1 Bornéo

Les forêts d'Asie du Sud-Est en général, et celles de Bornéo en particulier, n'ont pas été épargnées durant les dernières décennies par la déforestation (Figure 1.8). Si l'île restait en 2010 toujours couverte pour moitié par des forêts, la moitié de celles-ci pouvant être considérées comme naturelles (Gaveau *et al.*, 2014), les dernières tendances ne semblent pas indiquer une inflexion du rythme de perte des forêts naturelles (Margono *et al.*, 2014).

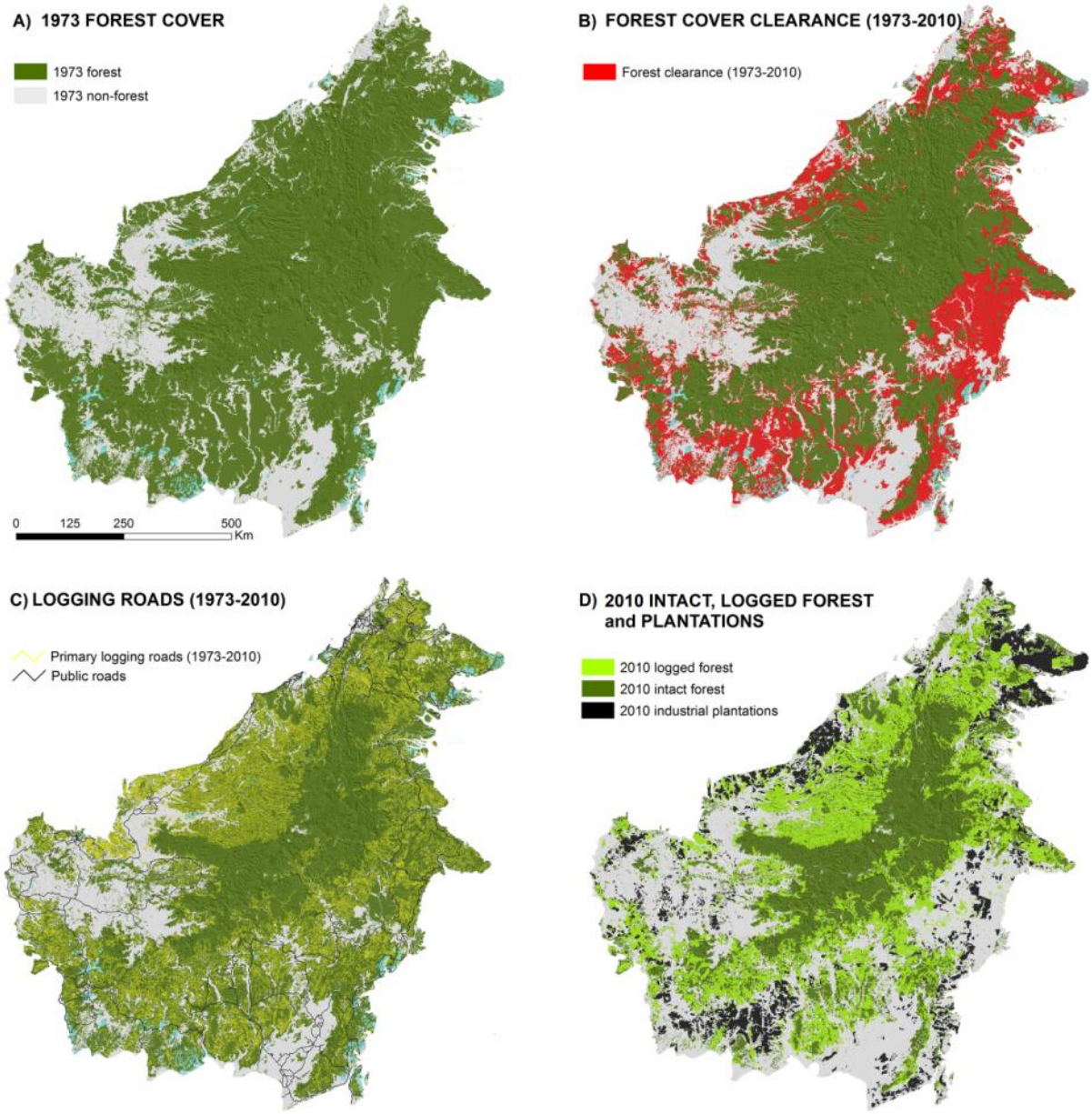

Figure 1.8. Bornéo a connu une déforestation importante sur la période 1973-2010, la couverture forestière sur l'île ayant diminué de 30% en l'espace d'environ 40 ans (Gaveau *et al.*, 2014).

Si l'intégralité des forêts de Bornéo est classée comme « forêts tropicales humides », il existe cependant de multiples types de forêts différents sur l'île. On y trouve notamment des forêts de plaine, de colline, de montagne mais aussi des forêts sur tourbe, sur sable blanc, sur sol calcaire ainsi que des forêts marécageuses et des mangroves (Whitmore, 1984).

1.3.2 Kapuas Hulu

L'étude a été réalisée à Kapuas Hulu, régence située dans la province de Kalimantan Ouest, en Indonésie (la régence, elle-même divisée en districts, étant l'échelon administratif directement sous celui de la province ; Figure 1.9). La majeure partie des quelques 31 000 km² que compte Kapuas Hulu est toujours couverte de forêts. A travers la régence, dont le climat est de type « tropical humide » (Köppen, 1936), l'altitude varie entre 0–2000 m (Jarvis *et al.*, 2008), les précipitations annuelles entre 2350–4300 mm, et les températures annuelles entre 17–27 °C (Hijmans *et al.*, 2005). Les sols se sont développés principalement à partir de roches sédimentaires (Noya *et al.*, 1993) et appartiennent en majorité aux ordres Ultisols, Inceptisols et Histosols (ISRIC – World Soil Information, 2013).

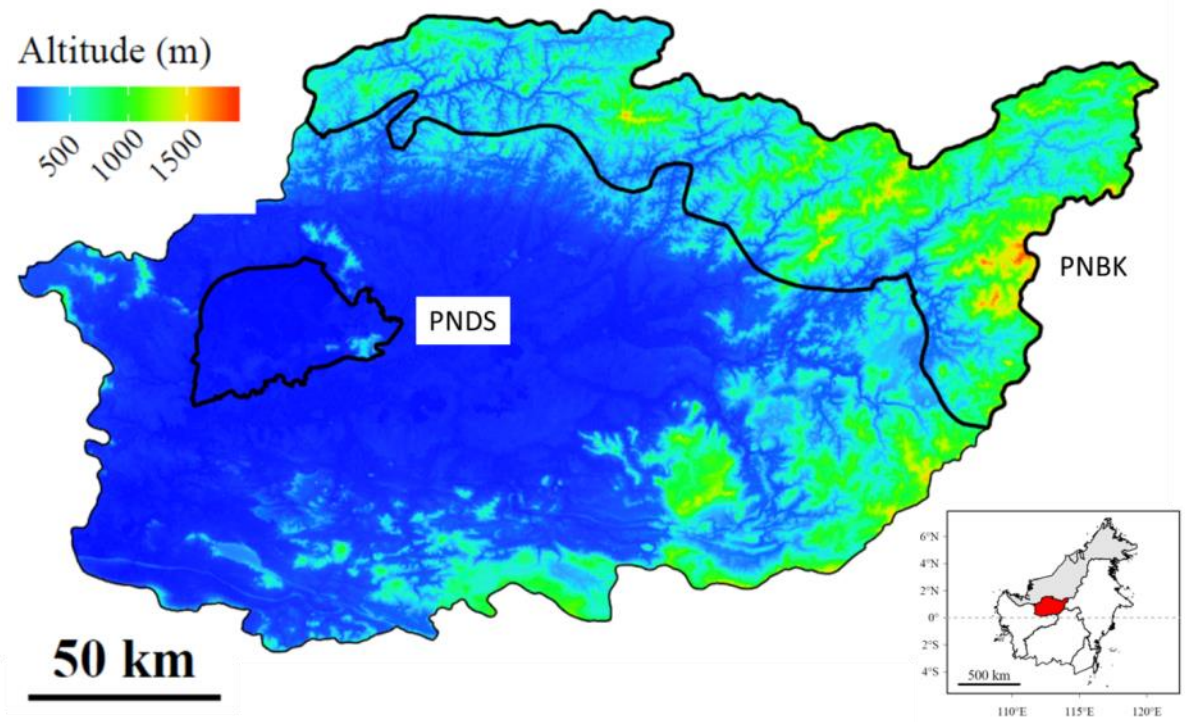

Figure 1.9. Topographie de la zone d'étude. Sont également représentés les deux parcs nationaux présents à Kapuas Hulu : le parc national Betung Kerihun (PNBK), et le parc national Danau Sentarum (PNDS).

Deux parc nationaux couvrent près de 30% de la surface de la régence : le parc national Betung Kerihun (PNBK) au nord-est, qui comporte une variété de types de forêts allant des forêts de plaine à celles de montagne, et le parc national Danau Sentarum (PNDS) au centre-ouest, un système hydrologique unique et complexe qui régule les régimes hydriques de la rivière Kapuas voisine et dans lequel sont présentes des forêts marécageuses, des forêts sur

tourbe ou encore des forêts riveraines. Suite à un décret de l'administration locale édicté en 2003, Kapuas Hulu a été déclarée « régence de conservation », soulignant la volonté d'y pratiquer une gestion raisonnée des ressources naturelles afin que soit préservée la fonctionnalité des écosystèmes (Shantiko *et al.*, 2013). Les forêts sur tourbe et plus généralement les forêts naturelles sont depuis 2011, à Kapuas Hulu comme dans le reste de l'Indonésie, protégées par un moratoire y interdisant l'attribution de nouvelles concessions pour leur exploitation forestière ou leur conversion en plantations, mais celui-ci ne couvre pas les concessions attribuées avant l'entrée en vigueur du moratoire (Sloan *et al.*, 2012).

1.4 Objectifs de la thèse et plan du manuscrit

Cette thèse porte sur l'analyse de la diversité d'espèces ligneuses (DEL) et de deux services écosystémiques (atténuation du changement climatique via stockage de carbone, contrôle de l'érosion des sols) à plusieurs échelles parmi celles locale, régionale et globale (Figure 1.10). L'objectif général de la thèse est d'aboutir à une meilleure compréhension de la distribution spatiale de la DEL et de deux services écosystémiques d'intérêt dans la zone d'étude, ainsi que d'approfondir les connaissances sur les relations qui existent entre eux.

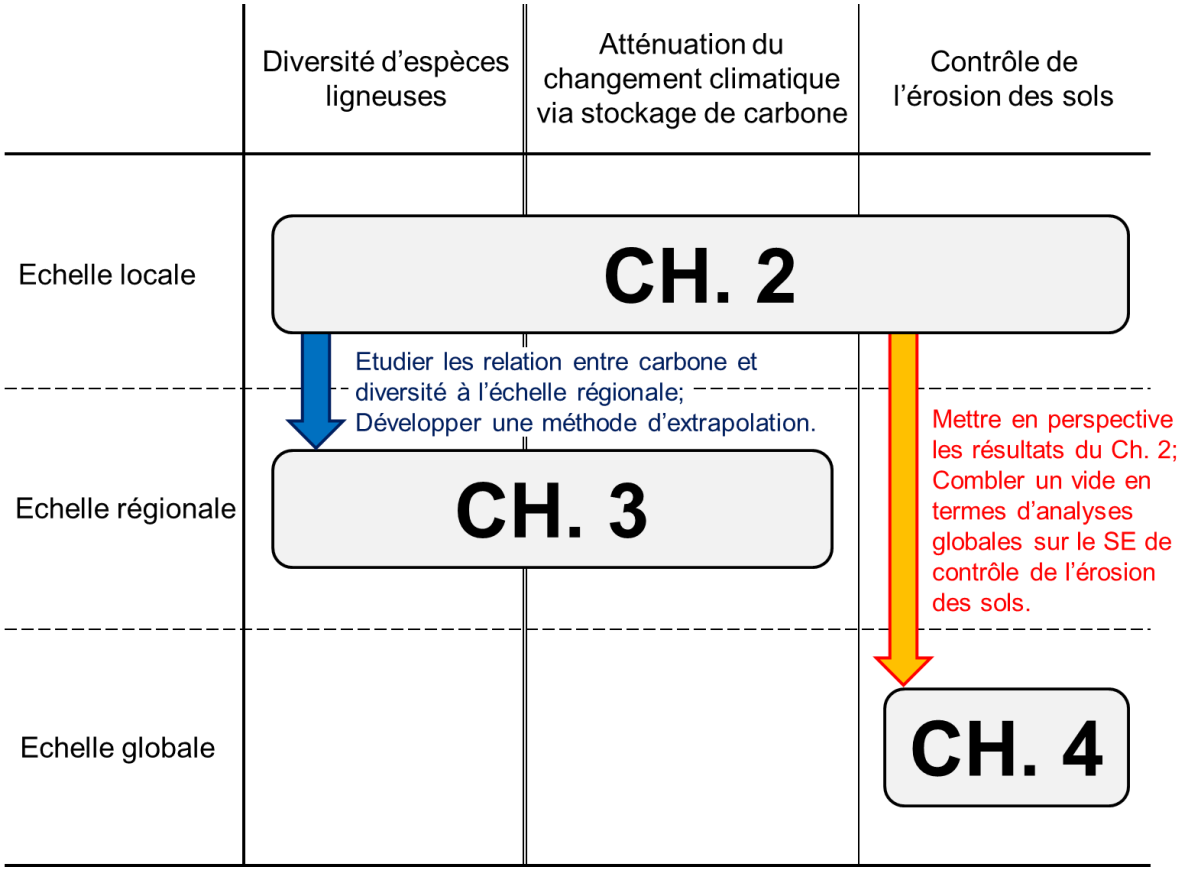

Figure 1.10. Plan schématique du manuscrit. Chacun des trois chapitres suivants (CH. 2 à CH. 4) aborde un ou plusieurs services ainsi qu'éventuellement la DEL à une échelle donnée.

Pour atteindre l'objectif principal, nous nous sommes notamment appuyés sur un échantillonnage stratifié des principaux types de végétation présents à Kapuas Hulu, à partir d'une carte au 1 : 50 000 réalisée dans le cadre du projet CoLUPSIA (« *Collaborative Land-Use Planning and Sustainable Institutional Arrangements* ») et qui utilise des images Landsat et SPOT (Satellite Pour l'Observation de la Terre) pour définir, notamment par le biais de la photo-interprétation, plus de 40 classes de végétation sur l'ensemble de la zone d'étude (Figure 1.11).

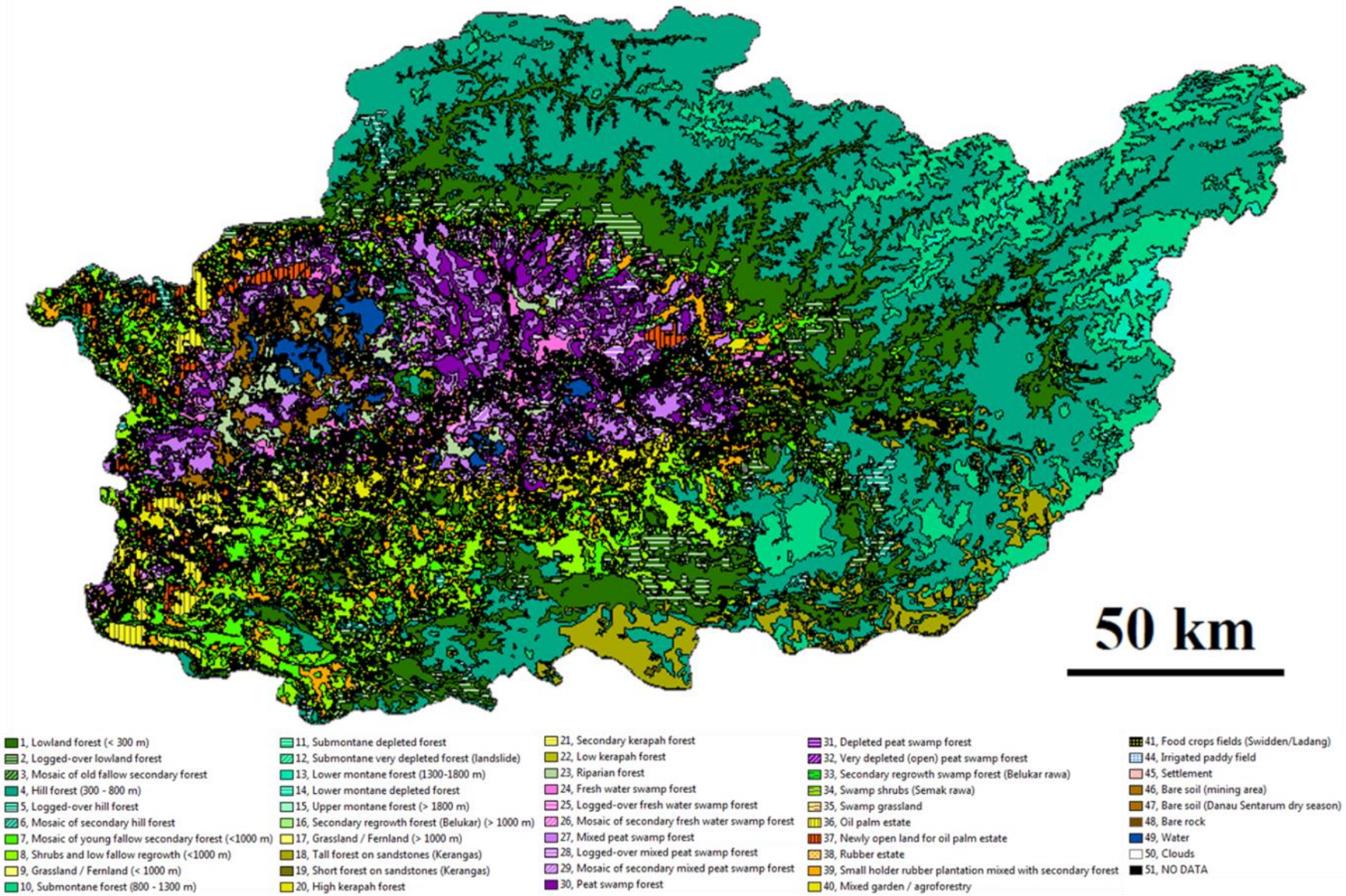

Figure 1.11. Carte de végétation du projet CoLUPSIA (données disponibles sur : http://www1.cifor.org/colupsia/home.html)

Dans le second chapitre, nous nous attachons à évaluer les niveaux de services écosystémiques produits par, et diversité d'espèces ligneuses abritée dans différents types d'occupation ou d'utilisation des sols au voisinage d'un village dont les moyens de subsistance sont liés à l'agriculture sur brûlis et la culture de l'hévéa (échelle locale). Nous cherchons à évaluer la façon dont les services écosystémiques et la diversité d'espèces ligneuses sont distribués au sein du paysage. Nous faisons l'hypothèse que, bien qu'à des niveaux moindres que dans le cas de milieux naturels, certains milieux perturbés par les activités anthropiques peuvent continuer de produire des SE et abriter une DEL dans des proportions relativement importantes.

Dans le troisième chapitre, nous élaborons des modèles régionaux de distribution de carbone (à la fois dans la biomasse aérienne et le sol) et de diversité d'espèces ligneuses, à partir d'inventaires botaniques et pédologiques réalisés sur l'ensemble de Kapuas Hulu (échelle régionale). Nous souhaitons, à l'aide des prédictions de nos modèles, discuter de la nature des relations spatiales qui existent entre carbone et diversité d'espèces ligneuses, et des stratégies qui pourraient conduire à la préservation de leurs « *hotspots* ». Nous faisons l'hypothèse que les zones d'importance pour la DEL et le carbone ne coïncident que partiellement au niveau de la zone d'étude, mais qu'il est possible d'optimiser la protection de la DEL et du carbone (tant celui de la biomasse aérienne que du sol) en choisissant des stratégies de conservation appropriées.

Dans le quatrième chapitre, nous conduisons une revue systématique des données de pertes de sol disponibles à l'échelle des tropiques humides (échelle globale) afin de synthétiser quantitativement l'influence du couvert végétal dans le contrôle de l'érosion des sols. Nous voulons, par le biais d'une classification fine des types d'utilisation des sols et de la végétation associée, obtenir une compréhension des éléments cruciaux dans le contrôle de l'érosion des sols, ce qui permettrait de proposer des mesures de conservation. Nous faisons l'hypothèse que le SE de contrôle de l'érosion des sols est fourni dès lors que le couvert végétal est suffisamment développé et ce, qu'importe le type d'occupation ou d'utilisation des sols.

Dans le cinquième chapitre, nous synthétisons les résultats des trois précédents chapitres et proposons différentes pistes de réflexion permettant de continuer à valoriser les travaux présentés.

Une conclusion générale du manuscrit fait office de sixième chapitre.

Note à l'attention du lecteur : les chapitres deux, trois et quatre ont été publiés ou soumis sous forme d'articles à des revues à comité de lecture. Il se peut qu'il y ait donc des redites, notamment dans les introductions des différents articles. La succession des chapitres ne suit pas la chronologie de publication des articles. Nous avons souhaité, par souci de cohérence, développer les chapitres du manuscrit selon une échelle d'étude croissante, en commençant par l'échelle locale, puis régionale et enfin globale, alors que la revue systématique (échelle globale) a été écrite en premier, suivie de l'article sur la production de SE dans le paysage (échelle locale) et enfin de celui traitant des distributions spatiales de SE sur l'ensemble de Kapuas Hulu (échelle régionale).

Chapitre 2

Services écosystémiques et biodiversité dans un paysage du nord de Bornéo en rapide mutation

Contexte de l'étude

Comme nous l'avons mentionné dans l'introduction, certains « *proxies* », bien que régulièrement utilisés pour évaluer la production de SE, ne présentent qu'une correspondance partielle avec les données primaires qu'ils sont censés représenter.

Afin d'estimer la pertinence du type d'occupation ou d'utilisation des sols comme « *proxy* », nous nous sommes attachés, au cours de l'étude suivante, à évaluer la diversité d'espèces ligneuses ainsi que la production de deux services écosystémiques (contrôle de l'érosion des sols, et atténuation du changement climatique via stockage de carbone dans les sols et la biomasse aérienne) dans différents types d'occupation ou d'utilisation des sols.

Nous avons travaillé dans les environs immédiats d'un village du nord de Bornéo dont les moyens de subsistance sont liés à l'agriculture itinérante sur brûlis et la culture de l'hévéa. Ce village a été choisi pour la diversité de types d'occupation ou d'utilisation des sols présents dans un périmètre relativement restreint : forêt naturelle, forêt post-exploitation, recrû secondaire, jardins à hévéa, champs de cultures vivrières (Figure 2.1).

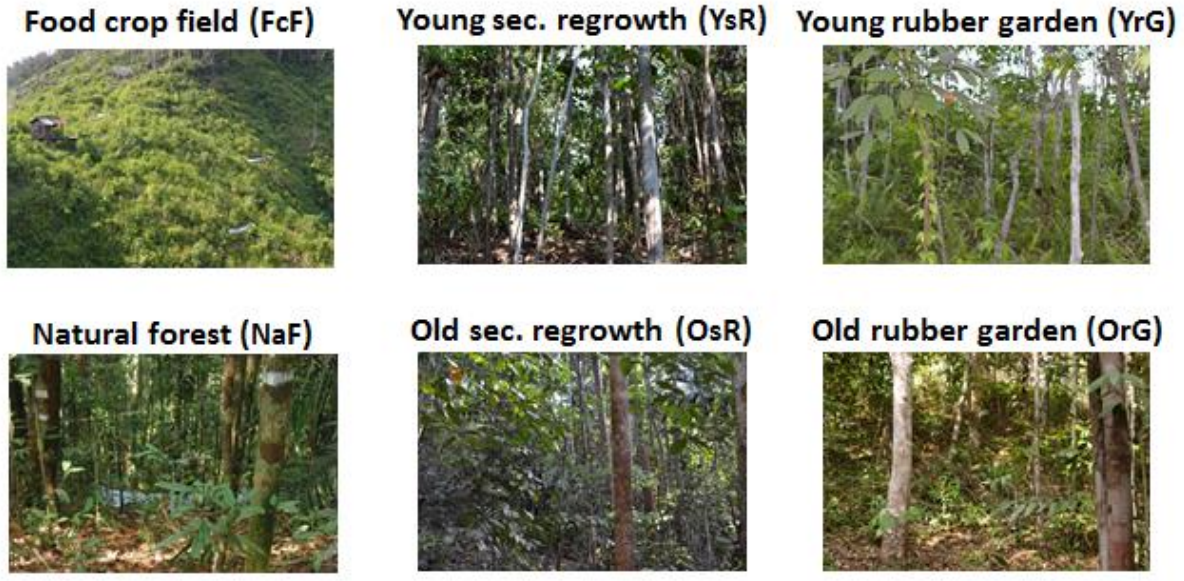

Figure 2.1. Types d'occupation ou d'utilisation des sols étudiés dans les environs de Keluin. Les forêts post-exploitation ne sont pas représentées, faute de photos.

Suivant des procédures standards, nous avons échantillonné la végétation dans les différents types d'occupation ou d'utilisation des sols (mesure du diamètre à hauteur de poitrine, estimation de la hauteur, récolte de feuilles pour identification). Nous avons ainsi pu déterminer, pour chaque parcelle de végétation, les densités de carbone contenues dans la biomasse aérienne, de même que la diversité d'espèces ligneuses.

Nous avons également établi un réseau de parcelles de mesure des pertes de sol. Environ 5 mètres en contrebas de rondins de bois placés sur une pente de 40%, nous avons disposé un géotextile (textile de taille de maille déterminée laissant passer l'eau mais pas les particules de sol) sur une largueur de 4 m en travers de la pente (Figure 2.2). Les textiles ont été nettoyés tous les mois pendant près de 2 ans, ce qui nous a permis de déterminer pour chacune parcelle un taux annuel d'érosion. Aux abords de ces parcelles, nous avons également collecté des échantillons de sol afin de déterminer les densités de carbone contenues dans les sols (0–20 cm).

Figure 2.2. Différentes étapes de la mise en place des parcelles de suivi des pertes de sol (© Imam Basuki)

L'un des buts de cette étude était notamment de voir si les valeurs mesurées (densités de carbone dans la biomasse aérienne et dans les sols, diversité d'espèces ligneuses, pertes de sol) sont homogènes au sein de chaque type d'occupation ou d'utilisation des sols. Il s'agit d'une condition nécessaire pour que le type d'occupation ou d'utilisation des sols puisse être considéré comme un « *proxy* » adéquat à l'échelle locale.

De plus, nous voulions également tester l'hypothèse suivante :
« Les milieux naturels produisent plus de SE et abritent une DEL plus importante que les milieux perturbés par les activités anthropiques. Cependant, certains milieux perturbés peuvent continuer de produire des SE et abriter une DEL dans des proportions relativement importantes. »

Ecosystem services and biodiversity in a rapidly transforming landscape in Northern Borneo

Article under review in PLOS ONE (first decision: minor corrections)

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Résumé

Alors que l'agriculture industrielle continue son expansion en Asie du Sud-Est aux dépens des forêts naturelles et des systèmes traditionnels liés à l'agriculture itinérante sur brûlis, il est nécessaire de comparer la biodiversité présente dans, et les services écosystémiques fournis par, ces systèmes traditionnels d'agriculture par rapport aux monocultures afin d'orienter la prise de décision en matière d'aménagement du territoire. Focalisant sur la diversité d'espèces ligneuses, le contrôle de l'érosion des sols et l'atténuation du changement climatique via stockage de carbone, nous avons échantillonné la végétation et suivi les pertes de sol dans des zones sous différents types d'occupation ou d'utilisation des sols au sein d'un paysage agricole du nord de Bornéo. Ce paysage a été façonné par l'agriculture itinérante sur brûlis, la récolte de caoutchouc et l'exploitation forestière, et des perturbations de type et d'intensité diverses y ont créé une fine mosaïque de végétation allant des champs de cultures vivrières à la forêt naturelle. Nous montrons que la diversité d'espèces ligneuses et la production de services écosystémiques sont maximales en forêt naturelle. Quant aux forêts post-exploitation, elles produisent des services semblables à ceux des forêts naturelles. La diversité d'espèces ligneuses et la production de services écosystémiques sont largement supérieures dans les types d'utilisation des sols liés à l'agriculture itinérante sur brûlis que dans les monocultures de palmiers à huile et d'hévéas. Les forêts naturelles et celles post-exploitation devraient être respectivement préservées et gérées comme parties intégrantes du système d'agriculture itinérante sur brûlis, et la multifonctionnalité des paysages recherchée. Etant donné que les forêts naturelles abritent une diversité d'espèces ligneuses unique et produisent des services écosystémiques en grande quantité, protéger leurs stocks de carbone, par exemple par le biais de mécanismes financiers tels que « Réduire les Emissions liées à la Déforestation et à la Dégradation de la forêt » (REDD+), profitera de façon synergétique à la biodiversité et de nombreux services écosystémiques. Cependant, la façon dont de tels mécanismes pourront également profiter aux communautés devra être évaluée attentivement afin de contrer les coûts d'opportunité importants liés à la conversion en monocultures qui peut certes générer des revenus plus conséquents, mais serait néfaste pour la production de bien des services écosystémiques.

Mots-clés

Services écosystémiques
Stockage de carbone
Diversité d'espèces ligneuses
Contrôle de l'érosion des sols
Système lié à l'agriculture itinérante sur brûlis
Agroforêt
Jardin à hévéa
Forêt post-exploitation

Abstract

Because industrial agriculture keeps expanding in Southeast Asia at the expense of natural forests and traditional swidden systems, comparing biodiversity and ecosystem services in the traditional forest–swidden agriculture system vs. monocultures is needed to guide decision making on land-use planning. Focusing on tree diversity, soil erosion control, and climate change mitigation through carbon storage, we surveyed vegetation and monitored soil loss in various land-use areas in a northern Bornean agricultural landscape shaped by swidden agriculture, rubber tapping, and logging, where various levels and types of disturbance have created a fine mosaic of vegetation from food crop fields to natural forest. Tree species diversity and ecosystem service production were highest in natural forests. Logged-over forests produced services similar to those of natural forests. Land uses related to the swidden agriculture system largely outperformed oil palm or rubber monocultures in terms of tree species diversity and service production. Natural and logged-over forests should be maintained or managed as integral parts of the swidden system, and landscape multifunctionality should be sustained. Because natural forests host a unique diversity of trees and produce high levels of ecosystem services, targeting carbon stock protection, e.g. through financial mechanisms such as Reducing Emissions from Deforestation and Forest Degradation (REDD+), will synergistically provide benefits for biodiversity and a wide range of other services. However, the way such mechanisms could benefit communities must be carefully evaluated to counter the high opportunity cost of conversion to monocultures that might generate greater income, but would be detrimental to the production of multiple ecosystem services.

Keywords

Ecosystem services
Carbon storage
Tree species diversity
Soil erosion control
Swidden system
Agroforest
Rubber garden
Logged-over forest

2.1 Introduction

Drastic land-use transformations have occurred in the tropical forest landscapes of Southeast Asia in the past decades, leading to the disappearance of natural forests and the replacement of traditional land-use systems with monoculture plantations. On the island of Borneo, the lowland rainforests are at the crossroads of multiple and divergent interests. While these rainforests are hotspots of biological diversity with a high rate of endemism and hold important carbon stocks, they are also a major source of valuable timber, and are situated on lands that are very suitable for conversion to oil palm or other large industrial plantations (Dixon *et al.*, 1994; Fisher *et al.*, 2011; Saatchi *et al.*, 2011).

Since the late 1960s, logging has affected most of the lowland forests (Brookfield & Byron, 1990), and following the logging boom era that lasted roughly until the 2000s, large areas of logged-over forest were left unmanaged. Although several studies demonstrated the important role that these forests play in supporting biodiversity and maintaining multiple ecosystem services (Meijaard *et al.*, 2005; Berry *et al.*, 2010; Edwards *et al.*, 2011; Putz *et al.*, 2012), these forests were slowly depleted through illegal logging and finally converted to oil palm plantations (Carlson *et al.*, 2013). The detrimental effect of such large-scale land clearing on biodiversity and other services is an accepted premise (Aratrakorn *et al.*, 2006; Fitzherbert *et al.*, 2008; Koh & Wilcove, 2008; Savilaakso *et al.*, 2014). At the same time, as the extent of industrial agricultural areas keeps increasing, the role of traditional agricultural systems (smallholder agroforestry and swidden, ie slash-and-burn and rotational fallow farming, systems) vs. alternative agricultural systems in providing goods and services has received much attention (Dove, 1993; Michon & de Foresta, 1995; de Jong, 1997; Sodhi *et al.*, 2010). To date, however, there has been little consensus about their role in supporting biodiversity and producing ecosystem services.

Since negative correlations usually exist between goods and services (e.g. Naidoo *et al.*, 2008; Raudsepp-Hearne *et al.*, 2010), human-modified land-use areas would not be expected to produce levels of services similar to those of natural forests. Yet, in Sumatra, under low management intensity conditions, mature rubber gardens were found to have a plant species richness similar to that of nearby natural or secondary forests and to store substantial amounts of carbon in aboveground biomass (Michon & de Foresta, 1995; Penot, 2004). Swidden fallows were also shown to reduce soil erosion and contribute to soil nutrient cycling to levels similar to those found in natural forests (Bruijnzeel, 2004; Bruun *et al.*, 2006; Sidle *et al.*, 2006). In contrast, studies in West Kalimantan found that an increasing number of shifting cultivation cycles naturally led to a decrease in tree species richness and important tree composition changes (Lawrence, 2004). Some argue that such human-modified land use will not allow any long-term conservation goal to be fulfilled, partly because maintaining tree diversity might hinder rubber garden productivity (Lawrence, 1996). Overall, despite current debates about the capacity of human-modified landscapes to protect biodiversity and support ecosystem services, these landscapes are getting increasing attention for their contribution to

biodiversity conservation in the global context of vanishing natural habitats (Chazdon *et al.*, 2009; Gardner *et al.*, 2009).

Research gaps concerning the effect of land-use changes on the ecosystem services produced by swidden systems have been identified through a systematic review currently under progress that aims to bring unbiased evidence to the debate (Dressler *et al.*, 2015). While demand for food and goods is growing worldwide, and biodiversity and services are being lost (Millennium Ecosystem Assessment, 2005), such information is essential to building sound land management strategies and guiding decision making on land-use planning.

In this study, we address the following question: What level of biodiversity and ecosystem services are found in the different land uses related to the traditional forest–swidden agriculture system? We conducted a case study from a northern Bornean agricultural landscape where we quantitatively estimated the contribution of various land uses to: (1) climate change mitigation through carbon storage in live aboveground biomass and topsoil, (2) tree species diversity, and (3) soil erosion control. The two services were chosen because of their relevance for multiple beneficiaries at different scales (local to regional for soil erosion control, and global for climate change mitigation). Tree species diversity, which we did not consider as an ecosystem service *per se*, was chosen because of its cross-cutting and cross-scale nature, as it jointly influences the delivery of goods (e.g. food, raw material, fruit, and timber for local people) and services (e.g. water regulation at the regional scale) (Diaz *et al.*, 2006).

2.2 Materials and Methods

2.2.1 Ethics statement

This study strictly complied with Indonesian laws. Authorizations to carry out research activities were obtained from appropriate sources both at national (Ministry of Forestry and Ministry of State for Research and Technology) and local level (Head of Kapuas Hulu regency). Permissions from local owners to work on their lands were obtained prior to any activity. Sending soil and herbarium samples from the field site to laboratories in Java for further analysis was done after authority approval. We did not collect endangered plants or any animals.

2.2.2 Study site and plot selection

Field work was carried out in the surroundings of Keluin (1°08'57" N, 112°15'37" E), a village located in the district of Batang Lupar, Kapuas Hulu regency, West Kalimantan province, Indonesia (Figure 2.3). This village is located near a river flowing directly toward the Danau Sentarum National Park, a very complex hydrological system that regulates the hydrological regime of the Kapuas River (the longest river in Borneo, which supplies water to the West Kalimantan capital city of Pontianak) (MacKinnon *et al.*, 1996). Altitude in the study area ranges from 50 to 450 m above sea level (Jarvis *et al.*, 2008). Soils have developed over sedimentary rocks (Noya *et al.*, 1993) and belong mostly to the Ultisols order (Hikmatullah *et al.*, 2007). Mean annual rainfall is 3300 mm (WorldClim data, interpolated estimate for the 1950−2000 period with a 30 arc-second resolution; Hijmans *et al.*, 2005). The study area has a tropical rainforest climate with a drier period from June to August, but monthly rainfall is highly variable throughout the year.

This site was chosen because of the diversity of land uses representative of northern Bornean traditional agricultural systems that were found within a limited perimeter (ca. 2 km W–E by 5 km N–S). Traditionally, the main crop, rice, is cultivated along with other annual crops (such as cassava, maize, etc.) in swiddens from either primary or secondary forest clearing before the plot is abandoned after 1−2 years of cultivation. Rubber seedlings and saplings, which are planted in some crop fields during the cultivation phase or just after plot abandonment, eventually lead to rubber-based secondary forests (also called “jungle rubber” gardens) as a result of plant succession. Past and current uses of land by the local community (swidden agriculture system mixed with rubber gardens) and past logging activities have created a mosaic of vegetation reflecting various disturbance types, ages and intensities in the Keluin area.

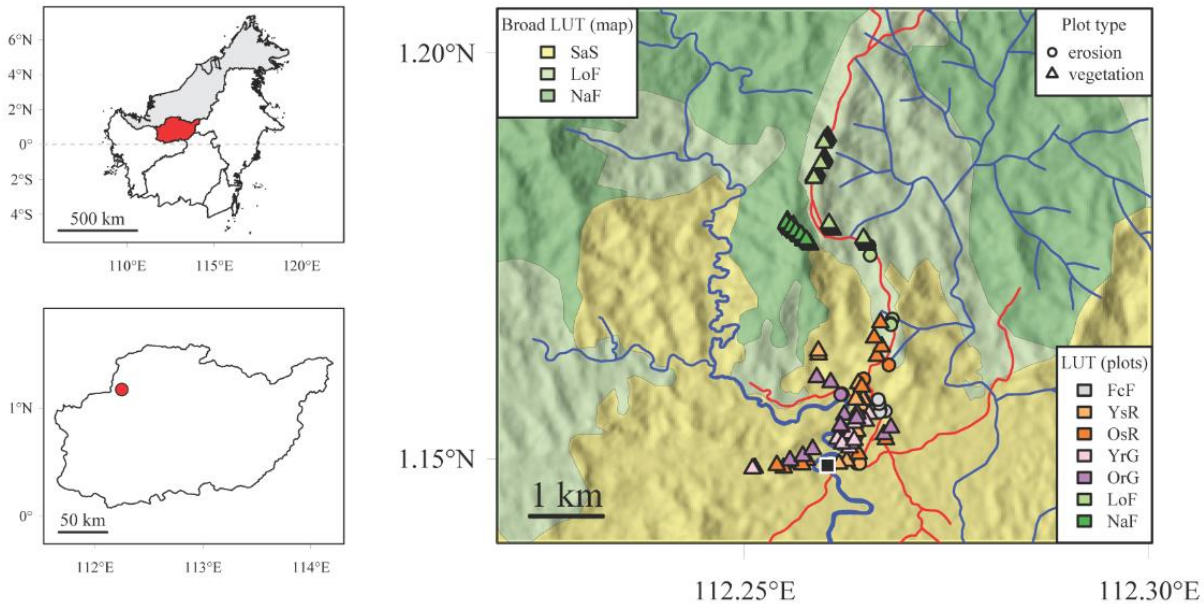

Figure 2.3. Plot location within the study area. The study area is located on the island of Borneo (top left panel), in the Indonesian province of West Kalimantan, in the regency of Kapuas Hulu (bottom left panel). In the main panel, plot location and broad land-use types (LUT) are displayed along with former logging roads (red) and rivers (blue). The black square indicates the location of the village. Broad land-use types (map): SaS = swidden agriculture system; LoF = logged-over forest; NaF = natural forest. Land-use types (plots): FcF = food crop field; YsR = young secondary regrowth area; OsR = old secondary regrowth forest; YrG = young rubber garden; OrG = old rubber garden; LoF = logged-over forest; NaF = natural forest.

We defined seven land-use types in the study area: (1) food crop fields where the main crop, rice (*Oryza sativa* L.), is planted after using the slash-and-burn method on the initial vegetation (natural forest or secondary vegetation), (2) young secondary regrowth following field abandonment after crops have been cultivated for 1 or 2 years, (3) old secondary regrowth forests further into the process of vegetation succession following field abandonment, (4) young rubber gardens resulting from the planting of rubber seedlings and saplings (*Hevea brasiliensis* (Willd. ex A.Juss.) Müll.Arg.) in some young fallows, (5) old rubber gardens with complex stand structure, (6) logged-over forest that was selectively logged from 1997 to 2005, and (7) natural forest with very little human disturbance.

Two distinct sets of vegetation and erosion plots were established based on a multi-stratified sampling first across land-use type and second across disturbance age for stands regenerating after slash and burn (see Table S1). For the purpose of this study, young and old stands (≤ 20 years and > 20 years following disturbance, respectively) were distinguished from each other because stand structure becomes more complex 20 years after initial disturbance (Werner, 1999; Guariguata & Ostertag, 2001). Plots for the vegetation sampling were scattered across the study area to encompass the variability of topographical situation (ridge, slope, valley bottom) and slope steepness (from flat to very steep) present in this low-elevation hilly

landscape. Plots for the erosion protocol were also scattered across the study area, with the additional constraint of having a homogenous slope of ca. 40% (ca. 22°). We chose relatively steep slopes (compared with the standard slope, i.e. 9%, of a typical erosion monitoring method such as the Wischmeier plot; Wischmeier & Smith, 1978), as erosion hardly occurs on non-bare slopes of low steepness in the study region (Sidle *et al.*, 2006).

2.2.3 Vegetation plots: estimating aboveground carbon stocks and tree species diversity

For young and old stands in both secondary regrowth areas and rubber gardens, 12 plots each of 20 × 20 m were randomly selected (for a total surveyed area of 0.48 ha for each of the four land-use types) to capture the variability of vegetation structure and composition within each land-use type (Figure 2.3, Table S1). For natural and logged-over forests, we surveyed a total area ca. twice as large as that of secondary regrowth areas and rubber gardens to encompass an even much higher variability of vegetation structure and composition: five rectangular plots each of 20 × 100 m (longer dimension along the contour line; 1 ha each forest type) were selected. Plots were contiguous but staggered down the slope for natural forest (all fitting in a 100 × 400 m area). For logged-over forest, they were scattered on either side of a former logging road built on a ridge, ca. 20 m downslope from the road.

All trees with diameter at breast height (DBH, 1.3 m) ≥ 5 cm were measured, tagged and mapped, and their height estimated, following standard procedures (Walker *et al.*, 2012). Leaf samples were collected at least once for each vernacular name (consistently given by the same group of highly knowledgeable local people using the Iban language) for both young and old secondary regrowth areas and rubber gardens, and for every individual tree for natural and logged-over forests. Identification of the herbarium vouchers were carried out at the Herbarium Bogoriense in Bogor, Indonesia.

We used three different indices to characterize tree species diversity at the plot level: species richness, Berger–Parker index, and Fisher's α. Species richness is the simplest measure of species diversity but does not take into account community evenness. Conversely, the Berger–Parker index (defined as the inverse of the proportion of individuals of the most common species in the community) depends only on evenness, and is sensitive to the dominance of a few species. Fisher's α is mathematically unrelated to the first two indices, is relatively independent of sample size, and is insensitive to the presence of rare species (Colwell, 2009).

We used the generic Chave *et al.* allometric equation for tropical forests (Chave *et al.*, 2014) to calculate tree dry biomass. Wood specific gravity, a multiplier included in the aforementioned equation, was obtained from the Global Wood Density Database (Zanne *et al.*, 2009*;* Chave *et al.*, 2009). When species were not found in the database, the genus-level average wood density was used instead. Aboveground biomass (AGB) was split into four fractions (according to tree DBH; 5–10 cm, 10–30 cm, 30–50 cm, and > 50 cm) of which

relative proportions were computed with no other analytical purpose than to identify the lowest and highest contributing fractions to total aboveground carbon stocks. Those were calculated from biomass values by application of the standard 0.47 conversion factor (McGroddy *et al.*, 2004).

Because of differences in sampling design (inter-plot distance ranged from 20 to 4650 m), we could not use tree diversity values aggregated over the total surveyed area (0.48 ha each for secondary regrowth areas and rubber gardens, 1 ha each for natural and logged-over forest) to compare the different land-use types (see Figure S1). Instead, we computed individual values–for tree diversity and aboveground carbon–for each 20 × 20 m plot (12 plots each for young and old secondary regrowth areas and rubber gardens, and 25 each for natural and logged-over forests; 98 plots in total) and used resulting mean values to characterize each land-use type. All details about individual plot coordinates, stand age (whenever relevant) and indicator–aboveground carbon and tree diversity–values can be found in Table S2.

2.2.4 Erosion plots: soil loss monitoring and topsoil carbon stock estimation

Silt fences (made from a nonwoven polyester geotextile) were used to measure hillslope erosion. Following guidelines from Robichaud and Brown (Robichaud & Brown, 2002), 4-meter-wide fences were set up across the slope, and heavy logs were positioned 15 m upslope from the fences to form the upper boundaries of laterally unbounded plots of ca. 60 m² contributing areas. Fences from 35 plots in total (five replicates for each of the seven land-use types) were cleaned monthly during 15 continuous months (from June 2012 to September 2013), and the collected material was dried, sieved (with a 1 mm sieve) and the weight of the resulting fine mineral fraction was recorded. Composite soil samples from four sampling points per plot (close to each plot corner) were taken for topsoils (0−20 cm). Dried samples (drying temperature T = 105 °C) were analyzed for carbon content (Walkley and Black method; Walkley & Black, 1934). In addition, for each plot, one sample of topsoil (using a 100 cm^3 ring) was taken at mid-slope and dry bulk density (in g cm^{-3}) was measured. Topsoil carbon stocks were then calculated using carbon content and dry bulk density. All details about individual plot coordinates, stand age (whenever relevant) and indicator–topsoil carbon and annual soil loss–values can be found in Table S3.

2.2.5 Statistical analysis

All statistical analyses were done using R 3.1.2 (R Core Team, 2013). Analyses were done on original values in case of normal data distribution and log_{10}-transformed values if transformation led to normal distributions. For each of the six indicators we studied (aboveground carbon, topsoil carbon, annual soil loss, tree species richness, Fisher's α and Berger-Parker index), we tested for spatial autocorrelation on both initial values and residuals of a linear model against land-use type using Moran's I. In case residuals were still spatially correlated, we used the Lagrange Multiplier diagnostics for spatial dependence to determine

the structure of the appropriate spatial regression model (ie spatial error model that accounts for error term correlation vs. spatial lag model that accounts for non-independence between observations; Haining, 1990) using various functions from the spdep package (Bivand *et al.*, 2013; Bivand & Piras, 2015). We tested for differences (at $p < 0.01$) in indicator values depending on land-use type using analysis of variance (ANOVA) followed by Tukey's honest significant difference (HSD) test on either (1) uncorrected values in case indicators or linear model residuals were non-spatially autocorrelated (which was the case for topsoil carbon, annual soil loss and Berger-Parker index), or (2) values corrected from spatial auto-correlation (by subtracting the "signal" term originating from spatial regression to the uncorrected value; Haining, 1990). Values of all statistical tests can be found in Table S4.

A nonmetric multidimensional scaling (NMDS) analysis was performed to illustrate plot similarity in terms of tree species composition (using the metaMDS function; see Oksanen *et al.*, 2014). NMDS analysis is an ordination technique aiming at iteratively collapsing multidimensional information (in this case, plot species composition) into an optimal—lower—number of dimensions while conserving the rank order of distances (Minchin, 1987). The closer the points in the initial and resulting spaces, the more similar are the tree species compositions of the corresponding plots. Using Spearman's rank-order correlation, we tested for correlations between plot distance in the field and in the NMDS plot to assess to what extent spatial autocorrelation influenced results from the NMDS analysis.

2.3 Results

2.3.1 Tree species diversity and composition

The three species diversity indices were highest in natural forests (Figure 2.4). However, differences in mean species richness and mean Fisher's α between natural and logged-over forests were not significant. Only Berger–Parker index values (exclusively dependent on community evenness) were significantly different between these two land-use types. Similarly, natural and logged-over forests had ca. 60% more species than do old secondary regrowth forests (next most species-rich land-use type).

Older stands (for rubber gardens and secondary regrowth forest) consistently showed higher index values compared with young ones, but the difference was only significant for mean Fisher's α. For similar time intervals since last disturbance, all the diversity indices were consistently higher in secondary regrowth areas compared with rubber gardens, but the difference was not significant.

In the two dimensions of the NMDS plot (Figure 2.5), tree species composition was markedly different in natural forest plots compared with other plots. Logged-over forests had the most similar tree species composition to natural forests. Tree species composition was highly variable among secondary regrowth areas and rubber gardens (both young and old). We found a moderate positive correlation between plot distance in the field and in the NMDS plot (Pearson's $r = 0.58$; $p < 0.001$). Even though point clustering for logged-over and natural forest might therefore result in part from the sampling design (spatial autocorrelation), a careful inspection of the species present in the different land-use types (see Table S5) strongly supports our finding that natural forest species are highly specific and different to all other land-use types.

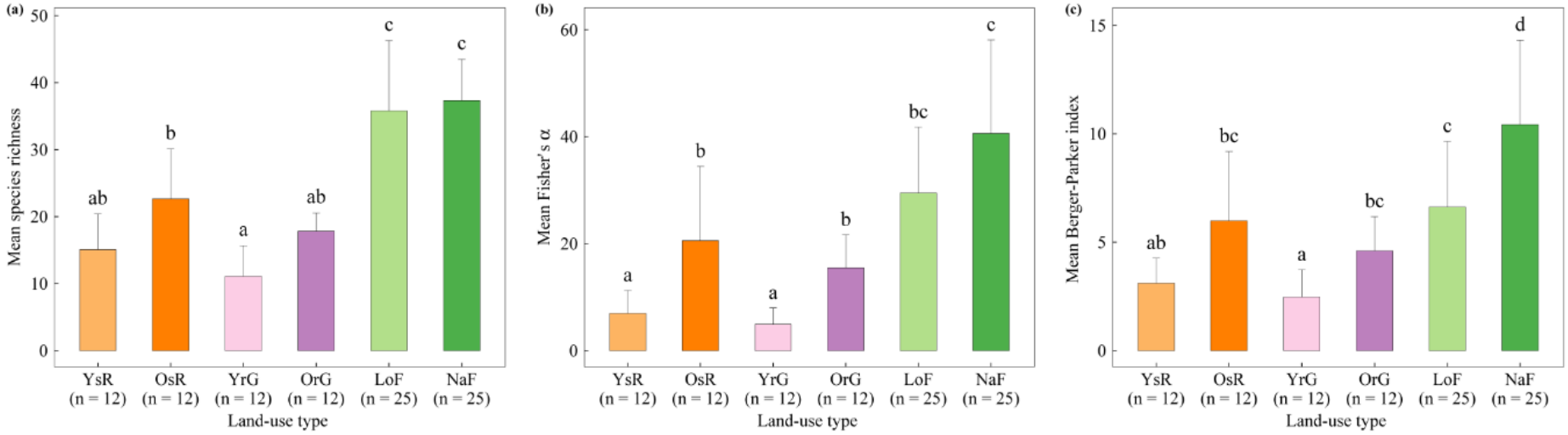

Figure 2.4. Tree species diversity indices depending on land-use type: (a) species richness; (b) Fischer's α; (c) Berger–Parker index. Indices were computed for each 20 × 20 m plot before being averaged by land-use type. Mean values with the same letter are not significantly different (Tukey's HSD test on uncorrected values in case no spatial autocorrelation was detected and corrected values otherwise, $p < 0.01$). Land-use types: YsR = young secondary regrowth area; OsR = old secondary regrowth forest; YrG = young rubber garden; OrG = old rubber garden; LoF = logged-over forest; NaF = natural forest.

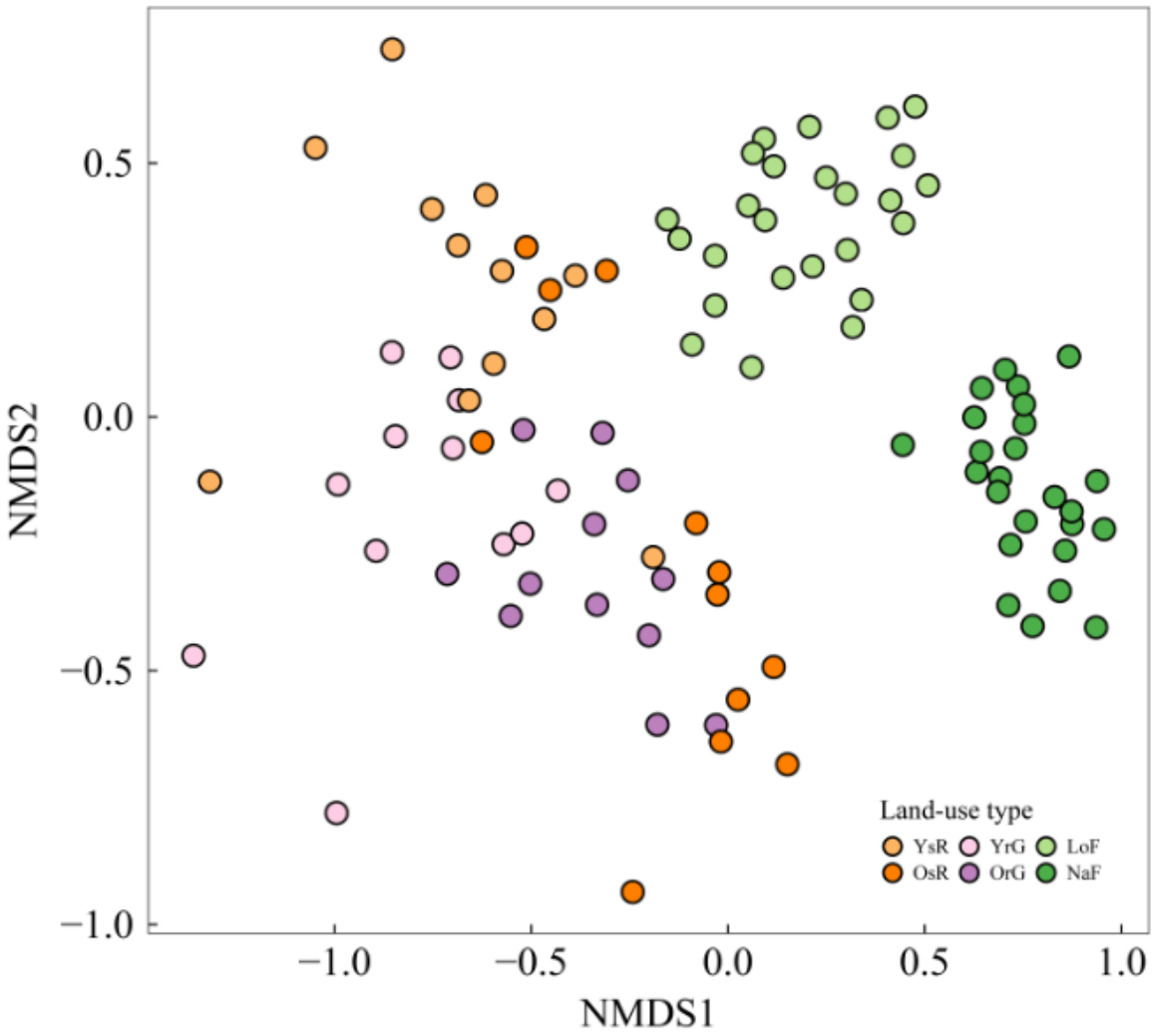

Figure 2.5. Nonmetric multidimensional scaling (NMDS) plot showing tree species composition similarity among plots under different land-use regimes. Each dot (98 in total) represents a 20 × 20 m plot. Land-use types: YsR = young secondary regrowth area; OsR = old secondary regrowth forest; YrG = young rubber garden; OrG = old rubber garden; LoF = logged-over forest; NaF = natural forest.

2.3.2 Carbon storage

Aboveground carbon stock levels were significantly higher in natural forests than in any other land-use types (Figure 2.6). Unsurprisingly, the lowest values were found in young stands (rubber gardens or secondary regrowth areas). Even old rubber gardens, old secondary regrowth forests, and logged-over forests had aboveground carbon stocks at levels half of those of natural forests.

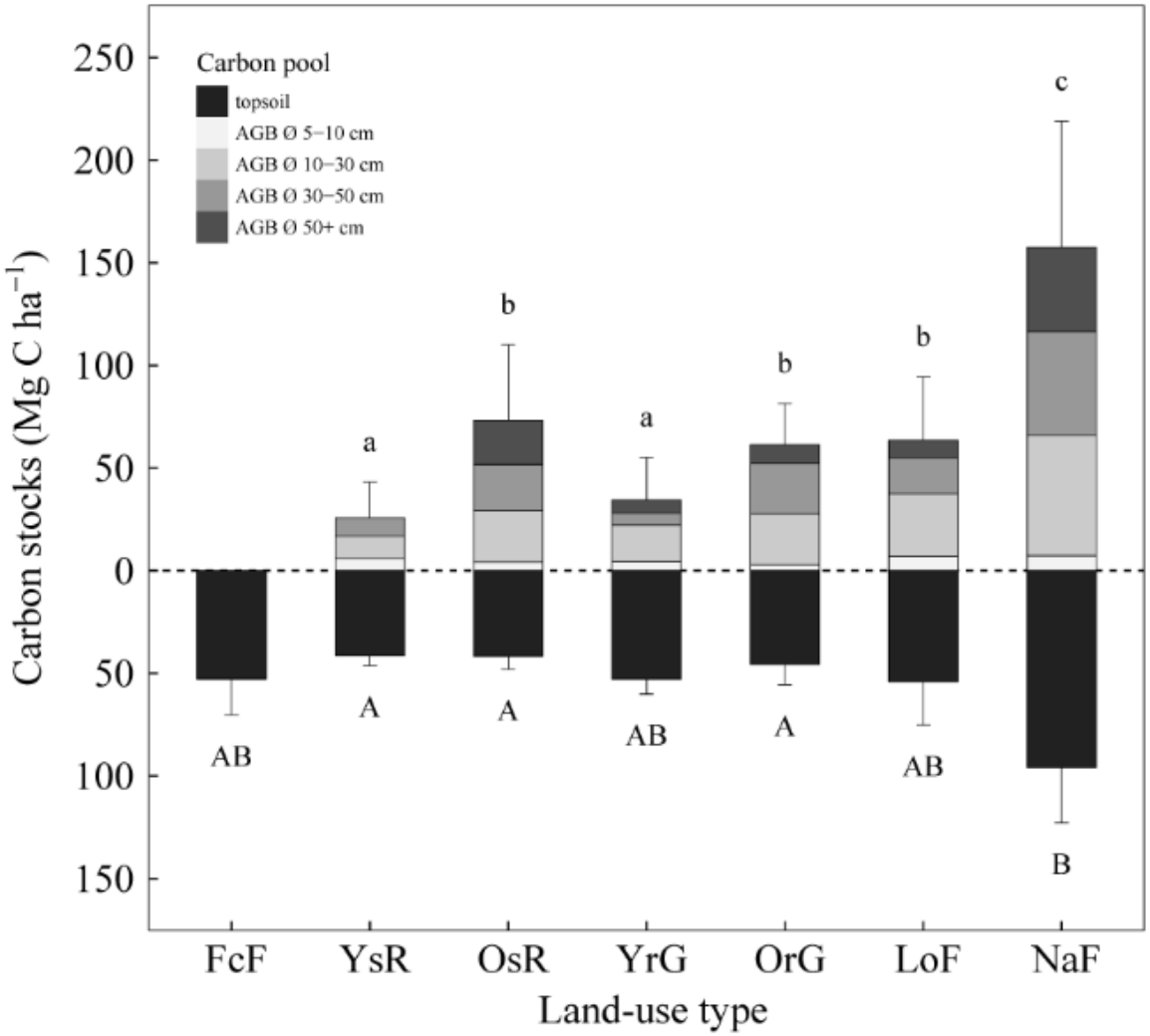

Figure 2.6. Mean carbon stocks (+ 1 SD) in topsoil (0–20 cm) and aboveground biomass. Means were computed over 12 to 25 replicates per land-use type for aboveground biomass, and over five replicates per land-use type for topsoil. Aboveground biomass (AGB) was split into four fractions according to tree diameter at breast height (Ø). Mean values with the same letter (lowercase for aboveground biomass, uppercase for topsoil) are not significantly different (Tukey's HSD test on uncorrected values in case no spatial autocorrelation was detected and corrected values otherwise, $p < 0.01$). Land-use types: FcF = food crop field; YsR = young secondary regrowth area; OsR = old secondary regrowth forest; YrG = young rubber garden; OrG = old rubber garden; LoF = logged-over forest; NaF = natural forest.

For all types of land use, the highest proportions of aboveground carbon were contained in trees with DBH = 10−30 cm, while the lowest non-null proportions were contained in trees with DBH = 5−10 cm. Yet, for recently disturbed stands such as those in young secondary regrowth areas, small trees (those with DBH = 5−10 cm) could represent up to ca. 25% of aboveground carbon.

Although natural forests stored on average twice as much carbon in topsoils as other land-use types, significant differences were observed only between natural forests and secondary regrowth areas (both young and old) or old rubber gardens due to high variability within land-use types (for logged-over and natural forests, especially).

2.3.3 Relationship between aboveground carbon stocks and species richness

The greater the aboveground carbon stocks, the greater the species richness in all land-use types, with the noticeable exception of natural forests for which the relationship is negative (cf. regression lines; Figure 2.7). Almost all plots with high tree diversity (richness higher than median) and low carbon (aboveground carbon stock below median) belonged to logged-over forests. The vast majority of young secondary regrowth areas and rubber garden plots had low diversity and low carbon. In contrast, all (but one corresponding to a tree-fall gap) natural forest plots showed high diversity and high carbon.

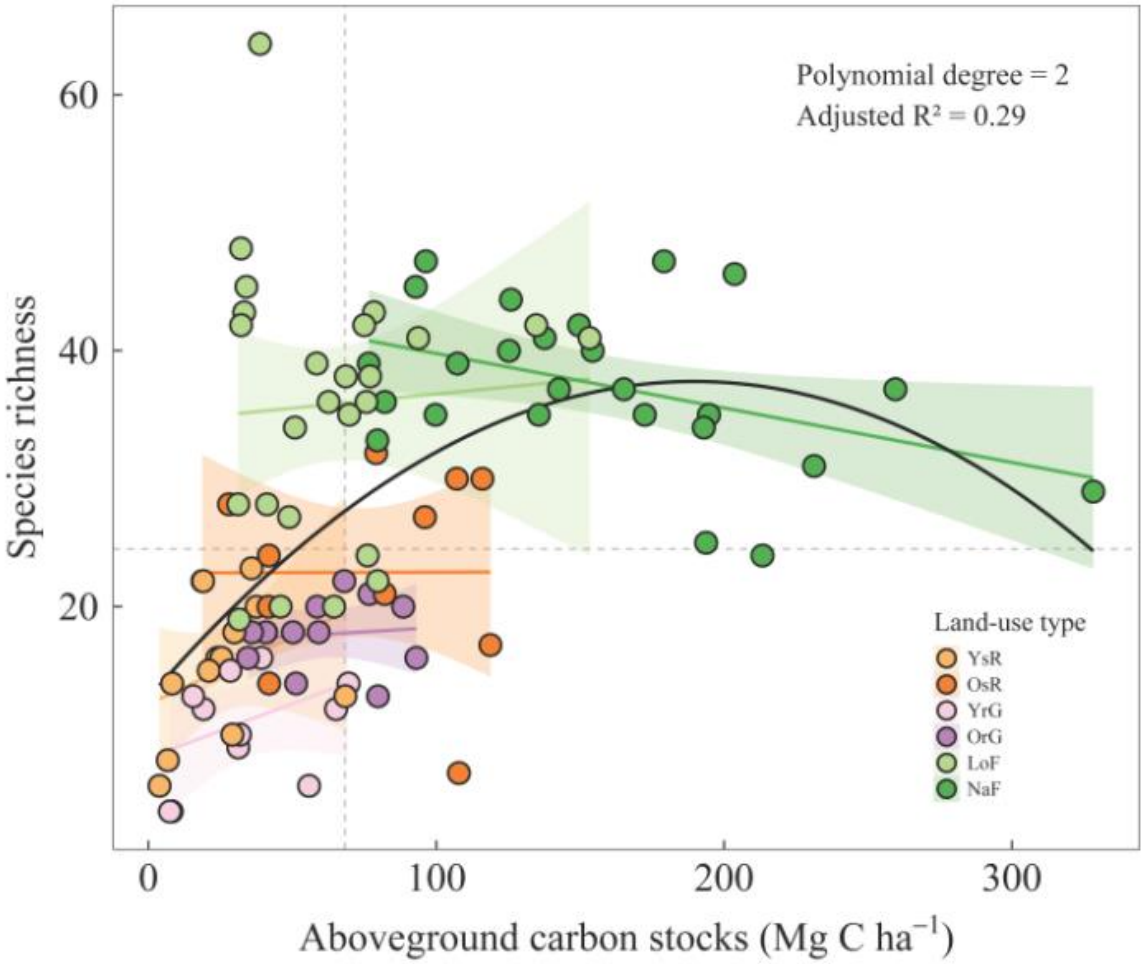

Figure 2.7. Species richness against aboveground carbon stocks. Each dot (98 in total) represents a 20 × 20 m plot. Horizontal and vertical dashed lines represent median values of species richness (n = 25) and carbon stocks in aboveground biomass (68 Mg C ha-1), respectively. Regression lines (along with standard error) are computed independently for each land-use type. A second-order regression model (best-fit significant model selected among polynomial models with degrees 0 to 3) over the whole data set is also displayed (in black). Land-use types: YsR = young secondary regrowth area; OsR = old secondary regrowth forest; YrG = young rubber garden; OrG = old rubber garden; LoF = logged-over forest; NaF = natural forest.

2.3.4 Soil erosion

Annual soil loss values ranged from 0.8 to 2.2 g m^{-2} yr^{-1}, with individual plot values varying from 0.5 to 2.7 g m^{-2} yr^{-1} (see table S3). Annual soil loss was significantly lower in natural forests and young rubber gardens compared with food crop fields (Figure 2.8). Other differences in annual soil loss between land-use types were not significant.

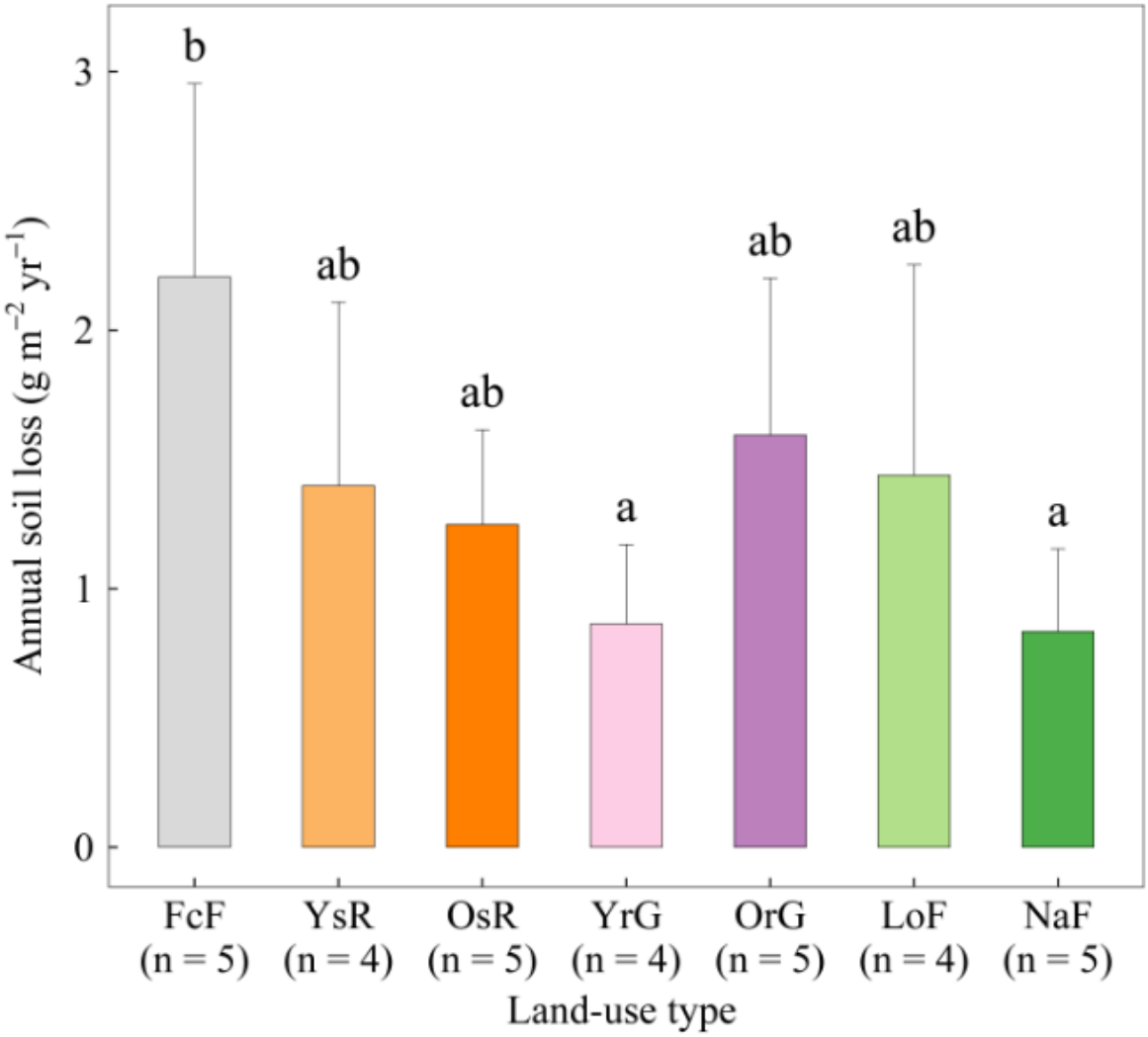

Figure 2.8. Mean annual soil loss (+ 1 SD) depending on land-use type. Data are averaged over the monitoring period (June 2012 to September 2013) and over the different replicates for each land-use type. Values from three replicates (one in young secondary regrowth area, one in young rubber garden, one in logged-over forest) were discarded because they were abnormally high (> two times mean value of the corresponding land-use type). Mean values with the same letter are not significantly different (Tukey's HSD test on uncorrected values in case no spatial autocorrelation was detected and corrected values otherwise, $p < 0.01$). Land-use types: FcF = food crop field; YsR = young secondary regrowth area; OsR = old secondary regrowth forest; YrG = young rubber garden; OrG = old rubber garden; LoF = logged-over forest; NaF = natural forest.

2.4 Discussion

2.4.1 Service production is highest in natural forest

As expected, service production was highest in natural forests (Figure 2.9). Natural forest plots clearly had high levels of both aboveground carbon stocks and tree species richness (top right corner, Figure 2.7), even though lower tree species richness was observed for the highest values of aboveground carbon stocks. This negative trend might be explained in light of Connell's intermediate disturbance hypothesis (Connell, 1978). According to this hypothesis, an intermediate level of disturbance is required for a given tree community to reach maximum species richness (Connell, 1978). Natural forest succession will lead to the competitive exclusion of early- and mid-successional species, therefore reducing overall species diversity. Our results corroborate this hypothesis because aboveground carbon stocks were positively correlated to disturbance age (Martin *et al.*, 2013).

Aboveground carbon stocks in human-modified land-use types did not reach half those of natural forests. Logged-over forests, agroforests and secondary regrowth areas had topsoil carbon stocks 40–60% lower than those of natural forests. This contrasts with results from Kessler *et al.* who found no significant reduction in soil carbon stocks between natural forests and cocoa agroforests in Sulawesi, Indonesia (Kessler *et al.*, 2012). This might in part be due to the fact that cocoa agroforests in their study region are obtained through gradual thinning of the natural forest with minimum impact on the root system (Kessler *et al.*, 2012), while transitions related to practices in our study area (logging, slash and burn) are more abrupt and therefore potentially more disturbing for topsoil.

Regarding soil erosion control, even if soil loss was lowest in natural forests and differed significantly between some pairs of land-use types, low absolute values of annual soil loss (2−3 orders of magnitude lower than the tolerable soil erosion rate; Montgomery, 2007) suggest that the service of soil erosion control is delivered as long as soils are protected by vegetation cover, as exemplified in a review for the humid tropics (Labrière *et al.*, 2015). However, it cannot be asserted that soil erosion is consistently negligible across the landscape and throughout time. We did not monitor soil loss on bare soil elements created by logging activities (e.g. dirt roads, landslides) or related to rubber tapping (e.g. walking tracks) that are known to contribute to erosion at the landscape scale disproportionately compared to their geographically restricted areas (Rijsdijk, 2005; Gómez-Delgado, 2010). Nor did we monitor soil loss immediately after a major disturbance (e.g. burning or opening of logging tracks). Since extreme rainfall events that occur while soil is temporarily bare can lead to dramatic soil loss, soil loss monitoring before, during and after disturbance is required to follow soil erosion control during land-use change (Costa Junior *et al.*, 2013).

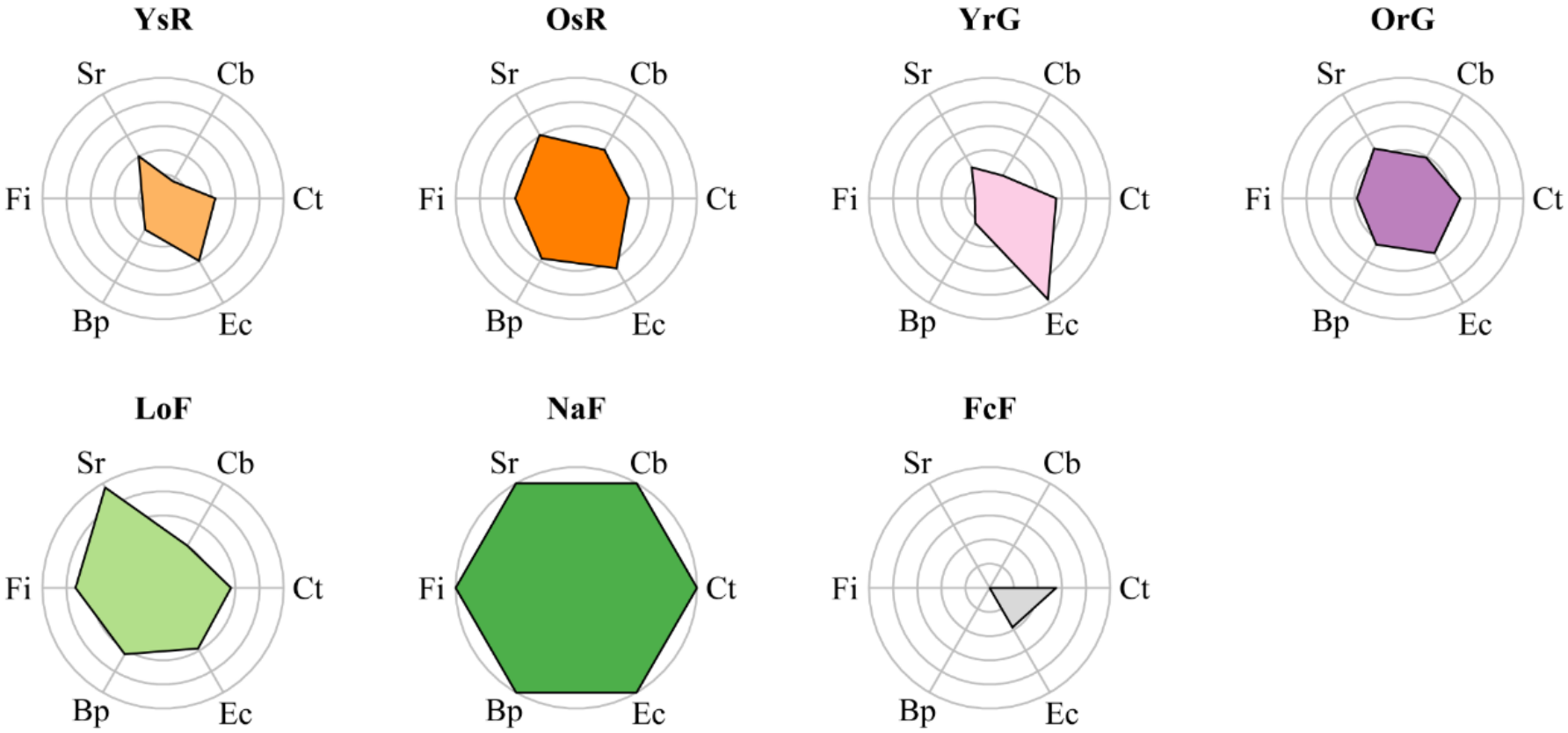

Figure 2.9. Spider chart of normalized service indicators for different land-use types. Indicators are normalized so that the minimum possible value of an indicator is at the center of the radial plot and the maximum observed values are on the outer circles (for the service of soil erosion control, the indicator is the inverse of the measured soil loss).Service indicators: Ct = carbon stocks in topsoil; Cb = carbon stocks in aboveground biomass; Sr = tree species richness; Fi = Fisher's α; Bp = Berger–Parker index; Ec = soil erosion control. Land-use types: YsR = young secondary regrowth area; OsR = old secondary regrowth forest; YrG = young rubber garden; OrG = old rubber garden; LoF = logged-over forest; NaF = natural forest; FcF = food crop field.

Our results on tree species diversity show that some areas of human-modified land-use types host high tree species richness (e.g. logged-over forests and old secondary regrowth forest). This has already been shown for various taxa and is a widely accepted phenomenon (Cannon *et al.*, 1998; Berry *et al.*, 2010; Putz *et al.*, 2012; Martin *et al.*, 2013). However, we also show that the tree species composition of natural forest is highly specific (cf. Figure 2.5), which strengthens the assertion that "primary forests are irreplaceable for sustaining tropical biodiversity" (Barlow *et al.*, 2007; Gibson *et al.*, 2011).

Overall, in our study site, natural forests irrefutably produce the highest levels of services across the landscape and this would lend support to land management strategies that promote their strict protection (Gilroy *et al.*, 2014). Schemes and financial mechanisms in this area that conserve one of these services (e.g. carbon with REDD+, a financial mechanism aiming at Reducing Emissions from Deforestation and Forest Degradation) would synergistically benefit the others, therefore increasing the effectiveness of natural forest protection. But correlations between services depend on the spatial resolution and the scope of a study (Anderson *et al.*, 2009; Strassburg *et al.*, 2010; Locatelli *et al.*, 2014). Therefore, more primary data are needed for inferring that mechanisms targeting carbon conservation would necessarily maximize benefits for biodiversity and other ecosystem services at the regional scale.

2.4.2 Logged-over forests and swidden agriculture system outperform monocultures in terms of service production

In addition to the need to preserve natural forests, another challenge is to maximize service production in human-modified land-use areas. With the noticeable exception of tree species richness and tree species composition, our data did not show significant differences in service production between logged-over forests, old rubber gardens and old secondary regrowth forests. Tree species richness is high in logged-over forests (one plot can simultaneously host a mixture of old growth and secondary species), but in such forests, aboveground carbon stocks are low. In contrast, aboveground carbon stocks can be large in some old rubber gardens and secondary regrowth forests, but tree species richness is low. Beyond the diversity of products from these land-use types, there is a complementarity in services produced by such human-modified landscapes. Despite continuous changes in land use and management, the diversification of human activities—farming, rubber tapping, and logging—ensures the sustained delivery of multiple services.

As anticipated, comparing our results with those in the literature emphasized that a mosaic of land uses produces far more services than do rubber or oil palm monocultures: biodiversity is greater (Savilaakso *et al.*, 2014), erosion is lower (especially when plantations are set up on steep slopes), and aboveground carbon stocks are more than twice as great (Germer & Sauerborn, 2008).

Our results support the finding that "a logged forest in Borneo is better than none at all" (Meijaard & Sheil, 2007). Hopefully, the strong case made by this study and many others

(e.g. Meijaard *et al.*, 2005; Putz *et al.*, 2012) will eventually raise awareness among decision-makers and land-use planners that logged-over forests are not just worth being converted but should be sustainably managed.

2.4.3 Is the swidden system in Keluin close to a sustainability threshold?

We found that carbon storage and tree diversity increased along a successional recovery of the forest after initial clearance: levels of service production were lowest in food crop fields, intermediate in young rubber gardens and secondary regrowth areas, and highest in old rubber gardens and secondary regrowth forests. More striking was no trend for carbon storage in topsoil and the slow recovery of different ecosystem services, either in old rubber gardens or secondary regrowth forests. Mean time since last disturbance for our old secondary regrowth forest plots was 47 years, and yet species richness was still significantly lower than for natural forests. Similarly, we found low similarity in tree species composition between old secondary regrowth forest and natural forest plots.

From a meta-analysis of the recovery of plant biodiversity and carbon stocks in secondary forests, 50 years are enough for species richness to reach natural forest levels, but with only a very low proportion of native forest species (mean value: 26%), even in old stands (Martin *et al.*, 2013). The aboveground carbon stocks we found in old secondary regrowth forests (ca. half those of natural forests) are consistent with the literature but lay in the lower part of the range compiled by the meta-analysis that reports aboveground carbon stock of 50-70% pre-disturbance levels after ca. 50 years of forest recovery (Martin *et al.*, 2013). Old rubber gardens also showed lower values of aboveground carbon stocks than those found in the literature (Lasco & Pulhin, 2004).

We found topsoil carbon stocks for food crop fields to be half those of natural forest. Our results are consistent with those of a meta-analysis that also showed that soil carbon stocks will eventually fully recover as croplands are allowed to revert to secondary forests (Guo & Gifford, 2002). Another study estimated that 40−50 years are needed for secondary forest soil carbon stocks to reach pre-disturbance levels (Brown & Lugo, 1990). Despite the mean time since last disturbance (42 years) being within this range, topsoil carbon in old secondary regrowth forests was far below the pre-disturbance levels in our study site.

One study that was also carried out in West Kalimantan found that an increasing number of cycles of cultivation and forest regrowth did not lead to total phosphorus decline, but had detrimental consequences for aboveground carbon sequestration (Lawrence & Schlesinger, 2001; Lawrence, 2005). The capacity of soils to recover carbon content after disturbances might also be reduced in plots where numerous rotations have already been done. The whole swidden agriculture system is sustainable if the condition that sufficient time is allowed for soil and vegetation to recover is met. Soil impoverishment related to reduction in rotation length is a serious threat likely to jeopardize the production of goods and services in the long-term from the traditional swidden system in the Keluin area.

2.5 Conclusion

In such a rapidly transforming traditional rural landscape in northern Bornean, natural forests host highly unique tree species diversity, have the lowest erosion rate, and store significantly more carbon (in aboveground biomass and topsoil) than do any other land-use type. Logged-over forests provide services similar to natural forest, except for soil erosion control, which is jeopardized by the presence of the remaining decaying road network that leads to soil loss at the landscape level.

All land uses related to the swidden agriculture system largely outperform oil palm or rubber monocultures in terms of tree diversity, carbon storage, and soil erosion control. Natural and logged-over forests should be maintained or managed as an integral part of the swidden system, and landscape multifunctionality should be sustained as a safety net against the price volatility of traded goods (e.g. rubber, palm oil, timber, tengkawang oil), upon which the economy of monocrop systems is much more dependent.

Because of the congruence of services in natural forest, protection of their carbon stocks, for example through financial mechanisms such as REDD+, will synergistically benefit biodiversity and a wide range of other services provided to communities in this area. However, how such mechanisms could benefit communities must be carefully evaluated to counter the high opportunity cost of conversion to monocultures; these may generate greater income, but may also be more detrimental to the production of multiple ecosystem services.

Ecosystem service recovery time following initial slash-and-burn practices on the vegetation is longer in the study area than has been reported in the literature for similar study situations. As rotation length appears to be a key factor in the sustainability of swidden systems, it is critical to understand the socio-cultural and economic drivers of the reduction in rotation length and the potential feedback of this reduction on social–ecological systems. In the rapidly transforming socio-environmental context of this region, questions remain about the long-term persistence of the swidden agriculture system.

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Author contributions

Conceived and designed the study: NL, YL, MC. Performed field work: NL, YL, MC. Analyzed the data: NL, BL. Contributed to the writing of the manuscript: NL, YL, BL, GV, MC.

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2.7 Appendices

Supplementary information for

Ecosystem services and biodiversity in a rapidly transforming landscape in Northern Borneo

Nicolas Labrière, Yves Laumonier, Bruno Locatelli, Ghislain Vieilledent, Marion Comptour

Figure S1. Individual-based rarefaction curves for every land-use type.

Table S2.1. Sampling design for vegetation and erosion plots.

Table S2. Vegetation plot features.

Table S3. Erosion plot features.

Table S4. Statistical analyses on ecosystem service and tree diversity indicators.

Table S5. Species surveyed in each land-use type.

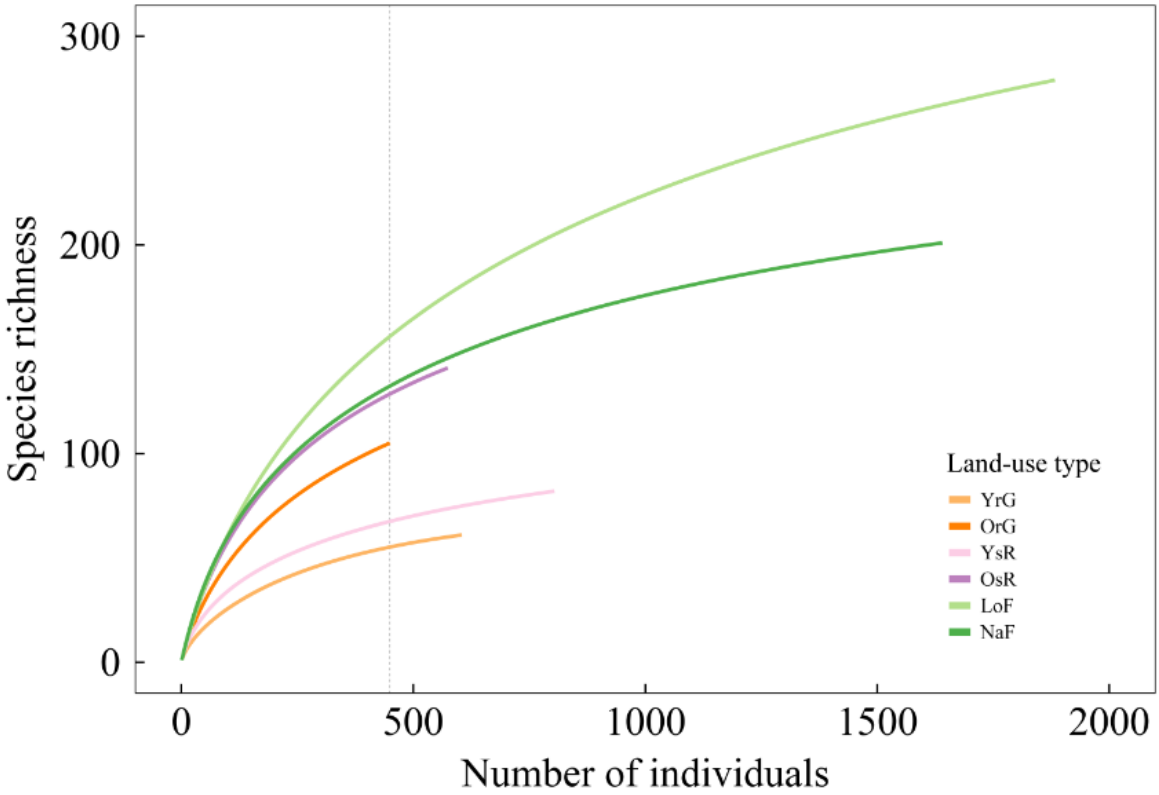

Figure S1. Individual-based rarefaction curves for every land-use type. Rarefaction level was the number of individuals surveyed in old rubber gardens (n = 449). Twelve plots (0.48 ha in total) were surveyed for fallows and rubber gardens (both young and old), and 25 plots (1 ha in total) for logged-over and natural forest. Land-use types: YsR = young secondary regrowth area; OsR = old secondary regrowth forest; YrG = young rubber garden; OrG = old rubber garden; LoF = logged-over forest; NaF = natural forest.

Table S2.2. Sampling design for vegetation and erosion plots. No vegetation plot was selected in food crop fields under the assumption that tree diversity and aboveground carbon would be null. The first plot size dimension is the dimension along the slope. Land-use types: FcF = food crop field; YsR = young secondary regrowth area; OsR = old secondary regrowth forest; YrG = young rubber garden; OrG = old rubber garden; LoF = logged-over forest; NaF = natural forest.

	Vegetation plots			Erosion plots	
Land-use type	Plot size (m)	Nb of plots *	Total surveyed area (ha)	Plot size (m)	Nb of plots
FcF	–	–	–	15 × 4	5
YsR	20 × 20	12	0.48	15 × 4	5
OsR	20 × 20	12	0.48	15 × 4	5
YrG	20 × 20	12	0.48	15 × 4	5
OrG	20 × 20	12	0.48	15 × 4	5
LoF	20 × 100	5 (25)	1	15 × 4	5
NaF	20 × 100	5 (25)	1	15 × 4	5
Total	–	58 (98)	3.92	–	35

* Values in parentheses show the number of corresponding 20 × 20 m plots after 20 × 100 m rectangular plots were resampled for comparison purposes.

Table S2. Vegetation plot features. Longitude and latitude of each plot are provided in decimal degrees (WSG84 datum). Plot mean diameter at breast height (DBH), height, wood specific gravity (WSG) and aboveground carbon (AGC) are also provided. Land-use types: YsR = young secondary regrowth area; OsR = old secondary regrowth forest; YrG = young rubber garden; OrG = old rubber garden; LoF = logged-over forest; NaF = natural forest.

Plot ID	Land-use type	Time since last disturbance	Latitude	Longitude	Nb trees	DBH (cm)	Height (m)	WSG (g cm-3)	AGC (Mg ha-1)	Species richness	Fisher's α	Berger-Parker index	Nb critically endangered species	Nb threatened species
VS_YsR_1	YsR	7	1.162828	112.259179	45	6.0	6.4	0.511	3.9	6	1.86	3.00	0	0
VS_YsR_2	YsR	7	1.163287	112.25914	75	6.0	6.7	0.494	6.8	8	2.27	3.57	0	0
VS_YsR_3	YsR	10	1.153252	112.263617	74	9.1	8.9	0.479	24.0	16	6.28	2.47	0	0
VS_YsR_4	YsR	18	1.15075	112.263333	41	11.5	7.8	0.474	29.9	18	12.25	2.93	0	0
VS_YsR_5	YsR	10	1.153408	112.263938	70	8.8	8.0	0.442	29.2	10	3.19	2.00	0	0
VS_YsR_6	YsR	8	1.157219	112.264822	75	10.8	9.9	0.387	25.4	16	6.23	2.14	0	0
VS_YsR_7	YsR	8	1.157269	112.264682	84	9.5	9.0	0.407	21.0	15	5.32	2.71	0	0
VS_YsR_8	YsR	20	1.149721	112.262653	55	11.8	8.4	0.489	68.4	13	5.37	3.93	0	0
VS_YsR_9	YsR	20	1.149363	112.261693	50	12.0	9.3	0.577	35.8	23	16.50	6.25	0	0
VS_YsR_10	YsR	5	1.156507	112.264442	123	7.5	7.6	0.461	19.0	22	7.80	2.62	0	0
VS_YsR_11	YsR	10	1.157285	112.263759	51	7.3	7.7	0.483	8.3	14	6.37	2.32	0	0
VS_YsR_12	YsR	20	1.159259	112.264087	61	10.1	10.0	0.520	37.6	20	10.37	3.39	0	0
VS_OsR_1	OsR	30	1.149513	112.256817	50	9.8	8.5	0.499	18.8	22	15.01	4.17	0	0
VS_OsR_2	OsR	45	1.148871	112.254856	45	15.0	10.3	0.550	107.2	30	39.33	11.25	0	0
VS_OsR_3	OsR	50	1.14919	112.254011	55	9.2	9.8	0.572	28.0	28	22.83	11.00	0	0
VS_OsR_4	OsR	70	1.14983	112.257725	35	17.3	10.8	0.597	118.8	17	13.03	5.83	0	0
VS_OsR_5	OsR	70	1.149265	112.257158	45	13.4	10.2	0.562	79.1	32	49.45	6.43	0	0
VS_OsR_6	OsR	38	1.158844	112.264522	59	12.9	10.7	0.468	42.0	14	5.80	1.51	0	0
VS_OsR_7	OsR	60	1.162628	112.266372	49	16.6	9.6	0.588	96.0	27	24.70	8.17	0	0
VS_OsR_8	OsR	40	1.152377	112.267492	52	12.5	9.5	0.574	41.9	24	17.29	5.78	0	0
VS_OsR_9	OsR	38	1.150595	112.264112	49	16.3	11.3	0.590	116.0	30	32.88	8.17	0	1
VS_OsR_10	OsR	30	1.163805	112.266972	56	10.3	11.1	0.524	41.7	20	11.13	4.31	0	0
VS_OsR_11	OsR	40	1.164912	112.266051	18	24.5	19.9	0.515	107.9	7	4.21	2.00	0	0
VS_OsR_12	OsR	50	1.166766	112.266824	61	11.9	11.3	0.497	82.1	21	11.33	3.21	0	0
VS_YrG_1	YrG	20	1.151362	112.262988	33	13.9	9.5	0.503	31.2	9	4.08	1.83	0	0
VS_YrG_2	YrG	7	1.151888	112.263212	60	6.8	8.5	0.461	8.1	4	0.96	1.11	0	0
VS_YrG_3	YrG	10	1.152897	112.26304	63	9.6	9.4	0.430	19.2	12	4.40	2.86	0	0
VS_YrG_4	YrG	10	1.153099	112.263091	41	11.8	9.8	0.483	40.9	18	12.25	2.93	0	0
VS_YrG_5	YrG	15	1.155507	112.265421	58	9.1	8.0	0.477	15.6	13	5.21	3.22	0	0

Plot ID	Land-use type	Time since last disturbance	Latitude	Longitude	Nb trees	DBH (cm)	Height (m)	WSG (g cm-3)	AGC (Mg ha-1)	Species richness	Fisher's α	Berger-Parker index	Nb critically endangered species	Nb threatened species
VS_YrG_6	YrG	18	1.148862	112.251283	51	11.8	10.4	0.468	31.8	10	3.72	1.42	0	0
VS_YrG_7	YrG	18	1.148775	112.251007	66	11.4	10.2	0.492	39.3	16	6.72	2.36	0	0
VS_YrG_8	YrG	17	1.152446	112.261493	46	12.2	9.7	0.490	69.6	14	6.85	5.11	0	0
VS_YrG_9	YrG	15	1.151842	112.262093	50	12.9	9.3	0.476	65.2	12	5.01	1.92	0	0
VS_YrG_10	YrG	5	1.152288	112.263582	51	6.8	7.1	0.541	7.5	4	1.02	1.50	0	0
VS_YrG_11	YrG	10	1.154632	112.265009	59	10.2	10.4	0.472	28.4	15	6.49	4.21	0	0
VS_YrG_12	YrG	20	1.154394	112.26363	26	20.1	12.3	0.473	55.8	6	2.45	1.24	0	0
VS_OrG_1	OrG	50	1.155404	112.262349	25	14.5	10.0	0.563	40.8	18	28.82	5.00	0	0
VS_OrG_2	OrG	50	1.155543	112.26397	51	15.1	10.9	0.531	76.8	21	13.35	6.38	0	0
VS_OrG_3	OrG	50	1.154957	112.263888	65	13.2	10.1	0.513	68.1	22	11.70	4.33	0	0
VS_OrG_4	OrG	50	1.153945	112.261974	31	18.6	10.7	0.461	88.5	20	24.37	7.75	0	0
VS_OrG_5	OrG	50	1.154049	112.261866	29	15.8	11.0	0.492	51.3	14	10.65	4.14	0	0
VS_OrG_6	OrG	40	1.152986	112.267278	44	14.7	10.4	0.547	59.2	18	11.37	2.75	0	0
VS_OrG_7	OrG	40	1.153834	112.268114	30	17.7	12.0	0.523	50.2	18	19.00	3.75	0	0
VS_OrG_8	OrG	35	1.159393	112.260663	35	12.2	9.5	0.533	36.0	18	14.88	5.00	0	0
VS_OrG_9	OrG	35	1.160023	112.258943	35	15.7	11.7	0.537	58.6	20	19.39	5.83	0	0
VS_OrG_10	OrG	30	1.149778	112.255639	45	12.1	10.8	0.487	34.5	16	8.87	2.05	0	0
VS_OrG_11	OrG	40	1.150328	112.257209	24	20.8	13.3	0.552	79.8	13	11.58	4.80	0	0
VS_OrG_12	OrG	50	1.151165	112.258446	35	19.7	13.5	0.515	93.1	16	11.40	3.50	0	0
VS_LoF_1	LoF	8-16	1.176356	112.265218	48	11.2	8.8	0.537	41.2	28	28.11	8.00	0	1
VS_LoF_2	LoF	8-16	1.176548	112.265099	59	12.7	9.3	0.517	75.8	36	39.20	6.56	0	0
VS_LoF_3	LoF	8-16	1.176776	112.264956	54	13.0	8.7	0.553	69.8	35	43.07	13.50	0	1
VS_LoF_4	LoF	8-16	1.176975	112.264841	75	12.5	8.8	0.575	78.4	43	41.92	9.38	0	2
VS_LoF_5	LoF	8-16	1.177177	112.264711	48	14.3	8.4	0.549	76.2	24	19.10	6.86	0	1
VS_LoF_6	LoF	8-16	1.17824	112.260935	54	13.3	10.7	0.533	79.7	22	13.84	5.40	0	0
VS_LoF_7	LoF	8-16	1.178416	112.2608	50	13.6	11.0	0.489	64.5	20	12.35	5.00	0	0
VS_LoF_8	LoF	8-16	1.178602	112.260686	58	10.4	9.5	0.486	45.9	20	10.80	1.87	0	0
VS_LoF_9	LoF	8-16	1.178793	112.260581	64	11.5	9.0	0.502	48.9	27	17.60	3.20	0	0
VS_LoF_10	LoF	8-16	1.17902	112.260457	59	10.6	9.3	0.480	31.6	19	9.71	3.47	0	0
VS_LoF_11	LoF	8-16	1.185483	112.258944	122	8.5	8.4	0.521	32.2	48	29.18	2.77	1	4
VS_LoF_12	LoF	8-16	1.185258	112.258855	125	8.4	8.5	0.493	34.1	45	25.22	5.21	0	0
VS_LoF_13	LoF	8-16	1.185067	112.258767	100	9.2	8.7	0.522	33.3	43	28.61	4.17	0	0
VS_LoF_14	LoF	8-16	1.184859	112.258688	114	8.7	9.1	0.506	32.2	42	24.02	2.43	0	1
VS_LoF_15	LoF	8-16	1.184593	112.258588	119	8.1	8.6	0.539	38.8	64	56.42	7.93	2	4
VS_LoF_16	LoF	8-16	1.187201	112.259896	68	13.2	11.3	0.553	153.3	41	43.67	7.56	3	6

Plot ID	Land-use type	Time since last disturbance	Latitude	Longitude	Nb trees	DBH (cm)	Height (m)	WSG (g cm-3)	AGC (Mg ha-1)	Species richness	Fisher's α	Berger-Parker index	Nb critically endangered species	Nb threatened species
VS_LoF_17	LoF	8-16	1.187025	112.259814	105	11.1	9.4	0.577	93.8	41	24.74	7.00	2	5
VS_LoF_18	LoF	8-16	1.186801	112.259702	67	12.8	10.1	0.577	75.0	42	48.21	9.57	0	3
VS_LoF_19	LoF	8-16	1.186574	112.259568	53	12.1	9.7	0.558	50.9	34	40.93	10.60	2	2
VS_LoF_20	LoF	8-16	1.18638	112.25944	88	12.9	10.7	0.563	134.8	42	31.50	7.33	2	3
VS_LoF_21	LoF	8-16	1.189754	112.260314	73	12.0	10.0	0.546	68.6	38	31.95	8.11	0	0
VS_LoF_22	LoF	8-16	1.189564	112.2602	67	11.7	9.4	0.579	58.5	39	39.01	11.17	0	0
VS_LoF_23	LoF	8-16	1.189362	112.260054	74	11.8	9.6	0.552	77.0	38	31.35	7.40	0	0
VS_LoF_24	LoF	8-16	1.189168	112.25995	78	11.8	9.5	0.518	62.7	36	25.93	8.67	0	0
VS_LoF_25	LoF	8-16	1.188938	112.259802	61	9.9	7.8	0.508	31.2	28	20.04	2.26	0	0
VS_NaF_1	NaF	nr	1.178268	112.255669	50	15.7	15.1	0.607	193.8	25	19.90	10.00	3	6
VS_NaF_2	NaF	nr	1.178472	112.255554	55	15.8	14.4	0.627	194.8	35	41.43	11.00	2	6
VS_NaF_3	NaF	nr	1.178649	112.255419	55	15.7	15.2	0.609	231.3	31	29.39	7.86	4	8
VS_NaF_4	NaF	nr	1.178833	112.25529	54	14.6	14.0	0.581	193.0	34	39.37	13.50	3	6
VS_NaF_5	NaF	nr	1.17903	112.255182	62	15.6	15.3	0.572	259.5	37	38.67	6.20	3	7
VS_NaF_6	NaF	nr	1.177839	112.256216	73	12.5	13.9	0.618	135.7	35	26.40	10.43	4	7
VS_NaF_7	NaF	nr	1.178036	112.256088	53	18.4	18.3	0.644	213.4	24	16.91	4.82	3	5
VS_NaF_8	NaF	nr	1.178193	112.25598	71	13.4	15.3	0.607	165.2	37	31.16	10.14	4	9
VS_NaF_9	NaF	nr	1.17837	112.255878	81	14.4	15.9	0.642	328.3	29	16.17	5.40	4	7
VS_NaF_10	NaF	nr	1.17856	112.255777	61	14.1	15.8	0.642	172.5	35	34.17	8.71	3	6
VS_NaF_11	NaF	nr	1.17741	112.256825	82	14.2	13.9	0.608	179.1	47	45.80	13.67	3	5
VS_NaF_12	NaF	nr	1.177553	112.256703	58	13.5	14.5	0.601	142.7	37	44.02	9.67	0	2
VS_NaF_13	NaF	nr	1.177716	112.256588	69	13.2	14.2	0.582	154.4	40	39.73	13.80	2	6
VS_NaF_14	NaF	nr	1.177879	112.25646	52	11.8	14.1	0.608	99.8	35	46.94	13.00	2	4
VS_NaF_15	NaF	nr	1.178063	112.256331	81	12.9	15.2	0.605	137.7	41	33.17	11.57	3	6
VS_NaF_16	NaF	nr	1.176906	112.257453	63	11.7	12.6	0.612	107.4	39	43.67	12.60	2	3
VS_NaF_17	NaF	nr	1.177089	112.257338	84	12.1	12.7	0.615	149.6	42	33.43	6.00	1	5
VS_NaF_18	NaF	nr	1.177253	112.25723	82	13.4	13.4	0.594	203.7	46	43.28	11.71	0	2
VS_NaF_19	NaF	nr	1.177409	112.257109	64	12.0	13.0	0.567	79.6	33	27.38	4.57	0	3
VS_NaF_20	NaF	nr	1.177573	112.256973	82	11.1	12.3	0.623	92.9	45	40.90	9.11	0	2
VS_NaF_21	NaF	nr	1.176388	112.258143	44	13.2	13.5	0.593	82.2	36	92.60	22.00	2	3
VS_NaF_22	NaF	nr	1.176538	112.258001	63	12.9	14.1	0.594	125.3	40	47.12	10.50	0	1
VS_NaF_23	NaF	nr	1.176681	112.257872	81	12.8	13.3	0.600	126.0	44	39.37	9.00	0	1
VS_NaF_24	NaF	nr	1.176831	112.257751	70	11.6	11.3	0.598	96.4	47	62.66	8.75	0	0
VS_NaF_25	NaF	nr	1.177001	112.257636	50	12.7	12.2	0.570	76.6	39	81.60	16.67	0	1

Table S3. Erosion plot features. Longitude and latitude of each plot are provided in decimal degrees (WSG84 datum). Plot annual soil loss (ASL) and topsoil carbon (TSC) are also provided. ASL values in grey-tinted cells were discarded for analyses. Land-use types: FcF = food crop field; YsR = young secondary regrowth area; OsR = old secondary regrowth forest; YrG = young rubber garden; OrG = old rubber garden; LoF = logged-over forest; NaF = natural forest.

Plot ID	Land-use type	Time since last disturbance	Latitude	Longitude	Area (m2)	ASL (g m-2 yr-1)	TSC (Mg ha-1)
EM_FcF_1	FcF	< 1	1.155889	112.267436	62.8	2.0	41.8
EM_FcF_2	FcF	< 1	1.156	112.266821	62.0	1.1	52.1
EM_FcF_3	FcF	< 1	1.155766	112.266752	62.9	2.2	81.5
EM_FcF_4	FcF	< 1	1.156822	112.266676	57.4	3.0	36.5
EM_FcF_5	FcF	< 1	1.157298	112.266562	61.0	2.7	52.5
EM_YsR_1	YsR	2	1.149453	112.263905	61.8	5.1	45.9
EM_YsR_2	YsR	2	1.14945	112.263943	60.6	1.3	41
EM_YsR_3	YsR	2	1.14943	112.264278	62.8	0.5	39.1
EM_YsR_4	YsR	7	1.157152	112.264705	60.6	2.1	46.4
EM_YsR_5	YsR	7	1.157101	112.264659	60.8	1.8	35.1
EM_OsR_1	OsR	40	1.158634	112.264258	61.4	1.6	46.8
EM_OsR_2	OsR	40	1.158658	112.264278	58.9	1.5	33.1
EM_OsR_3	OsR	50	1.159828	112.264782	62.0	0.7	47.3
EM_OsR_4	OsR	60	1.159854	112.264761	61.5	1.2	44.1
EM_OsR_5	OsR	60	1.161566	112.267882	62.0	1.3	37.6
EM_YrG_1	YrG	6	1.151945	112.263198	64.9	8.1	45.2
EM_YrG_2	YrG	6	1.152062	112.263361	66.4	0.6	57.6
EM_YrG_3	YrG	7	1.152608	112.263779	61.8	1.0	52
EM_YrG_4	YrG	8	1.152592	112.26304	64.8	0.7	47.1
EM_YrG_5	YrG	8	1.152697	112.262982	63.8	1.2	62.6
EM_OrG_1	OrG	40	1.152559	112.262313	64.1	2.2	54.9
EM_OrG_2	OrG	40	1.155363	112.263976	60.4	1.1	46.2
EM_OrG_3	OrG	40	1.155421	112.263962	61.4	0.9	39.2
EM_OrG_4	OrG	50	1.158001	112.262115	60.8	1.8	32.6
EM_OrG_5	OrG	50	1.157935	112.261928	64.3	2.1	55.4
EM_LoF_1	LoF	8-16	1.176274	112.265437	60.8	2.6	56.4
EM_LoF_2	LoF	8-16	1.175116	112.265564	61.0	0.6	88.6
EM_LoF_3	LoF	8-16	1.167234	112.268307	60.8	4.2	31.6
EM_LoF_4	LoF	8-16	1.16671	112.268058	62.0	1.3	48.1
EM_LoF_5	LoF	8-16	1.166541	112.26813	63.9	1.3	45.5
EM_NaF_1	NaF	nr	1.17767	112.256766	61.0	0.9	116.9
EM_NaF_2	NaF	nr	1.178084	112.256603	61.0	1.3	63.5
EM_NaF_3	NaF	nr	1.178816	112.255753	60.6	0.7	69.9
EM_NaF_4	NaF	nr	1.177916	112.256138	57.6	0.5	110
EM_NaF_5	NaF	nr	1.177873	112.256286	59.5	0.7	119.2

Table S4. Statistical analyses on ecosystem service and tree diversity indicators. We used original indicator values when the distribution was normal and log_{10}-transformed values otherwise. The vegetation set did not include food crop field plots under the assumption that tree diversity and aboveground carbon would be null. Depicted values are either test statistics (for Moran's I, Lagrange Multiplier and the selected model) or model coefficients, and are presented along with information on statistical significance. For the Berger-Parker index, despite some spatial auto-correlation, the spatial dependence coefficient of the spatial error model was not significant. We therefore used a regular linear model and acknowledge that results for this indicator might be slightly biased due to spatial auto-correlation.

Plot set (nb plots)		Vegetation set (98)				Erosion set (35)	
Indicator [1]		AGC	Species richness	Fisher's α	Berger-Parker index	TSC	ASL
Data format		log_{10}	original	log_{10}	log_{10}	log_{10}	log_{10}
Moran's I	on variable	0.41 ***	0.57 ***	0.46 ***	0.38 ***	0.46 ***	0.21 ns
	on linear model residuals	0.08 ***	0.19 ***	0.08 ***	0.05 **	-0.11 ns	0.01 ns
Lagrange Multiplier (LM)	LM_{err}	4.52 *	18.73 ***	4.93 ***	1.74 ns	–	–
	LM_{lag}	2.74 ns	12.92 ***	1.16 ns	0.66 ns	–	–
Selected model type [2]		sem	sem	sem	lm	lm	lm
Model statistic [3]		10.73 **	96.81 ***	11.82 ***	21.32 ***	6.20 ***	2.80 *
Model coefficients	Intercept (NaF)	2.18 ***	40.27 ***	1.62 ***	0.99 ***	1.97 ***	-0.11 ns
	FcF	–	–	–	–	-0.26 ***	0.43 **
	LoF	-0.42 ***	-5.11 ns	-0.2 ns	-0.22 ***	-0.26 ***	0.21 ns
	OrG	-0.42 ***	-22.78 ***	-0.48 ***	-0.35 ***	-0.32 ***	0.29 *
	OsR	-0.39 ***	-17.55 ***	-0.42 ***	-0.28 ***	-0.35 ***	0.19 ns
	YrG	-0.76 ***	-30.07 ***	-1.05 ***	-0.64 ***	-0.25 **	0.03 ns
	YsR	-0.87 ***	-24.93 ***	-0.84 ***	-0.52 ***	-0.35 ***	0.20 ns
	Spatial dependence [4]	0.59 *	0.86 ***	0.61 *	–	–	–

[1] Indicator: AGC = aboveground carbon; TSC = topsoil carbon; ASL = annual soil loss

[2] sem = spatial error model; lm = linear model

[3] F statistic for linear models; Wald statistic for spatial error/lag model

[4] Rho in case of spatial lag model, Lambda in case of spatial error model

n.s. non-significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table S5. Species surveyed in each land-use type. Data from plots under the same land-use type (12 for young and old rubber gardens and fallows and 25 for logged-over and natural forests) were pooled together. IUCN conservation status is provided for each species (CR = Critically Endangered; EN = Endangered; VU = Vulnerable; LR/cd = Lower Risk: Conservation Dependent; LR/nt = Lower Risk: Near Threatened; DD = Data Deficient; LC or LR/lc = Least Concern). In order to be conservative, any species identified to the genus level only (e.g. *Aglaia* sp.3) or absent from the IUCN Red List was given a "LC" status.

1) YsR (young secondary regrowth area)

Genus	Species	Author(s)	Family	IUCN status
Adinandra	*dumosa*	Jack	Pentaphylacaceae	LC
Anisophyllea	*corneri*	Ding Hou	Anisophylleaceae	LR/lc
Antidesma	*leucopodum*	Miq.	Phyllanthaceae	LC
Antidesma	*neurocarpum*	Miq.	Phyllanthaceae	LC
Archidendron	*clypearia*	(Jack) I.C.Nielsen	Leguminosae	LC
Archidendron	*havilandii*	(Ridl.) I.C.Nielsen	Leguminosae	LC
Artocarpus	*kemando*	Miq.	Moraceae	LC
Artocarpus	*odoratissimus*	Blanco	Moraceae	LC
Baccaurea	*polyneura*	Hook.f.	Phyllanthaceae	LR/cd
Baccaurea	*sumatrana*	(Miq.) Müll.Arg.	Phyllanthaceae	LC
Bacopa	*paraguariensis*	subsp. congesta (Chodat & Hassl.) Hassl.	Plantaginaceae	LC
Bellucia	*pentamera*	Naudin	Melastomataceae	LC
Brookea	*tomentosa*	Benth.	Plantaginaceae	LC
Buchanania	*sessilifolia*	Blume	Anacardiaceae	LC
Calophyllum	*pseudomolle*	P.F.Stevens	Clusiaceae	LC
Cratoxylum	*arborescens*	(Vahl) Blume	Hypericaceae	LR/lc
Cratoxylum	*formosum*	(Jacq.) Benth. & Hook.f. ex Dyer	Hypericaceae	LR/lc
Crypteronia	*cumingii*	(Planch.) Endl.	Penaeaceae	LC
Dillenia	*suffruticosa*	(Griff.) Martelli	Dilleniaceae	LC
Durio	*graveolens*	Becc.	Malvaceae	LC
Elaeocarpus	*mastersii*	King	Elaeocarpaceae	LC
Elaeocarpus	*stipularis*	var. castaneus (Merr.) Coode	Elaeocarpaceae	LC
Ellipanthus	*tomentosus*	Kurz	Connaraceae	LC
Endertia	*spectabilis*	Steenis & de Wit	Leguminosae	LC
Endospermum	*diadenum*	(Miq.) Airy Shaw	Euphorbiaceae	LC
Fagraea	*racemosa*	Jack	Gentianaceae	LC
Ficus	*aurata*	(Miq.) Miq.	Moraceae	LC
Ficus	*fulva*	Reinw. ex Blume	Moraceae	LC
Ficus	*grossularioides*	Burm.f.	Moraceae	LC
Ficus	*obscura*	Blume	Moraceae	LC
Ficus	*recurva*	var. pedicellata Corner	Moraceae	LC
Ficus	sp.1		Moraceae	LC
Ficus	*variegata*	Blume	Moraceae	LC
Garcinia	*caudiculata*	Ridl.	Clusiaceae	LC
Glochidion	*lutescens*	Blume	Phyllanthaceae	LC
Glochidion	*philippicum*	(Cav.) C.B.Rob.	Phyllanthaceae	LC
Glochidion	*rubrum*	Blume	Phyllanthaceae	LC
Guioa	*pleuropteris*	(Blume) Radlk.	Sapindaceae	LC
Hevea	*brasiliensis*	(Willd. ex A.Juss.) Müll.Arg.	Euphorbiaceae	LC
Horsfieldia	*grandis*	(Hook.f.) Warb.	Myristicaceae	LR/lc
Ilex	*cissoidea*	Loes.	Aquifoliaceae	LC
Ixonanthes	*petiolaris*	Blume	Ixonanthaceae	LC
Koompassia	*malaccensis*	Benth.	Leguminosae	LR/cd
Lansium	*parasiticum*	(Osbeck) K.C.Sahni & Bennet	Meliaceae	LC
Leea	*indica*	(Burm. f.) Merr.	Vitaceae	LC
Lithocarpus	*coopertus*	(Blanco) Rehder	Fagaceae	LC
Litsea	*elliptica*	Blume	Lauraceae	LC
Macaranga	*beccariana*	Merr.	Euphorbiaceae	LC
Macaranga	*conifera*	(Rchb.f. & Zoll.) Müll.Arg.	Euphorbiaceae	LC
Macaranga	*costulata*	Pax & K.Hoffm.	Euphorbiaceae	LC
Macaranga	*gigantea*	(Rchb.f. & Zoll.) Müll.Arg.	Euphorbiaceae	LC

Genus	Species	Author(s)	Family	IUCN status
Macaranga	*hypoleuca*	(Rchb.f. & Zoll.) Müll.Arg.	Euphorbiaceae	LC
Macaranga	*pearsonii*	Merr.	Euphorbiaceae	LC
Macaranga	*recurvata*	Gage	Euphorbiaceae	LC
Macaranga	sp.1		Euphorbiaceae	LC
Mallotus	*paniculatus*	(Lam.) Müll.Arg.	Euphorbiaceae	LC
Melicope	*glabra*	(Blume) T.G. Hartley	Rutaceae	LC
Nauclea	*officinalis*	(Pierre ex Pit.) Merr. & Chun	Rubiaceae	LC
Nephelium	*uncinatum*	Radlk. ex Leenh.	Sapindaceae	LC
Phyllanthus	*borneensis*	Müll.Arg.	Phyllanthaceae	LC
Prunus	*arborea*	(Blume) Kalkman	Rosaceae	LR/lc
Prunus	*arborea*	var. stipulacea (King) Kalkman	Rosaceae	LR/lc
Pseuduvaria	*reticulata*	(Blume) Miq.	Annonaceae	LC
Santiria	*tomentosa*	Blume	Burseraceae	LR/lc
Saurauia	*reinwardtiana*	Blume	Actinidiaceae	LC
Saurauia	*subcordata*	Korth.	Actinidiaceae	LC
Symplocos	*fasciculata*	Zoll.	Symplocaceae	LC
Syzygium	*fastigiatum*	(Blume) Merr. & L.M.Perry	Myrtaceae	LC
Syzygium	*glomeratum*	(Lam.) DC.	Myrtaceae	LC
Syzygium	*grande*	(Wight) Walp.	Myrtaceae	LC
Syzygium	*oligomyrum*	Diels	Myrtaceae	LC
Syzygium	*pallidilimbum*	Merr. & L.M.Perry	Myrtaceae	LC
Syzygium	*polyanthum*	(Wight) Walp.	Myrtaceae	LC
Syzygium	sp.1		Myrtaceae	LC
Timonius	*borneensis*	Valeton	Rubiaceae	LC
Triadica	*cochinchinensis*	Lour.	Euphorbiaceae	LC
Urophyllum	*corymbosum*	(Blume) Korth.	Rubiaceae	LC
Vernonia	*arborea*	Buch.-Ham.	Compositae	LC
Vitex	*pinnata*	L.	Lamiaceae	LC
Vitex	*quinata*	(Lour.) F.N.Williams	Lamiaceae	LC
Xanthophyllum	*adenotus*	Miq.	Polygalaceae	LC
Xanthophyllum	*ellipticum*	Korth. ex Miq.	Polygalaceae	LC
Xylopia	*ferruginea*	(Hook.f. & Thomson) Baill.	Annonaceae	LC

2) OsR (old secondary regrowth forest)

Genus	Species	Author(s)	Family	IUCN status
Adinandra	*dumosa*	Jack	Pentaphylacaceae	LC
Aglaia	*silvestris*	(M.Roem.) Merr.	Meliaceae	LR/nt
Anisophyllea	*corneri*	Ding Hou	Anisophylleaceae	LR/lc
Antidesma	*leucopodum*	Miq.	Phyllanthaceae	LC
Antidesma	*neurocarpum*	Miq.	Phyllanthaceae	LC
Aporosa	*confusa*	Gage	Phyllanthaceae	LC
Aporosa	*falcifera*	Hook.f.	Phyllanthaceae	LC
Archidendron	*clypearia*	(Jack) I.C.Nielsen	Leguminosae	LC
Ardisia	*sanguinolenta*	Blume	Primulaceae	LC
Artocarpus	*dadah*	Miq.	Moraceae	LC
Artocarpus	*elasticus*	Reinw. ex Blume	Moraceae	LC
Artocarpus	*integer*	(Thunb.) Merr.	Moraceae	LC
Artocarpus	*nitidus*	Trécul	Moraceae	LC
Artocarpus	*odoratissimus*	Blanco	Moraceae	LC
Baccaurea	*macrophylla*	(Müll.Arg.) Müll.Arg.	Phyllanthaceae	LC
Baccaurea	*polyneura*	Hook.f.	Phyllanthaceae	LR/cd
Baccaurea	*sumatrana*	(Miq.) Müll.Arg.	Phyllanthaceae	LC
Baccaurea	*tetrandra*	(Baill.) Müll.Arg.	Phyllanthaceae	LC
Barringtonia	*lanceolata*	(Ridl.) Payens	Lecythidaceae	LC
Barringtonia	*macrostachya*	(Jack) Kurz	Lecythidaceae	LC
Beilschmiedia	*rivularis*	Kosterm.	Lauraceae	LC
Bellucia	*pentamera*	Naudin	Melastomataceae	LC
Bhesa	*paniculata*	Arn.	Centroplacaceae	LR/lc
Buchanania	*sessilifolia*	Blume	Anacardiaceae	LC
Byttneria	sp.1		Malvaceae	LC
Calophyllum	*pseudomolle*	P.F.Stevens	Clusiaceae	LC
Calophyllum	sp.2		Calophyllaceae	LC
Calophyllum	*teysmannii*	Miq.	Clusiaceae	LC
Campnosperma	*coriaceum*	(Jack) Hallier f.	Anacardiaceae	LC

Genus	Species	Author(s)	Family	IUCN status
Castanopsis	*hypophoenicea*	(Seemen) Soepadmo	Fagaceae	LC
Castanopsis	*inermis*	(Lindl.) Benth. & Hook.f.	Fagaceae	LC
Cephalomappa	*malloticarpa*	J.J.Sm.	Euphorbiaceae	LC
Cratoxylum	*arborescens*	(Vahl) Blume	Hypericaceae	LR/lc
Crypteronia	*cumingii*	(Planch.) Endl.	Penaeaceae	LC
Dacryodes	*rostrata*	(Blume) H.J.Lam	Burseraceae	LR/lc
Dialium	*indum*	L.	Leguminosae	LC
Dillenia	*excelsa*	(Jack) Martelli ex Gilg.	Dilleniaceae	LC
Dillenia	*suffruticosa*	(Griff.) Martelli	Dilleniaceae	LC
Dimocarpus	*longan*	var. malaiensis Lour.	Sapindaceae	LR/nt
Diospyros	*borneensis*	Hiern	Ebenaceae	LC
Diospyros	*venosa*	Wall. ex A.DC.	Ebenaceae	LC
Dipterocarpus	*crinitus*	Dyer	Dipterocarpaceae	EN
Drepananthus	*ramuliflorus*	Maingay ex Hook.f. & Thomson	Annonaceae	LC
Durio	*zibethinus*	L.	Malvaceae	LC
Elaeocarpus	*mastersii*	King	Elaeocarpaceae	LC
Elaeocarpus	*polystachyus*	Wall. ex Müll.Berol.	Elaeocarpaceae	LC
Endospermum	*diadenum*	(Miq.) Airy Shaw	Euphorbiaceae	LC
Fagraea	*racemosa*	Jack	Gentianaceae	LC
Ficus	*aurata*	(Miq.) Miq.	Moraceae	LC
Ficus	*fulva*	Reinw. ex Blume	Moraceae	LC
Ficus	*obscura*	Blume	Moraceae	LC
Ficus	*variegata*	Blume	Moraceae	LC
Ficus	*vasculosa*	Wall. ex Miq.	Moraceae	LC
Fordia	*splendidissima*	(Miq.) Buijsen	Leguminosae	LC
Garcinia	*bancana*	Miq.	Clusiaceae	LC
Garcinia	*caudiculata*	Ridl.	Clusiaceae	LC
Garcinia	*lateriflora*	Blume	Clusiaceae	LC
Garcinia	*mangostana*	L.	Clusiaceae	LC
Garcinia	*parvifolia*	(Miq.) Miq.	Clusiaceae	LC
Gardenia	*tubifera*	Wall. ex Roxb.	Rubiaceae	LC
Gironniera	*subaequalis*	Planch.	Cannabaceae	LC
Glochidion	*philippicum*	(Cav.) C.B.Rob.	Phyllanthaceae	LC
Gynotroches	*axillaris*	Blume	Rhizophoraceae	LC
Hancea	*penangensis*	(Müll.Arg.) S.E.C.Sierra, Kulju & Welzen	Euphorbiaceae	LC
Hevea	*brasiliensis*	(Willd. ex A.Juss.) Müll.Arg.	Euphorbiaceae	LC
Horsfieldia	*grandis*	(Hook.f.) Warb.	Myristicaceae	LR/lc
Hydnocarpus	*castanea*	Hook.f. & Thomson	Achariaceae	LC
Ilex	*cissoidea*	Loes.	Aquifoliaceae	LC
Ilex	*cymosa*	Blume	Aquifoliaceae	LC
Intsia	*palembanica*	Miq.	Leguminosae	LC
Ixonanthes	*petiolaris*	Blume	Ixonanthaceae	LC
Knema	*latericia*	Elmer	Myristicaceae	LC
Knema	*laurina*	Warb.	Myristicaceae	LC
Kokoona	*ochracea*	Merr.	Celastraceae	LC
Koompassia	*excelsa*	(Becc.) Taub.	Leguminosae	LR/cd
Koompassia	*malaccensis*	Benth.	Leguminosae	LR/cd
Lithocarpus	*coopertus*	(Blanco) Rehder	Fagaceae	LC
Lithocarpus	*gracilis*	(Korth.) Soepadmo	Fagaceae	LC
Lithocarpus	*leptogyne*	(Korth.) Soepadmo	Fagaceae	LC
Lithocarpus	*urceolaris*	(Jack) Merr.	Fagaceae	LC
Litsea	*elliptica*	Blume	Lauraceae	LC
Litsea	*sessiliflora*	Hook.f.	Lauraceae	LC
Maasia	*glauca*	(Hassk.) Mols, Kessler & Rogstad	Annonaceae	LC
Macaranga	*gigantea*	(Rchb.f. & Zoll.) Müll.Arg.	Euphorbiaceae	LC
Macaranga	*pearsonii*	Merr.	Euphorbiaceae	LC
Macaranga	*recurvata*	Gage	Euphorbiaceae	LC
Macaranga	sp.1		Euphorbiaceae	LC
Mallotus	*paniculatus*	(Lam.) Müll.Arg.	Euphorbiaceae	LC
Mastixia	*cuspidata*	Blume	Cornaceae	LC
Microcos	*crassifolia*	Burret	Malvaceae	LC
Microcos	*latifolia*	Burret	Malvaceae	LC
Myristica	*maxima*	Warb.	Myristicaceae	LR/lc
Nauclea	*officinalis*	(Pierre ex Pit.) Merr. & Chun	Rubiaceae	LC
Nephelium	*cuspidatum*	Blume	Sapindaceae	LC
Nephelium	*mangayi*	Hiern	Sapindaceae	LC

Genus	Species	Author(s)	Family	IUCN status
Nephelium	*ramboutan-ake*	(Labill.) Leenh.	Sapindaceae	LC
Nephelium	*uncinatum*	Radlk. ex Leenh.	Sapindaceae	LC
Norrisia	*maior*	Soler.	Loganiaceae	LC
Ochanostachys	*amentacea*	Mast.	Olacaceae	DD
Palaquium	*dasyphyllum*	Pierre ex Dubard	Sapotaceae	LC
Palaquium	*quercifolium*	(de Vriese) Burck	Sapotaceae	LC
Parastemon	*urophyllus*	(Wall. ex A.DC.) A.DC.	Chrysobalanaceae	LC
Pellacalyx	*axillaris*	Korth.	Rhizophoraceae	LC
Pimelodendron	*griffithianum*	(Müll.Arg.) Benth. ex Hook.f.	Euphorbiaceae	LC
Porterandia	*anisophylla*	(Jack ex Roxb.) Ridl.	Rubiaceae	LC
Prunus	*arborea*	(Blume) Kalkman	Rosaceae	LR/lc
Prunus	*grisea*	(Blume ex Müll.Berol.) Kalkman	Rosaceae	LR/lc
Prunus	*javanica*	(Teijsm. & Binn.) Miq.	Rosaceae	LR/lc
Pternandra	*crassicalyx*	J.F.Maxwell	Melastomataceae	LC
Santiria	*rubiginosa*	Blume	Burseraceae	LC
Santiria	sp.		Burseraceae	LC
Santiria	*tomentosa*	Blume	Burseraceae	LR/lc
Sarcotheca	*diversifolia*	Hallier f.	Connaraceae	LC
Saurauia	*subcordata*	Korth.	Actinidiaceae	LC
Semecarpus	*glauca*	Engl.	Anacardiaceae	LC
Shorea	*beccariana*	Burck	Dipterocarpaceae	LC
Shorea	*beccariana*	cf. Burck	Dipterocarpaceae	LC
Shorea	*confusa*	P.S.Ashton	Dipterocarpaceae	LC
Sloetia	*elongata*	Koord.	Moraceae	LC
Sterculia	sp.1		Malvaceae	LC
Symplocos	*fasciculata*	Zoll.	Symplocaceae	LC
Symplocos	*henschelii*	(Moritzi) Benth. ex C.B. Clarke	Symplocaceae	LC
Syzygium	*fastigiatum*	(Blume) Merr. & L.M.Perry	Myrtaceae	LC
Syzygium	*glomeratum*	(Lam.) DC.	Myrtaceae	LC
Syzygium	*grande*	(Wight) Walp.	Myrtaceae	LC
Syzygium	*lineatum*	(DC.) Merr. & L.M.Perry	Myrtaceae	LC
Syzygium	*oligomyrum*	Diels	Myrtaceae	LC
Syzygium	*pallidilimbum*	Merr. & L.M.Perry	Myrtaceae	LC
Syzygium	*polyanthum*	(Wight) Walp.	Myrtaceae	LC
Syzygium	sp.1		Myrtaceae	LC
Syzygium	*tawahense*	(Korth.) Merr. & L.M.Perry	Myrtaceae	LC
Timonius	*borneensis*	Valeton	Rubiaceae	LC
Trigonopleura	*malayana*	Hook.f.	Peraceae	LC
Tristaniopsis	*obovata*	(Benn.) Peter G.Wilson & J.T.Waterh.	Myrtaceae	LC
Tristaniopsis	*whiteana*	(Griff.) Peter G.Wilson & J.T.Waterh.	Myrtaceae	LC
Urophyllum	*corymbosum*	(Blume) Korth.	Rubiaceae	LC
Vernonia	*arborea*	Buch.-Ham.	Compositae	LC
Vitex	*pinnata*	L.	Lamiaceae	LC
Vitex	*quinata*	(Lour.) F.N.Williams	Lamiaceae	LC
Xanthophyllum	*amoenum*	Chodat	Polygalaceae	LC
Xylopia	*altissima*	Boerl.	Annonaceae	LC
Xylopia	*ferruginea*	(Hook.f. & Thomson) Baill.	Annonaceae	LC

3) YrG (young rubber garden)

Genus	Species	Author(s)	Family	IUCN status
Adinandra	*dumosa*	Jack	Pentaphylacaceae	LC
Antidesma	*leucopodum*	Miq.	Phyllanthaceae	LC
Aporosa	*confusa*	Gage	Phyllanthaceae	LC
Archidendron	*clypearia*	(Jack) I.C.Nielsen	Leguminosae	LC
Archidendron	*havilandii*	(Ridl.) I.C.Nielsen	Leguminosae	LC
Artocarpus	*elasticus*	Reinw. ex Blume	Moraceae	LC
Artocarpus	*integer*	(Thunb.) Merr.	Moraceae	LC
Artocarpus	*kemando*	Miq.	Moraceae	LC
Artocarpus	*teysmannii*	Miq.	Moraceae	LC
Baccaurea	*macrophylla*	(Müll.Arg.) Müll.Arg.	Phyllanthaceae	LC
Bellucia	*pentamera*	Naudin	Melastomataceae	LC
Bhesa	*paniculata*	Arn.	Centroplacaceae	LR/lc
Buchanania	*sessilifolia*	Blume	Anacardiaceae	LC
Calophyllum	*pseudomolle*	P.F.Stevens	Clusiaceae	LC

Genus	Species	Author(s)	Family	IUCN status
Citrus	*aurantium*	L.	Rutaceae	LC
Cratoxylum	*arborescens*	(Vahl) Blume	Hypericaceae	LR/lc
Cratoxylum	*formosum*	(Jacq.) Benth. & Hook.f. ex Dyer	Hypericaceae	LR/lc
Cratoxylum	*sumatranum*	(Jack) Blume	Hypericaceae	LC
Dacryodes	*rostrata*	(Blume) H.J.Lam	Burseraceae	LR/lc
Dillenia	*indica*	L.	Dilleniaceae	LC
Dillenia	*suffruticosa*	(Griff.) Martelli	Dilleniaceae	LC
Dimocarpus	*longan*	Lour.	Sapindaceae	LR/nt
Durio	*graveolens*	Becc.	Malvaceae	LC
Durio	*zibethinus*	L.	Malvaceae	LC
Elaeocarpus	*stipularis*	var. castaneus (Merr.) Coode	Elaeocarpaceae	LC
Endospermum	*diadenum*	(Miq.) Airy Shaw	Euphorbiaceae	LC
Ficus	*aurata*	(Miq.) Miq.	Moraceae	LC
Ficus	*fulva*	Reinw. ex Blume	Moraceae	LC
Hevea	*brasiliensis*	(Willd. ex A.Juss.) Müll.Arg.	Euphorbiaceae	LC
Horsfieldia	*grandis*	(Hook.f.) Warb.	Myristicaceae	LR/lc
Ilex	*cissoidea*	Loes.	Aquifoliaceae	LC
Ilex	*cymosa*	Blume	Aquifoliaceae	LC
Ixonanthes	*petiolaris*	Blume	Ixonanthaceae	LC
Koompassia	*excelsa*	(Becc.) Taub.	Leguminosae	LR/cd
Lithocarpus	*blumeanus*	(Korth.) Rehder	Fagaceae	LC
Lithocarpus	*leptogyne*	(Korth.) Soepadmo	Fagaceae	LC
Litsea	*elliptica*	Blume	Lauraceae	LC
Macaranga	*beccariana*	Merr.	Euphorbiaceae	LC
Macaranga	*gigantea*	(Rchb.f. & Zoll.) Müll.Arg.	Euphorbiaceae	LC
Macaranga	*pearsonii*	Merr.	Euphorbiaceae	LC
Macaranga	*recurvata*	Gage	Euphorbiaceae	LC
Mangifera	*laurina*	Blume	Anacardiaceae	LC
Mangifera	*longipetiolata*	King	Anacardiaceae	LC
Melanochyla	*fulvinervia*	(Blume) Ding Hou	Anacardiaceae	LC
Nauclea	*officinalis*	(Pierre ex Pit.) Merr. & Chun	Rubiaceae	LC
Nephelium	*juglandifolium*	Blume	Sapindaceae	LC
Nephelium	*lappaceum*	L.	Sapindaceae	LR/lc
Norrisia	*maior*	Soler.	Loganiaceae	LC
Norrisia	*malaccensis*	Gardner	Loganiaceae	LC
Parkia	*timoriana*	(DC.) Merr.	Leguminosae	LC
Pimelodendron	*griffithianum*	(Müll.Arg.) Benth. ex Hook.f.	Euphorbiaceae	LC
Prunus	*arborea*	(Blume) Kalkman	Rosaceae	LR/lc
Prunus	*arborea*	var. stipulacea (King) Kalkman	Rosaceae	LR/lc
Saurauia	*bracteolata*	DC.	Actinidiaceae	LC
Shorea	*beccariana*	cf. Burck	Dipterocarpaceae	LC
Syzygium	*polyanthum*	(Wight) Walp.	Myrtaceae	LC
Tarenna	*confusa*	(Blume) Valeton	Rubiaceae	LC
Timonius	*borneensis*	Valeton	Rubiaceae	LC
Vernonia	*arborea*	Buch.-Ham.	Compositae	LC
Vitex	*pinnata*	L.	Lamiaceae	LC
Vitex	*quinata*	(Lour.) F.N.Williams	Lamiaceae	LC
Xylopia	*ferruginea*	(Hook.f. & Thomson) Baill.	Annonaceae	LC

4) OrG (old rubber garden)

Genus	Species	Author(s)	Family	IUCN status
Adinandra	*dumosa*	Jack	Pentaphylacaceae	LC
Anisophyllea	*corneri*	Ding Hou	Anisophylleaceae	LR/lc
Antidesma	*leucopodum*	Miq.	Phyllanthaceae	LC
Antidesma	*neurocarpum*	Miq.	Phyllanthaceae	LC
Aporosa	*confusa*	Gage	Phyllanthaceae	LC
Archidendron	*clypearia*	(Jack) I.C.Nielsen	Leguminosae	LC
Archidendron	*havilandii*	(Ridl.) I.C.Nielsen	Leguminosae	LC
Artocarpus	*anisophyllus*	Miq.	Moraceae	LC
Artocarpus	*elasticus*	Reinw. ex Blume	Moraceae	LC
Artocarpus	*integer*	(Thunb.) Merr.	Moraceae	LC
Artocarpus	*kemando*	Miq.	Moraceae	LC
Artocarpus	*odoratissimus*	Blanco	Moraceae	LC
Baccaurea	*edulis*	Merr.	Phyllanthaceae	LC

Genus	Species	Author(s)	Family	IUCN status
Baccaurea	*macrophylla*	(Müll.Arg.) Müll.Arg.	Phyllanthaceae	LC
Baccaurea	*minor*	Hook.f.	Phyllanthaceae	LC
Baccaurea	*polyneura*	Hook.f.	Phyllanthaceae	LR/cd
Baccaurea	*sumatrana*	(Miq.) Müll.Arg.	Phyllanthaceae	LC
Barringtonia	*lanceolata*	(Ridl.) Payens	Lecythidaceae	LC
Bellucia	*pentamera*	Naudin	Melastomataceae	LC
Bhesa	*paniculata*	Arn.	Centroplacaceae	LR/lc
Buchanania	*arborescens*	(Blume) Blume	Anacardiaceae	LC
Buchanania	*sessilifolia*	Blume	Anacardiaceae	LC
Calophyllum	*pseudomolle*	P.F.Stevens	Clusiaceae	LC
Calophyllum	*soulattri*	Burm.f.	Clusiaceae	LR/lc
Calophyllum	*tetrapterum*	Miq.	Clusiaceae	LR/lc
Calophyllum	*teysmannii*	Miq.	Clusiaceae	LC
Campnosperma	*coriaceum*	(Jack) Hallier f.	Anacardiaceae	LC
Castanopsis	*megacarpa*	Gamble	Fagaceae	LC
Cratoxylum	*arborescens*	(Vahl) Blume	Hypericaceae	LR/lc
Cratoxylum	*formosum*	(Jacq.) Benth. & Hook.f. ex Dyer	Hypericaceae	LR/lc
Cratoxylum	*sumatranum*	(Jack) Blume	Hypericaceae	LC
Crypteronia	*cumingii*	(Planch.) Endl.	Penaeaceae	LC
Dacryodes	*rostrata*	(Blume) H.J.Lam	Burseraceae	LR/lc
Dialium	*indum*	L.	Leguminosae	LC
Dialium	*platysepalum*	Baker	Leguminosae	LC
Dillenia	*suffruticosa*	(Griff.) Martelli	Dilleniaceae	LC
Dimocarpus	*longan*	var. malaiensis Lour.	Sapindaceae	LR/nt
Elaeocarpus	*mastersii*	King	Elaeocarpaceae	LC
Elaeocarpus	*stipularis*	var. castaneus (Merr.) Coode	Elaeocarpaceae	LC
Engelhardtia	*serrata*	Blume	Juglandaceae	LR/lc
Ficus	*glandulifera*	(Wall. ex Miq.) King	Moraceae	LC
Garcinia	*caudiculata*	Ridl.	Clusiaceae	LC
Garcinia	*mangostana*	L.	Clusiaceae	LC
Garcinia	*parvifolia*	(Miq.) Miq.	Clusiaceae	LC
Gardenia	*tubifera*	Wall. ex Roxb.	Rubiaceae	LC
Gironniera	*nervosa*	Planch.	Cannabaceae	LC
Gironniera	*subaequalis*	Planch.	Cannabaceae	LC
Guioa	*pleuropteris*	(Blume) Radlk.	Sapindaceae	LC
Hevea	*brasiliensis*	(Willd. ex A.Juss.) Müll.Arg.	Euphorbiaceae	LC
Homalanthus	*populneus*	(Geiseler) Pax	Euphorbiaceae	LC
Horsfieldia	*grandis*	(Hook.f.) Warb.	Myristicaceae	LR/lc
Ixonanthes	*petiolaris*	Blume	Ixonanthaceae	LC
Knema	*laurina*	Warb.	Myristicaceae	LC
Koompassia	*malaccensis*	Benth.	Leguminosae	LR/cd
Lansium	*parasiticum*	(Osbeck) K.C.Sahni & Bennet	Meliaceae	LC
Lithocarpus	*bennettii*	(Miq.) Rehder	Fagaceae	LC
Lithocarpus	*urceolaris*	(Jack) Merr.	Fagaceae	LC
Litsea	*elliptica*	Blume	Lauraceae	LC
Litsea	*garciae*	Vidal	Lauraceae	LC
Macaranga	*depressa*	(Müll.Arg.) Müll.Arg.	Euphorbiaceae	LC
Macaranga	*hypoleuca*	(Rchb.f. & Zoll.) Müll.Arg.	Euphorbiaceae	LC
Macaranga	*pearsonii*	Merr.	Euphorbiaceae	LC
Macaranga	*recurvata*	Gage	Euphorbiaceae	LC
Mallotus	*mollissimus*	(Geiseler) Airy Shaw	Euphorbiaceae	LC
Nauclea	*officinalis*	(Pierre ex Pit.) Merr. & Chun	Rubiaceae	LC
Nephelium	*cuspidatum*	Blume var. robustum (Radlk.) Leenh.	Sapindaceae	LC
Nephelium	*cuspidatum*	Blume	Sapindaceae	LC
Nephelium	*juglandifolium*	Blume	Sapindaceae	LC
Nephelium	*lappaceum*	L.	Sapindaceae	LR/lc
Nephelium	*mangayi*	Hiern	Sapindaceae	LC
Nephelium	*ramboutan-ake*	(Labill.) Leenh.	Sapindaceae	LC
Nephelium	*uncinatum*	Radlk. ex Leenh.	Sapindaceae	LC
Norrisia	*maior*	Soler.	Loganiaceae	LC
Norrisia	*malaccensis*	Gardner	Loganiaceae	LC
Ochanostachys	*amentacea*	Mast.	Olacaceae	DD
Palaquium	*quercifolium*	(de Vriese) Burck	Sapotaceae	LC
Pentace	*triptera*	Mast.	Malvaceae	LC
Pimelodendron	*griffithianum*	(Müll.Arg.) Benth. ex Hook.f.	Euphorbiaceae	LC
Porterandia	*anisophylla*	(Jack ex Roxb.) Ridl.	Rubiaceae	LC

Genus	Species	Author(s)	Family	IUCN status
Prunus	*arborea*	(Blume) Kalkman	Rosaceae	LR/lc
Psychotria	*viridiflora*	Reinw. ex Blume	Rubiaceae	LC
Pternandra	*crassicalyx*	J.F.Maxwell	Melastomataceae	LC
Santiria	*rubiginosa*	Blume	Burseraceae	LC
Santiria	sp.		Burseraceae	LC
Sarcotheca	*diversifolia*	Hallier f.	Connaraceae	LC
Semecarpus	*glauca*	Engl.	Anacardiaceae	LC
Shorea	*beccariana*	cf. Burck	Dipterocarpaceae	LC
Sympetalandra	*borneensis*	Stapf	Leguminosae	LC
Symplocos	*fasciculata*	Zoll.	Symplocaceae	LC
Syzygium	*glomeratum*	(Lam.) DC.	Myrtaceae	LC
Syzygium	*grande*	(Wight) Walp.	Myrtaceae	LC
Syzygium	*leptostemon*	(Korth.) Merr. & L.M.Perry	Myrtaceae	LC
Syzygium	*pallidilimbum*	Merr. & L.M.Perry	Myrtaceae	LC
Syzygium	*polyanthum*	(Wight) Walp.	Myrtaceae	LC
Syzygium	sp.1		Myrtaceae	LC
Syzygium	*tawahense*	(Korth.) Merr. & L.M.Perry	Myrtaceae	LC
Syzygium	*valdevenosum*	(Duthie) Merr. & L.M.Perry	Myrtaceae	LC
Tabernaemontana	*macrocarpa*	Jack	Apocynaceae	LC
Timonius	*borneensis*	Valeton	Rubiaceae	LC
Trigonopleura	*malayana*	Hook.f.	Peraceae	LC
Tristaniopsis	*obovata*	(Benn.) Peter G.Wilson & J.T.Waterh.	Myrtaceae	LC
Vernonia	*arborea*	Buch.-Ham.	Compositae	LC
Vitex	*quinata*	(Lour.) F.N.Williams	Lamiaceae	LC
Xanthophyllum	*flavescens*	Roxb.	Polygalaceae	LC
Xylopia	*altissima*	Boerl.	Annonaceae	LC
Xylopia	*ferruginea*	(Hook.f. & Thomson) Baill.	Annonaceae	LC

5) LoF (logged-over forest)

Genus	Species	Author(s)	Family	IUCN status
Actinodaphne	*borneensis*	Meisn.	Lauraceae	LC
Actinodaphne	sp.1		Lauraceae	LC
Adinandra	*cordifolia*	Ridl.	Pentaphylacaceae	LC
Adinandra	*dumosa*	Jack	Pentaphylacaceae	LC
Adinandra	*sarosanthera*	Miq.	Pentaphylacaceae	LC
Aglaia	*exstipulata*	(Griff.) W.Theob.	Meliaceae	LR/nt
Aglaia	*sexipetala*	Griff.	Meliaceae	LR/nt
Aglaia	sp.1		Meliaceae	LC
Aglaia	sp.2		Meliaceae	LC
Aglaia	sp.3		Meliaceae	LC
Agrostistachys	*indica*	Dalzell	Euphorbiaceae	LC
Alangium	*ridleyi*	King	Cornaceae	LC
Amyxa	*pluricornis*	(Radlk.) Domke	Thymelaeaceae	LC
Anisophyllea	*ferruginea*	Ding Hou	Anisophylleaceae	VU
Antidesma	*leucopodum*	Miq.	Phyllanthaceae	LC
Aporosa	*falcifera*	Hook.f.	Phyllanthaceae	LC
Aporosa	*lucida*	(Miq.) Airy Shaw	Phyllanthaceae	LC
Aporosa	*prainiana*	King ex Gage	Phyllanthaceae	LC
Aporosa	*subcaudata*	Merr.	Phyllanthaceae	LC
Archidendron	*clypearia*	(Jack) I.C.Nielsen	Leguminosae	LC
Archidendron	*microcarpum*	(Benth.) I.C.Nielsen	Leguminosae	LC
Archidendron	sp.		Leguminosae	LC
Ardisia	*fuliginosa*	Blume	Primulaceae	LC
Ardisia	sp.1		Primulaceae	LC
Artocarpus	*elasticus*	Reinw. ex Blume	Moraceae	LC
Artocarpus	*nitidus*	Trécul	Moraceae	LC
Artocarpus	*odoratissimus*	Blanco	Moraceae	LC
Artocarpus	*rigidus*	Blume	Moraceae	LC
Atuna	*racemosa*	Raf.	Chrysobalanaceae	LC
Baccaurea	*macrocarpa*	(Miq.) Müll.Arg.	Phyllanthaceae	LC
Baccaurea	*macrophylla*	cf. macrophylla (Müll.Arg.) Müll.Arg.	Phyllanthaceae	LC
Baccaurea	*parviflora*	(Müll.Arg.) Müll.Arg.	Phyllanthaceae	LC
Baccaurea	sp.1		Phyllanthaceae	LC
Baccaurea	*sumatrana*	(Miq.) Müll.Arg.	Phyllanthaceae	LC

Genus	Species	Author(s)	Family	IUCN status
Barringtonia	*lanceolata*	(Ridl.) Payens	Lecythidaceae	LC
Barringtonia	*macrostachya*	(Jack) Kurz	Lecythidaceae	LC
Beilschmiedia	*gemmiflora*	(Blume) Kosterm.	Lauraceae	LC
Beilschmiedia	sp.1		Lauraceae	LC
Bellucia	*pentamera*	Naudin	Melastomataceae	LC
Bhesa	*paniculata*	Arn.	Centroplacaceae	LR/lc
Buchanania	*insignis*	Blume	Anacardiaceae	LC
Calophyllum	*biflorum*	M.R.Hend. & Wyatt-Sm.	Clusiaceae	LC
Calophyllum	*dasypodium*	Miq.	Clusiaceae	LC
Calophyllum	*pseudomolle*	P.F.Stevens	Clusiaceae	LC
Calophyllum	*pulcherrimum*	Wall. ex Choisy	Clusiaceae	LC
Calophyllum	*rigidum*	Miq.	Clusiaceae	LC
Calophyllum	*sclerophyllum*	Vesque	Clusiaceae	LC
Calophyllum	*soulattri*	Burm.f.	Clusiaceae	LR/lc
Calophyllum	sp.1		Clusiaceae	LC
Calophyllum	*venulosum*	Zoll.	Clusiaceae	LC
Campnosperma	*auriculatum*	(Blume) Hook.f.	Anacardiaceae	LC
Canarium	*littorale*	Blume	Burseraceae	LR/lc
Canarium	*patentinervium*	Miq.	Burseraceae	LR/lc
Canarium	sp.1		Burseraceae	LC
Castanopsis	*inermis*	(Lindl.) Benth. & Hook.f.	Fagaceae	LC
Castanopsis	*malaccensis*	Gamble	Fagaceae	LC
Castanopsis	sp.1		Fagaceae	LC
Cephalomappa	*paludicola*	Airy Shaw	Euphorbiaceae	LC
Chionanthus	*pluriflorus*	(Knobl.) Kiew	Oleaceae	LC
Cinnamomum	*pendulum*	Cammerl.	Lauraceae	LC
Cleistanthus	sp.1		Phyllanthaceae	LC
Cratoxylum	*arborescens*	(Vahl) Blume	Hypericaceae	LR/lc
Crypteronia	*cumingii*	(Planch.) Endl.	Penaeaceae	LC
Cryptocarya	*densiflora*	Blume	Lauraceae	LC
Cryptocarya	*lucida*	Blume	Lauraceae	LC
Ctenolophon	*parvifolius*	Oliv.	Ctenolophonaceae	LC
Cyathocalyx	*sumatranus*	Scheff.	Annonaceae	LR/lc
Dacryodes	*costata*	(A.W.Benn.) H.J.Lam	Burseraceae	LR/lc
Dacryodes	*laxa*	(A.W.Benn.) H.J.Lam	Burseraceae	LR/lc
Dacryodes	*rugosa*	(Blume) H.J.Lam	Burseraceae	LC
Dialium	*indum*	L.	Leguminosae	LC
Dialium	sp.		Leguminosae	LC
Dillenia	*eximia*	Miq.	Dilleniaceae	LC
Diospyros	*foxworthyi*	Bakh.	Ebenaceae	LR/lc
Diospyros	*korthalsiana*	Hiern	Ebenaceae	LC
Diospyros	*rostrata*	(Merr.) Bakh.	Ebenaceae	LC
Diospyros	*venosa*	Wall. ex A.DC.	Ebenaceae	LC
Diospyros	*vera*	(Lour.) A.Chev.	Ebenaceae	LC
Dipterocarpus	*caudiferus*	Merr.	Dipterocarpaceae	LC
Dipterocarpus	*pachyphyllus*	cf. pachyphyllus Meijer	Dipterocarpaceae	LC
Drepananthus	*biovulatus*	(Boerl.) Survesw. & R.M.K.Saunders	Annonaceae	LC
Drepananthus	*havilandii*	(Boerl.) Survesw. & R.M.K.Saunders	Annonaceae	LC
Drimycarpus	*luridus*	(Hook.f.) Ding Hou	Anacardiaceae	LC
Dryobalanops	*beccarii*	Dyer	Dipterocarpaceae	EN
Drypetes	*crassipes*	Pax & K.Hoffm.	Putranjivaceae	LC
Durio	*carinatus*	Mast.	Malvaceae	LC
Dysoxylum	sp.1		Meliaceae	LC
Dysoxylum	sp.2		Meliaceae	LC
Elaeocarpus	*floribundus*	Blume	Elaeocarpaceae	LC
Elaeocarpus	*mastersii*	King	Elaeocarpaceae	LC
Elaeocarpus	*nitidus*	Jack	Elaeocarpaceae	LC
Elaeocarpus	*polystachyus*	Wall. ex Müll.Berol.	Elaeocarpaceae	LC
Elaeocarpus	sp.1		Elaeocarpaceae	LC
Elaeocarpus	sp.2		Elaeocarpaceae	LC
Elaeocarpus	sp.3		Elaeocarpaceae	LC
Elaeocarpus	*stipularis*	var. castaneus (Merr.) Coode	Elaeocarpaceae	LC
Endiandra	sp.		Lauraceae	LC
Endospermum	*diadenum*	(Miq.) Airy Shaw	Euphorbiaceae	LC
Erycibe	*borneensis*	(Merr.) Hoogland	Convolvulaceae	LC
Fagraea	*elliptica*	Roxb.	Gentianaceae	LC

Genus	Species	Author(s)	Family	IUCN status
Fagraea	*racemosa*	Jack	Gentianaceae	LC
Ficus	*aurata*	(Miq.) Miq.	Moraceae	LC
Ficus	*binnendijkii*	Miq.	Moraceae	LC
Ficus	*obscura*	Blume	Moraceae	LC
Ficus	*recurva*	var. pedicellata Corner	Moraceae	LC
Ficus	*trachypison*	K.Schum. & Lauterb.	Moraceae	LC
Fissistigma	sp.		Annonaceae	LC
Fordia	*splendidissima*	(Miq.) Buijsen	Leguminosae	LC
Garcinia	*caudiculata*	Ridl.	Clusiaceae	LC
Garcinia	*parvifolia*	(Miq.) Miq.	Clusiaceae	LC
Garcinia	*rigida*	Miq.	Clusiaceae	LC
Garcinia	sp.		Clusiaceae	LC
Garcinia	*vidua*	Ridl.	Clusiaceae	LC
Gardenia	*forsteniana*	Miq.	Rubiaceae	LC
Gironniera	*nervosa*	Planch.	Cannabaceae	LC
Gironniera	*subaequalis*	Planch.	Cannabaceae	LC
Glochidion	*philippicum*	(Cav.) C.B.Rob.	Phyllanthaceae	LC
Glochidion	sp.1		Phyllanthaceae	LC
Glochidion	sp.2		Phyllanthaceae	LC
Glochidion	*zeylanicum*	(Gaertn.) A.Juss.	Phyllanthaceae	LC
Gluta	*aptera*	(King) Ding Hou	Anacardiaceae	LC
Gluta	*renghas*	L.	Anacardiaceae	LC
Gluta	*wallichii*	(Hook.f.) Ding Hou	Anacardiaceae	LC
Gomphia	*serrata*	(Gaertn.) Kanis	Ochnaceae	LR/lc
Goniothalamus	*tapis*	Miq.	Annonaceae	LC
Gonocaryum	*gracile*	Miq.	Cardiopteridaceae	LC
Gonystylus	*forbesii*	Gilg	Thymelaeaceae	LC
Gonystylus	sp.		Thymelaeaceae	LC
Gordonia	sp.		Theaceae	LC
Gymnacranthera	*forbesii*	(King) Warb.	Myristicaceae	LC
Hopea	*myrtifolia*	Miq.	Dipterocarpaceae	LC
Hopea	*pachycarpa*	(F.Heim) Symington	Dipterocarpaceae	VU
Hopea	*tenuivervula*	P.S.Ashton	Dipterocarpaceae	CR
Horsfieldia	*crassifolia*	(Hook.f. & Thomson) Warb.	Myristicaceae	LR/nt
Horsfieldia	*grandis*	(Hook.f.) Warb.	Myristicaceae	LR/lc
Horsfieldia	*polyspherula*	(Hook.f. ex King) J.Sinclair	Myristicaceae	LC
Hydnocarpus	*castanea*	Hook.f. & Thomson	Achariaceae	LC
Hydnocarpus	*gracilis*	(Slooten) Sleumer	Achariaceae	LC
Hydnocarpus	*kunstleri*	(King) Warb.	Achariaceae	LC
Hydnocarpus	sp.1		Achariaceae	LC
Hydnocarpus	*woodii*	Merr.	Achariaceae	LC
Ilex	*cissoidea*	Loes.	Aquifoliaceae	LC
Ixonanthes	*petiolaris*	Blume	Ixonanthaceae	LC
Ixora	sp.		Rubiaceae	LC
Knema	*cinerea*	Warb.	Myristicaceae	LC
Knema	*conferta*	(King) Warb.	Myristicaceae	LR/lc
Knema	*furfuracea*	(Hook. f. & Thomson) Warb.	Myristicaceae	LR/lc
Knema	sp.		Myristicaceae	LC
Knema	sp.1		Myristicaceae	LC
Knema	sp.2		Myristicaceae	LC
Kokoona	*ochracea*	Merr.	Celastraceae	LC
Lithocarpus	*blumeanus*	(Korth.) Rehder	Fagaceae	LC
Lithocarpus	sp.		Fagaceae	LC
Lithocarpus	sp.3		Fagaceae	LC
Lithocarpus	sp.4		Fagaceae	LC
Litsea	*costalis*	var. nidularis (Gamble) Ng	Lauraceae	LC
Litsea	*firma*	(Blume) Hook.f.	Lauraceae	LC
Litsea	*lanceolata*	(Blume) Kosterm.	Lauraceae	LC
Litsea	*sessiliflora*	Hook.f.	Lauraceae	LC
Litsea	sp.1		Lauraceae	LC
Lophopetalum	*beccarianum*	Pierre	Celastraceae	LC
Lophopetalum	*multinervium*	Ridl.	Celastraceae	LC
Maasia	*glauca*	(Hassk.) Mols, Kessler & Rogstad	Annonaceae	LC
Maasia	*sumatrana*	(Miq.) Mols, Kessler & Rogstad	Annonaceae	LC
Macaranga	*beccariana*	Merr.	Euphorbiaceae	LC
Macaranga	*gigantea*	(Rchb.f. & Zoll.) Müll.Arg.	Euphorbiaceae	LC

Genus	Species	Author(s)	Family	IUCN status
Macaranga	*hullettii*	King ex Hook.f.	Euphorbiaceae	LC
Macaranga	*lowii*	King ex Hook.f.	Euphorbiaceae	LC
Macaranga	*pearsonii*	Merr.	Euphorbiaceae	LC
Macaranga	*pruinosa*	(Miq.) Müll.Arg.	Euphorbiaceae	LC
Macaranga	*triloba*	(Thunb.) Müll.Arg.	Euphorbiaceae	LC
Madhuca	*korthalsii*	(Pierre ex Burck) H.J.Lam	Sapotaceae	LC
Madhuca	*sericea*	(Miq.) S.Moore	Sapotaceae	LC
Madhuca	sp.1		Sapotaceae	LC
Magnolia	*liliifera*	(L.) Baill.	Magnoliaceae	LC
Mallotus	*peltatus*	(Geiseler) Müll.Arg.	Euphorbiaceae	LC
Mallotus	*rufidulus*	(Miq.) Müll.Arg.	Euphorbiaceae	LC
Mangifera	*laurina*	Blume	Anacardiaceae	LC
Mangifera	sp.		Anacardiaceae	LC
Mangifera	*swintonioides*	Kosterm.	Anacardiaceae	LC
Melanochyla	*caesia*	(Blume) Ding Hou	Anacardiaceae	LC
Melanochyla	*fulvinervia*	(Blume) Ding Hou	Anacardiaceae	LC
Melicope	*accedens*	(Blume) T.G. Hartley	Rutaceae	LC
Mesua	*beccariana*	(Baill.) Kosterm.	Calophyllaceae	LC
Mesua	*elmeri*	(Merr.) Kosterm.	Calophyllaceae	LC
Mesua	*macrantha*	(Baill.) Kosterm.	Calophyllaceae	LC
Microcos	*crassifolia*	Burret	Malvaceae	LC
Microcos	*hirsuta*	(Korth.) Burret	Malvaceae	LC
Myristica	*iners*	Blume	Myristicaceae	LR/lc
Neonauclea	*calycina*	(Bartl. ex DC.) Merr.	Rubiaceae	LC
Nephelium	*cuspidatum*	Blume	Sapindaceae	LC
Nephelium	*mangayi*	Hiern	Sapindaceae	LC
Nephelium	*ramboutan-ake*	(Labill.) Leenh.	Sapindaceae	LC
Ochanostachys	*amentacea*	Mast.	Olacaceae	DD
Palaquium	*dasyphyllum*	Pierre ex Dubard	Sapotaceae	LC
Palaquium	*quercifolium*	(de Vriese) Burck	Sapotaceae	LC
Parishia	*insignis*	Hook.f.	Anacardiaceae	LC
Payena	*lucida*	A.DC.	Sapotaceae	LC
Pellacalyx	*axillaris*	Korth.	Rhizophoraceae	LC
Pentace	*borneensis*	Pierre	Malvaceae	LC
Pentace	*polyantha*	Hassk.	Malvaceae	LC
Pentace	sp.		Malvaceae	LC
Phoebe	*grandis*	(Nees) Merr.	Lauraceae	LC
Phyllanthus	*borneensis*	Müll.Arg.	Phyllanthaceae	LC
Polyalthia	*cauliflora*	Hook.f. & Thomson	Annonaceae	LC
Polyalthia	*rumphii*	(Blume ex Hensch.) Merr.	Annonaceae	LC
Porterandia	*anisophylla*	(Jack ex Roxb.) Ridl.	Rubiaceae	LC
Prunus	*arborea*	(Blume) Kalkman	Rosaceae	LR/lc
Psydrax	*dicoccos*	Gaertn.	Rubiaceae	VU
Pternandra	*azurea*	(DC.) Burkill	Melastomataceae	LC
Pternandra	*caerulescens*	Jack	Melastomataceae	LC
Pternandra	*crassicalyx*	J.F.Maxwell	Melastomataceae	LC
Quercus	*subsericea*	A.Camus	Fagaceae	LC
Rinorea	*bengalensis*	(Wall.) Kuntze	Violaceae	LC
Santiria	*apiculata*	A.W.Benn.	Burseraceae	LR/lc
Santiria	*griffithii*	Engl.	Burseraceae	LR/lc
Santiria	*laevigata*	Blume	Burseraceae	LR/lc
Santiria	*mollissima*	Ridl.	Burseraceae	LC
Santiria	*oblongifolia*	Blume	Burseraceae	LC
Santiria	*tomentosa*	Blume	Burseraceae	LR/lc
Saurauia	*nudiflora*	DC.	Actinidiaceae	LC
Scaphium	*macropodum*	(Miq.) Beumée ex K.Heyne	Malvaceae	LR/lc
Semecarpus	*cuneiformis*	Blanco	Anacardiaceae	LC
Semecarpus	*glauca*	Engl.	Anacardiaceae	LC
Shorea	*beccariana*	Burck	Dipterocarpaceae	LC
Shorea	*elliptica*	Burck	Dipterocarpaceae	CR
Shorea	*faguetiana*	F.Heim	Dipterocarpaceae	EN
Shorea	*gibbosa*	Brandis	Dipterocarpaceae	CR
Shorea	*glauca*	cf. glauca King	Dipterocarpaceae	EN
Shorea	*laevis*	Ridl.	Dipterocarpaceae	LR/lc
Shorea	*macroptera*	Dyer	Dipterocarpaceae	LC
Shorea	*maxwelliana*	King	Dipterocarpaceae	EN

Genus	Species	Author(s)	Family	IUCN status
Shorea	*parvifolia*	Dyer	Dipterocarpaceae	LC
Shorea	*peltata*	Symington	Dipterocarpaceae	CR
Shorea	*pilosa*	P.S.Ashton	Dipterocarpaceae	LC
Shorea	*pinanga*	Scheff.	Dipterocarpaceae	LC
Shorea	*retinodes*	Slooten	Dipterocarpaceae	LC
Shorea	*sagittata*	P.S.Ashton	Dipterocarpaceae	CR
Sterculia	sp.		Malvaceae	LC
Strombosia	*ceylanica*	Gardner	Olacaceae	LC
Swintonia	*glauca*	Engl.	Anacardiaceae	LC
Syzygium	*claviflorum*	(Roxb.) Wall. ex A.M.Cowan & Cowan	Myrtaceae	LC
Syzygium	*fastigiatum*	(Blume) Merr. & L.M.Perry	Myrtaceae	LC
Syzygium	*grande*	(Wight) Walp.	Myrtaceae	LC
Syzygium	*incarnatum*	(Elmer) Merr. & L.M.Perry	Myrtaceae	LC
Syzygium	*leptostemon*	(Korth.) Merr. & L.M.Perry	Myrtaceae	LC
Syzygium	*lineatum*	(DC.) Merr. & L.M.Perry	Myrtaceae	LC
Syzygium	*napiforme*	(Koord. & Valeton) Merr. & L.M.Perry	Myrtaceae	LC
Syzygium	*oligomyrum*	Diels	Myrtaceae	LC
Syzygium	*rosaceum*	Diels	Myrtaceae	LC
Syzygium	sp.		Myrtaceae	LC
Syzygium	sp.1		Myrtaceae	LC
Syzygium	sp.2		Myrtaceae	LC
Syzygium	sp.3		Myrtaceae	LC
Syzygium	sp.4		Myrtaceae	LC
Syzygium	sp.5		Myrtaceae	LC
Syzygium	sp.6		Myrtaceae	LC
Syzygium	sp.7		Myrtaceae	LC
Syzygium	sp.8		Myrtaceae	LC
Syzygium	*valdevenosum*	(Duthie) Merr. & L.M.Perry	Myrtaceae	LC
Tabernaemontana	*macrocarpa*	Jack	Apocynaceae	LC
Tarenna	*dasyphylla*	(Miq.) Valeton ex Steenis	Rubiaceae	LC
Teijsmanniodendron	*coriaceum*	(C.B.Clarke) Kosterm.	Lamiaceae	LC
Timonius	*borneensis*	Valeton	Rubiaceae	LC
Trigonopleura	*malayana*	Hook.f.	Peraceae	LC
Tristaniopsis	*whiteana*	(Griff.) Peter G.Wilson & J.T.Waterh.	Myrtaceae	LC
undetermined	n°1		Magnoliaceae	LC
Urophyllum	*arboreum*	(Reinw. ex Blume) Korth.	Rubiaceae	LC
Urophyllum	*corymbosum*	(Blume) Korth.	Rubiaceae	LC
Urophyllum	*enneandrum*	(Wight) Ridl.	Rubiaceae	LC
Vatica	*micrantha*	Slooten	Dipterocarpaceae	LC
Vatica	*pauciflora*	cf. Blume	Dipterocarpaceae	EN
Vatica	*pauciflora*	Blume	Dipterocarpaceae	EN
Vatica	sp.1		Dipterocarpaceae	LC
Vatica	*venulosa*	Blume	Dipterocarpaceae	CR
Xanthophyllum	*flavescens*	Roxb.	Polygalaceae	LC
Xanthophyllum	*obscurum*	A.W.Benn.	Polygalaceae	LC
Xerospermum	*laevigatum*	Radlk.	Sapindaceae	LC
Xylopia	*ferruginea*	(Hook.f. & Thomson) Baill.	Annonaceae	LC
Xylopia	*malayana*	Hook.f. & Thomson	Annonaceae	LC

6) NaF (natural forest.

Genus	Species	Author(s)	Family	IUCN status
Actinodaphne	*borneensis*	Meisn.	Lauraceae	LC
Aglaia	*exstipulata*	(Griff.) W.Theob.	Meliaceae	LR/nt
Aglaia	*sexipetala*	Griff.	Meliaceae	LR/nt
Aglaia	*simplicifolia*	(Bedd.) Harms	Meliaceae	LR/nt
Aglaia	sp.		Meliaceae	LC
Agrostistachys	*sessilifolia*	(Kurz) Pax & K.Hoffm.	Euphorbiaceae	LC
Alangium	*ridleyi*	King	Cornaceae	LC
Amyxa	*pluricornis*	(Radlk.) Domke	Thymelaeaceae	LC
Anisophyllea	*corneri*	Ding Hou	Anisophylleaceae	LR/lc
Anisophyllea	*disticha*	(Jack) Baill.	Anisophylleaceae	LR/lc
Antidesma	*leucopodum*	Miq.	Euphorbiaceae	LC
Aporosa	*lunata*	(Miq.) Kurz	Phyllanthaceae	LC
Aporosa	*octandra*	(Buch.-Ham. ex D.Don) Vickery	Phyllanthaceae	LC

Genus	Species	Author(s)	Family	IUCN status
Aporosa	*subcaudata*	Merr.	Phyllanthaceae	LC
Ardisia	*fuliginosa*	Blume	Primulaceae	LC
Ardisia	sp.1		Primulaceae	LC
Artocarpus	*dadah*	Miq.	Moraceae	LC
Artocarpus	*kemando*	Miq.	Moraceae	LC
Artocarpus	*odoratissimus*	Blanco	Moraceae	LC
Atuna	*racemosa*	Raf.	Chrysobalanaceae	LC
Baccaurea	*macrocarpa*	(Miq.) Müll.Arg.	Phyllanthaceae	LC
Baccaurea	*sumatrana*	(Miq.) Müll.Arg.	Phyllanthaceae	LC
Barringtonia	*macrostachya*	(Jack) Kurz	Lecythidaceae	LC
Beilschmiedia	*gemmiflora*	(Blume) Kosterm.	Lauraceae	LC
Beilschmiedia	*kunstleri*	Gamble	Lauraceae	LC
Beilschmiedia	*lucidula*	(Miq.) Kosterm.	Lauraceae	LC
Beilschmiedia	*pulverulenta*	(Blume) Kosterm.	Lauraceae	LC
Beilschmiedia	*rivularis*	cf. rivularis Kosterm.	Lauraceae	LC
Beilschmiedia	sp.		Lauraceae	LC
Bhesa	*paniculata*	Arn.	Centroplacaceae	LR/lc
Blumeodendron	*tokbrai*	(Blume) Kurz	Euphorbiaceae	LC
Buchanania	*sessilifolia*	Blume	Anacardiaceae	LC
Calophyllum	*canum*	Hook.f. ex T.Anderson	Clusiaceae	LC
Calophyllum	*inophyllum*	L.	Clusiaceae	LR/lc
Calophyllum	*lowei*	Planch. & Triana	Clusiaceae	LC
Calophyllum	*pulcherrimum*	Wall. ex Choisy	Clusiaceae	LC
Canarium	*littorale*	Blume	Burseraceae	LR/lc
Canarium	sp.		Burseraceae	LC
Cephalomappa	*malloticarpa*	J.J.Sm.	Euphorbiaceae	LC
Cephalomappa	*paludicola*	Airy Shaw	Euphorbiaceae	LC
Chaetocarpus	*castanocarpus*	(Roxb.)	Peraceae	LC
Cleistanthus	sp.		Euphorbiaceae	LC
Cleistanthus	*sumatranus*	(Miq.) Müll.Arg.	Phyllanthaceae	LC
Cratoxylum	*arborescens*	(Vahl) Blume	Hypericaceae	LR/lc
Crudia	*wrayi*	Prain	Leguminosae	LC
Crypteronia	*cumingii*	(Planch.) Endl.	Penaeaceae	LC
Cryptocarya	*lucida*	Blume	Lauraceae	LC
Dacryodes	*rugosa*	(Blume) H.J.Lam	Burseraceae	LC
Dehaasia	*caesia*	Blume	Lauraceae	LC
Dialium	*platysepalum*	Baker	Leguminosae	LC
Diospyros	sp.1		Ebenaceae	LC
Dipterocarpus	*crinitus*	Dyer	Dipterocarpaceae	EN
Dipterocarpus	*grandiflorus*	(Blanco) Blanco	Dipterocarpaceae	CR
Dipterocarpus	sp.1		Dipterocarpaceae	LC
Dipterocarpus	*tempehes*	Slooten	Dipterocarpaceae	CR
Dipterocarpus	*validus*	Blume	Dipterocarpaceae	CR
Dracaena	*angustifolia*	(Medik.) Roxb.	Asparagaceae	LC
Drepananthus	*biovulatus*	(Boerl.) Survesw. & R.M.K.Saunders	Annonaceae	LC
Drepananthus	*ramuliflorus*	Maingay ex Hook.f. & Thomson	Annonaceae	LC
Drimycarpus	sp.		Anacardiaceae	LC
Drypetes	sp.		Putranjivaceae	LC
Durio	*carinatus*	Mast.	Malvaceae	LC
Dysoxylum	sp.		Meliaceae	LC
Elaeocarpus	*floribundus*	Blume	Elaeocarpaceae	LC
Elaeocarpus	*mastersii*	King	Elaeocarpaceae	LC
Elaeocarpus	*petiolatus*	(Jacq.) Wall.	Elaeocarpaceae	LC
Elaeocarpus	sp.		Elaeocarpaceae	LC
Erycibe	*crassipes*	Ridl. ex Hoogland	Convolvulaceae	LC
Ficus	*recurva*	var. pedicellata Corner	Moraceae	LC
Ficus	*sundaica*	Blume	Moraceae	LC
Garcinia	*borneensis*	Pierre	Clusiaceae	LC
Garcinia	*havilandii*	Stapf	Clusiaceae	LC
Garcinia	*rigida*	Miq.	Clusiaceae	LC
Garcinia	*rostrata*	(Hassk.) Miq.	Clusiaceae	LC
Garcinia	*vidua*	Ridl.	Clusiaceae	LC
Gironniera	*nervosa*	Planch.	Cannabaceae	LC
Gironniera	*subaequalis*	Planch.	Cannabaceae	LC
Gluta	*wallichii*	(Hook.f.) Ding Hou	Anacardiaceae	LC
Gomphia	*serrata*	(Gaertn.) Kanis	Ochnaceae	LR/lc

Genus	Species	Author(s)	Family	IUCN status
Goniothalamus	sp.		Annonaceae	LC
Gonocaryum	*gracile*	Miq.	Cardiopteridaceae	LC
Gonystylus	*keithii*	Airy Shaw	Thymelaeaceae	VU
Gymnacranthera	*contracta*	Warb.	Myristicaceae	LC
Gymnacranthera	*forbesii*	(King) Warb.	Myristicaceae	LC
Hancea	*penangensis*	(Müll.Arg.) S.E.C.Sierra, Kulju & Welzen	Euphorbiaceae	LC
Haplolobus	*anisander*	(Lauterb.) H.J.Lam	Burseraceae	LC
Hopea	*dryobalanoides*	Miq.	Dipterocarpaceae	LC
Hopea	*dyeri*	F.Heim	Dipterocarpaceae	LC
Hopea	*myrtifolia*	cf. myrtifolia Miq.	Dipterocarpaceae	LC
Hopea	sp.1		Dipterocarpaceae	LC
Horsfieldia	*glabra*	(Reinw. ex Blume) Warb.	Myristicaceae	LC
Hydnocarpus	*castanea*	Hook.f. & Thomson	Achariaceae	LC
Hydnocarpus	sp.		Achariaceae	LC
Hydnocarpus	*sumatrana*	Koord.	Achariaceae	LC
Hydnocarpus	*woodii*	Merr.	Achariaceae	LC
Knema	*cinerea*	var. sumatrana (Warb.)	Myristicaceae	LC
Knema	*cinerea*	Warb.	Myristicaceae	LC
Knema	*furfuracea*	(Hook. f. & Thomson) Warb.	Myristicaceae	LR/lc
Knema	*galeata*	J.Sinclair	Myristicaceae	LC
Knema	*latifolia*	Warb.	Myristicaceae	LR/lc
Knema	*mandaharan*	Warb.	Myristicaceae	LC
Knema	sp.1		Myristicaceae	LC
Lepisanthes	*amoena*	(Hassk.) Leenh.	Sapindaceae	LC
Lepisanthes	*tetraphylla*	Radlk.	Sapindaceae	LC
Lithocarpus	*daphnoideus*	(Blume) A.Camus	Fagaceae	LC
Lithocarpus	*ewyckii*	(Korth.) Rehder	Fagaceae	LC
Lithocarpus	*gracilis*	(Korth.) Soepadmo	Fagaceae	LC
Lithocarpus	sp.1		Fagaceae	LC
Litsea	*firma*	(Blume) Hook.f.	Lauraceae	LC
Litsea	*lanceolata*	(Blume) Kosterm.	Lauraceae	LC
Litsea	*sessiliflora*	Hook.f.	Lauraceae	LC
Lophopetalum	*beccarianum*	Pierre	Celastraceae	LC
Lophopetalum	sp.		Celastraceae	LC
Maasia	*glauca*	(Hassk.) Mols, Kessler & Rogstad	Annonaceae	LC
Macaranga	*lowii*	King ex Hook.f.	Euphorbiaceae	LC
Macaranga	*recurvata*	Gage	Euphorbiaceae	LC
Macaranga	*triloba*	(Thunb.) Müll.Arg.	Euphorbiaceae	LC
Madhuca	sp.1		Sapotaceae	LC
Mangifera	*swintonioides*	Kosterm.	Anacardiaceae	LC
Melanochyla	*caesia*	(Blume) Ding Hou	Anacardiaceae	LC
Melanochyla	*fulvinervia*	(Blume) Ding Hou	Anacardiaceae	LC
Melanochyla	sp.		Anacardiaceae	LC
Memecylon	*kunstleri*	King	Melastomataceae	VU
Memecylon	*myrsinoides*	Blume	Melastomataceae	LC
Mesua	*elmeri*	(Merr.) Kosterm.	Calophyllaceae	LC
Microcos	*crassifolia*	Burret	Malvaceae	LC
Microcos	sp.		Malvaceae	LC
Millettia	sp.		Leguminosae	LC
Myristica	*iners*	Blume	Myristicaceae	LR/lc
Nauclea	sp.		Rubiaceae	LC
Nephelium	*cuspidatum*	Blume	Sapindaceae	LC
Nephelium	*lappaceum*	L.	Sapindaceae	LR/lc
Nephelium	sp.		Sapindaceae	LC
Ochanostachys	*amentacea*	Mast.	Olacaceae	DD
Ormosia	sp.		Leguminosae	LC
Palaquium	*dasyphyllum*	Pierre ex Dubard	Sapotaceae	LC
Palaquium	*quercifolium*	(de Vriese) Burck	Sapotaceae	LC
Payena	*leerii*	(Teijsm. & Binn.) Kurz	Sapotaceae	LC
Payena	*lucida*	A.DC.	Sapotaceae	LC
Pentace	sp.		Malvaceae	LC
Phoebe	*grandis*	(Nees) Merr.	Lauraceae	LC
Porterandia	sp.		Rubiaceae	LC
Prunus	*polystachya*	(Hook.f.) Kalkman	Rosaceae	LR/lc
Pternandra	*azurea*	(DC.) Burkill	Melastomataceae	LC
Quercus	*subsericea*	A.Camus	Fagaceae	LC

Genus	Species	Author(s)	Family	IUCN status
Ryparosa	*hullettii*	King	Achariaceae	LC
Santiria	*apiculata*	A.W.Benn.	Burseraceae	LR/lc
Santiria	*griffithii*	Engl.	Burseraceae	LR/lc
Santiria	*laevigata*	Blume	Burseraceae	LR/lc
Santiria	*mollissima*	Ridl.	Burseraceae	LC
Santiria	*oblongifolia*	Blume	Burseraceae	LC
Santiria	*pilosa*	Engl.	Burseraceae	LC
Santiria	*tomentosa*	Blume	Burseraceae	LR/lc
Sarcotheca	*griffithii*	Hallier f.	Oxalidaceae	LC
Scaphium	*macropodum*	(Miq.) Beumée ex K.Heyne	Malvaceae	LR/lc
Shorea	*beccariana*	Burck	Dipterocarpaceae	LC
Shorea	*bracteolata*	Dyer	Dipterocarpaceae	EN
Shorea	*brunnescens*	P.S.Ashton	Dipterocarpaceae	EN
Shorea	*dasyphylla*	Foxw.	Dipterocarpaceae	EN
Shorea	*faguetiana*	F.Heim	Dipterocarpaceae	EN
Shorea	*falcifera*	Dyer ex Brandis	Dipterocarpaceae	EN
Shorea	*gibbosa*	Brandis	Dipterocarpaceae	CR
Shorea	*macroptera*	Dyer	Dipterocarpaceae	LC
Shorea	*maxwelliana*	King	Dipterocarpaceae	EN
Shorea	*mujongensis*	P.S.Ashton	Dipterocarpaceae	CR
Shorea	*pachyphylla*	Ridl. ex Symington	Dipterocarpaceae	CR
Shorea	*parvifolia*	Dyer	Dipterocarpaceae	LC
Shorea	*peltata*	Symington	Dipterocarpaceae	CR
Shorea	*sagittata*	P.S.Ashton	Dipterocarpaceae	CR
Shorea	*seminis*	Slooten	Dipterocarpaceae	CR
Shorea	sp.		Dipterocarpaceae	LC
Stemonurus	*secundiflorus*	Blume	Stemonuraceae	LC
Sterculia	*oblongata*	R.Br.	Malvaceae	LC
Sterculia	sp.		Malvaceae	LC
Strombosia	*ceylanica*	Gardner	Olacaceae	LC
Swintonia	*schwenckii*	Teijsm. & Binn. ex Hook.f.	Anacardiaceae	LC
Symplocos	*crassipes*	C.B.Clarke	Symplocaceae	LC
Syzygium	*bankense*	(Hassk.) Merr. & L.M.Perry	Myrtaceae	LC
Syzygium	*caudatilimbum*	(Merr.) Merr. & L.M.Perry	Myrtaceae	LC
Syzygium	*cymosum*	(Lam.) DC.	Myrtaceae	LC
Syzygium	*garciniifolium*	(King) Merr. & L.M.Perry	Myrtaceae	LC
Syzygium	*grande*	(Wight) Walp.	Myrtaceae	LC
Syzygium	*leptostemon*	(Korth.) Merr. & L.M.Perry	Myrtaceae	LC
Syzygium	*lineatum*	(DC.) Merr. & L.M.Perry	Myrtaceae	LC
Syzygium	*pycnanthum*	Merr. & L.M.Perry	Myrtaceae	LC
Syzygium	*scortechinii*	(King) Chantaran. & J.Parn.	Myrtaceae	LC
Syzygium	sp.1		Myrtaceae	LC
Syzygium	*tawahense*	(Korth.) Merr. & L.M.Perry	Myrtaceae	LC
Tabernaemontana	*sphaerocarpa*	Blume	Apocynaceae	LC
Teijsmanniodendron	*bogoriense*	Koord.	Lamiaceae	LC
Teijsmanniodendron	*coriaceum*	(C.B.Clarke) Kosterm.	Lamiaceae	LC
Trigonopleura	*malayana*	Hook.f.	Peraceae	LC
Tristaniopsis	*whiteana*	(Griff.) Peter G.Wilson & J.T.Waterh.	Myrtaceae	LC
Urophyllum	*enneandrum*	(Wight) Ridl.	Rubiaceae	LC
Vatica	*chartacea*	P.S.Ashton	Dipterocarpaceae	CR
Vatica	*micrantha*	Slooten	Dipterocarpaceae	LC
Vatica	sp.		Dipterocarpaceae	LC
Vatica	*teysmanniana*	Burck	Dipterocarpaceae	CR
Xanthophyllum	*excelsum*	Blume ex Miq.	Polygalaceae	LC
Xanthophyllum	*flavescens*	Roxb.	Polygalaceae	LC
Xanthophyllum	*stipitatum*	A.W.Benn.	Polygalaceae	LC
Xylopia	*caudata*	Hook.f. & Thomson	Annonaceae	LC

Conclusions de l'étude

Malgré une double stratification de notre échantillonnage, à la fois en fonction du type d'occupation ou d'utilisation des sols et de la période écoulée depuis la dernière perturbation majeure (pour les types d'occupation ou d'utilisation des sols pour lesquels cela s'avère pertinent), nous avons constaté qu'il existe encore au sein des classes étudiées une variabilité importante des variables mesurées (voir Figure 2.4, ainsi que Figures 2.6–2.8). De fait, l'utilisation du type d'occupation ou d'utilisation des sols comme « *proxy* » pour l'estimation de la production de SE tels le contrôle de l'érosion des sols ou l'atténuation du changement climatique via stockage de carbone, ou pour l'évaluation de la DEL ne semble pas pertinente à l'échelle du paysage.

Revenons à présent sur l'hypothèse principale liée à l'étude que nous avons menée : « Les milieux naturels produisent plus de SE et abritent une DEL plus importante que les milieux perturbés par les activités anthropiques. Cependant, certains milieux perturbés peuvent continuer de produire des SE et abriter une DEL dans des proportions relativement importantes. »

☑ Nous avons montré que les densités de carbone dans la biomasse aérienne et dans les sols de surface, le contrôle de l'érosion des sols et la DEL sont maximaux (mais pas toujours significativement supérieures) en forêt naturelle que dans les milieux perturbés par les activités anthropiques.

☑ Nous avons également mis en évidence que certains milieux perturbés continuent de produire des SE en quantité relativement importante et/ou d'abriter une grande DEL (voir par exemple la richesse spécifique comparable en forêt post-exploitation et forêt naturelle).

☒ Nous avons constaté que les SE et la DEL ne parvenaient pas à retrouver leurs niveaux pré-perturbation, même après de longues périodes (> 50 ans) écoulées depuis la dernière perturbation majeure. Alors que les types d'occupation ou d'utilisation des sols liés à la pratique de l'agriculture itinérante sur brûlis produisent plus de SE que des monocultures de palmiers à huile ou d'hévéas, le système est peut-être en passe de franchir un seuil de soutenabilité dans cette partie de la zone d'étude, potentiellement en lien avec la réduction des temps de jachère.

☒ Si, au travers des données récoltées, la forêt post-exploitation produit des SE et abrite une DEL semblables à ceux de la forêt naturelle, nous avons constaté que des éléments du paysage liés à l'exploitation forestière pourraient drastiquement réduire la fourniture du SE de contrôle de l'érosion des sols à l'échelle du bassin versant (Figure 2.10). Si l'érosion n'est effectivement pas significativement plus importante en forêt post-exploitation qu'en forêt naturelle, il ne faudrait pas pour autant en conclure que l'exploitation forestière n'augmente pas les pertes de sol.

Figure 2.10. L'un des multiples glissements de terrain que nous avons observés le long du principal chemin d'exploitation forestière (photo prise en Juin 2012)

Chapitre 3

Congruence spatiale entre carbone et biodiversité dans un paysage forestier de Bornéo

Contexte de l'étude

Nous avons dans le Chapitre précédent évalué la production de services écosystémiques (SE) et la diversité d'espèces ligneuses (DEL) au sein d'une mosaïque paysagère dont la végétation est influencée par les activités anthropiques passées et présentes. En étudiant la relation entre stocks de carbone dans la biomasse aérienne et DEL, nous avons mis en évidence une relation de nature parabolique, les plus fortes valeurs de DEL étant atteintes pour des valeurs intermédiaires de stocks de carbone.

Etant donné que la relation entre deux SE (et par extension entre un SE et la DEL) dépend de l'échelle à laquelle elle est considérée, comme mentionné au cours de l'introduction, nous avons choisi d'étudier les relations entre la DEL et le SE d'atténuation du changement climatique via stockage de carbone dans la biomasse aérienne et dans le sol à l'échelle de la zone d'étude. Pour ce faire, les principaux types de végétation ont été échantillonnés (Figure 3.1). Au total, dans les 18.4 ha de végétation échantillonnés, 14155 arbres ont été mesurés, et 4480 échantillons prélevés puis identifiés.

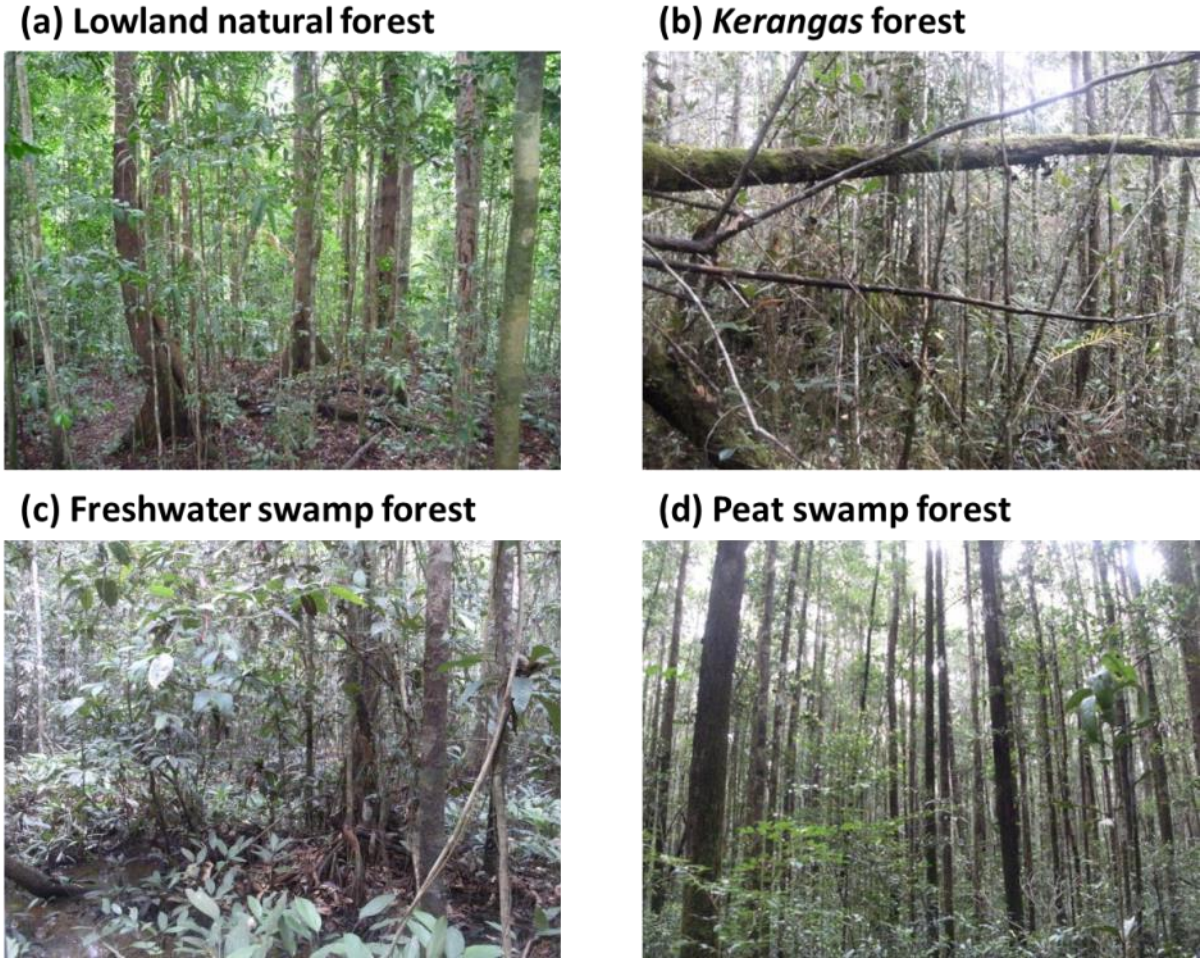

Figure 3.1. Quelques-uns des types de végétation échantillonnés lors des campagnes de terrain dans la zone d'étude : (a) forêts de plaine, (b) forêts sur sable blanc, (c) forêts marécageuses, (d) forêts sur tourbe (en bas à droite)

A l'aide de ces inventaires et de données facilement accessibles, nous avons élaboré des modèles régionaux de distribution de carbone (dans la biomasse aérienne et le sol) et de DEL. Nous avons utilisé les prédictions pour étudier les corrélations entre stocks de carbone et DEL, ainsi que les congruences spatiales entre leurs « *hotspots* » respectifs. Cette étude, conjuguée à une évaluation des menaces potentielles pesant sur les « *hotspots* » de carbone et de DEL, nous a permis d'émettre des recommandations en termes de conservation et de développement.

Au travers de cette étude, nous voulions tester l'hypothèse suivante : « Les zones d'importance pour la DEL et le carbone ne coïncident que partiellement au niveau de la zone d'étude, mais il est possible d'optimiser la protection de la DEL et du carbone (tant celui de la biomasse aérienne que du sol) en choisissant des stratégies de conservation appropriées. ».

Spatial congruence between carbon and biodiversity in a Bornean forest landscape

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Résumé

Comprendre comment le carbone et la biodiversité varient au sein des paysages forestiers tropicaux est essentiel afin de pouvoir en conserver les « *hotspots* » dans un contexte général de forte déforestation. Que les stratégies de conservation visant à protéger les « *hotspots* » de carbone fournissent conjointement des bénéfices pour la protection de la biodiversité, et vice-versa, dépend principalement du degré auquel carbone et biodiversité coïncident à l'échelle du paysage. Nous avons utilisé des mesures de terrain et des variables explicatives facilement accessibles pour modéliser la densité de carbone de la biomasse aérienne, la densité de carbone du sol et la diversité d'espèces ligneuses (variables-réponses) au niveau de paysages forestiers du nord de Bornéo. Nous avons évalué la corrélation spatiale entre variables-réponses ainsi que la congruence spatiale de leurs « *hotspots* ». Nous avons trouvé une forte corrélation positive entre le carbone de la biomasse aérienne et la diversité d'espèces ligneuses, et une congruence spatiale de leurs « hotspots » plus importante qu'attendue si les distributions avaient été aléatoires. En conséquence, la protection de zones aux fortes densités de carbone dans la biomasse aérienne par l'intermédiaire de mécanismes financiers tels que REDD+ devrait être bénéfique pour la conservation de la diversité d'espèces ligneuses dans la zone d'étude. En revanche, les corrélations entre densité de carbone du sol et densité de carbone contenu dans la biomasse aérienne ou bien diversité d'espèces ligneuses se sont avérées négatives, et les congruences spatiales nulles. Les « *hotspots* » de densité de carbone du sol, situés pour la plupart dans les tourbières, requièrent donc des réglementations spécifiques afin d'assurer leur protection. Le moratoire actuel sur la conversion des tourbières en Indonésie constitue un premier pas dans cette direction.

Mots-clés

Services écosystémiques
Spatialisation
Relation spatiale
REDD+
Aires protégées
Aménagement du territoire

Points-clés

• Nous avons modélisé la diversité d’espèces ligneuses et la densité de carbone en utilisant des données de terrain et d’autres données facilement accessibles.
• La densité de carbone dans la biomasse aérienne et la diversité d’espèces ligneuses sont fortement corrélées.
• Les zones présentant de fortes valeurs de carbone du sol ne correspondent pas à celles ayant de fortes valeurs de carbone dans la biomasse ou bien de diversité d’espèces ligneuses.
• La protection de zones à forte densité de carbone dans la biomasse aérienne devrait être bénéfique pour la conservation de la diversité d’espèces ligneuses.
• Les stocks importants de carbone contenus dans les tourbières doivent être protégés par des réglementations adéquates.

Abstract

Understanding how carbon and biodiversity vary across tropical forest landscapes is essential to achieving effective conservation of their respective hotspots in a global context of high deforestation. Whether conservation strategies aimed at protecting carbon hotspots can provide co-benefits for biodiversity protection, and vice versa, mostly depends on the extent to which carbon and biodiversity co-occur at the landscape level. We used field measurements and easily accessible explanatory variables to model aboveground carbon density, soil carbon density and tree alpha diversity (response variables) over a tropical forest landscape of northern Borneo. We assessed the spatial correlation between response variables and the spatial congruence of their hotspots. We found a strong positive correlation between aboveground carbon density and tree alpha diversity, and an above-than-expected-by-chance spatial congruence of their hotspots. Consequently, the protection of areas of high aboveground carbon density through financial mechanisms such as REDD+ is expected to benefit tree diversity conservation in the study area. On the other hand, correlations between soil carbon density and both aboveground carbon density and tree alpha diversity were negative and spatial congruences null. Hotspots of soil carbon density, mostly located in peatlands, therefore need conservation regulations, which the current moratorium on peat conversion in Indonesia is a first step toward.

Keywords

Ecosystem services
Spatialization
Spatial relationship
REDD+
Protected areas
Land-use planning

Highlights

• We modeled tree diversity and carbon density using field measurements and accessible data
• Aboveground carbon density and tree diversity were strongly correlated
• High soil carbon density did not overlap with high aboveground carbon density or tree diversity
• Protecting areas of high aboveground carbon density will benefit tree diversity
• High soil carbon in peatlands must be protected with specific regulations

3.1 Introduction

Information on the nature, strength and extent of spatial relationships between multiple ecosystem services (ES) and biodiversity (which is not an ES but a determinant of the delivery of other ES; see Diaz et al., 2006) is crucial for sound ecosystem management and land-use planning (de Groot et al., 2010; Egoh et al., 2008; Naidoo et al., 2008), especially in tropical forest landscapes where conservation versus development goals are at stake (Malhi et al., 2014). Considering multiple ES together constitutes a major challenge in ecosystem management (Raudsepp-Hearne et al., 2010) but is necessary for managing trade-offs between ES and creating new funding opportunities for conservation by bundling co-occurring ES (Carpenter et al., 2006; Wendland et al., 2010).

Tropical forests have long received much attention for conservation, initially with respect to the extraordinary biodiversity that they host (15 of the 25 biodiversity hotspots sensu Myers include tropical forests; see Myers et al., 2000). The number of tree species in tropical forests, for example, is estimated to lie between 40,000–53,000 compared to only 124 tree species across temperate Europe (Slik et al., 2015). To date, the conservation of biodiversity has mostly relied on a network of protected areas. However, the efficiency and effectiveness of this strategy has been challenged because protected areas are too few, too small (at least many of them) and often lack sufficient funding, with only a small fraction of them shown to succeed in disrupting biodiversity erosion (Kramer et al., 1997; Laurance et al., 2012).

In the last decade, the development of REDD+, a United Nations initiative aimed at Reducing Emissions from Deforestation and forest Degradation, has shed new light on the necessity to protect tropical forests. Because tropical forests store large amounts of carbon, mostly in living woody biomass (Baccini et al., 2012) and soils (especially in peatlands; see Page et al., 2011), and are currently disappearing fast (Kim et al., 2015), their protection is particularly relevant for climate change mitigation (Pan et al., 2011). The REDD+ mechanism, which aims to provide financial incentives to maintain and enhance forest carbon stocks, appears to some as an unprecedented opportunity for biodiversity conservation provided strong safeguards are incorporated (Gardner et al., 2012; Paoli et al., 2010; Phelps et al., 2012). However, biodiversity monitoring as part of the social and environmental safeguards for REDD+ has not received much attention, with the focus clearly remaining on greenhouse gas emission estimations (Dickson and Kapos, 2012).

Schemes dedicated to biodiversity and carbon protection are not meant to be mutually exclusive. Yet many challenges (institutional, political, social, economic, etc.) need to be overcome for protection scheme optimization, for example, protected areas benefiting from the financial support of REDD+ despite seemingly lack of additionality (a project is ‘additional’ when emission reductions are linked to its implementation and would not have occurred without it; Macdonald et al., 2011), or REDD+ positively integrating biodiversity safeguards. Beyond scheme design, whether biodiversity conservation could benefit from climate change mitigation-oriented financial schemes, and vice versa, depends mostly on the

extent to which carbon and biodiversity co-occur at the landscape level (Strassburg et al., 2010).

So far, there is little agreement on the spatial relationship between carbon storage and biodiversity. At a global scale reports are contradictory, with one study pointing out an "overall lack of spatial concordance between biodiversity and ecosystem services" (including carbon storage; see Naidoo et al., 2008) while another found a "high congruence between species richness and biomass carbon" (Strassburg et al., 2010). The same seemingly conflicting results arose at national (e.g. see Egoh et al., 2009 vs. Locatelli et al., 2014) and local scales (e.g. see Kessler et al., 2012 vs. Ruiz-Jaen and Potvin, 2010).

Three key elements might shed some light on the apparent contradiction between these findings. First, as pointed out by Eigenbrod et al. (2010), proxies used to assess ES distribution may poorly fit primary data, impacting the quality of resulting ES maps and, therefore, the identification of ES hotspots and areas of spatial congruence (i.e. overlap) between multiple ES. Second, the nature, strength and extent of spatial relationships between carbon and biodiversity clearly depend on the metrics selected for carbon (e.g. aboveground carbon only vs. aboveground and soil organic carbon) and biodiversity (e.g. richness, threat, restricted range) in each study (Murray et al., 2015). Third, spatial covariance of ES provision can be influenced by data spatial resolution and study spatial extent (Anderson et al., 2009; Murray et al., 2015).

There is a need for more primary data to help understand the spatial relationship between carbon storage and biodiversity, especially at the landscape level where most management decisions are made. Working in an area of northern Borneo that is mostly forested but facing clearance with the development of oil palm plantations, we assessed aboveground carbon density (ACD), soil carbon density (SCD, for the 0−20 cm soil layer) and tree alpha diversity (TAD, using Fisher's α) in sampling plots scattered across the study area. The following research questions were addressed: (1) are there correlations between carbon density and tree diversity across the study area; (2) do carbon and tree diversity hotspots overlap in the study area; and (3) to what extent can biodiversity conservation policies also protect carbon stocks and vice versa. We modelled ACD, SCD and TAD (response variables) with explanatory variables that are easily accessible at the landscape scale. We applied the resulting models over the whole study area and compared our predictions with existing maps for ACD, SCD and TAD. We then explored correlations between response variables and spatial congruence of their respective hotspots. We finally assessed threats and opportunities for carbon storage and tree diversity based on hotspot location, and quantified trade-offs in ES protection from different conservation strategies.

3.2 Materials and Methods

3.2.1 Study area

Fieldwork was conducted in the Kapuas Hulu regency (hereafter referred to as the "study area") in the Indonesian province of West Kalimantan. The study area spans ca. 31,000 km² of mostly forested land where altitude ranges from 0 to ca. 2000 masl. Mean annual precipitation varies from 2350–4300 mm with an average of ca. 3450 mm, and mean annual temperature varies from 17–27 °C with an average of ca. 25 °C (Hijmans et al., 2005). The majority of soils have developed on sedimentary parent material and belong to the Ultisols, Inceptisols and Histosols orders (RePPProT, 1990).

Two national parks (Betung Kerihun and Danau Sentarum) cover about 30% of the study area (Shantiko et al., 2013). In 2003, Kapuas Hulu was declared a conservation area by the local government, a commitment to improved natural resource management and ecosystem functionality preservation (Prasetyo et al., 2007).

3.2.2 Field sampling and index computation for carbon and tree diversity

We sampled the main vegetation types between 2011 and 2013. Of the 120 plots sampled, 85 were 100 × 20 m with natural and/or moderately disturbed vegetation, and 35 were 20 × 20 m with rubber gardens and/or secondary regrowth. Smaller plots were preferred for rubber gardens and secondary regrowth to ensure that plot vegetation was homogeneous despite landscape heterogeneity associated with swidden practices. In each plot, all trees with ≥ 10 cm diameter at breast height (1.3 m above ground) were measured, tagged and mapped, and their height estimated (for details, see Walker et al., 2012). Leaf samples were collected and identified at the Herbarium Bogoriense in Bogor, Indonesia. In total, over the 18.4 ha of surveyed vegetation, 14,155 trees were measured and 4480 herbarium vouchers collected and identified.

Tree dry biomass was computed using a pantropical allometric model that includes tree diameter, tree height and wood specific gravity as explanatory variables (Chave et al., 2014), and carbon content was derived using the standard conversion factor of 0.47 (McGroddy et al., 2004). Wood specific gravity, a constitutive factor of the aforementioned equation, was obtained from the Global Wood Density Database (Zanne et al., 2009). When species were not found in the database, the genus-level average wood density was used instead. Any unresolved cases were assigned the value of the mean wood density for tropical Southeast Asia (0.57 g cm^{-3}; see Chave et al., 2009). ACD (in Mg ha^{-1}) was calculated by averaging total plot carbon content over plot area.

Composite soil samples were taken for topsoils (0−20 cm; collected using an auger at four different locations for each composite sample) in half of the vegetation plots. Samples were dried at 105 °C and further analyzed for carbon content (using Walkley and Black method;

see Landon, 1984). Topsoil cores were also collected using 100 cm^3 sample rings to measure dry bulk density (in g cm^{-3}). SCD (in Mg ha^{-1} for the 0−20 cm soil layer) was calculated using carbon content and dry bulk density. As we did not collect soil samples for the plots in peatlands and swamp areas, we used values from the literature. For plots in peatlands, we assigned a value of 53% for carbon content and 0.10 g cm^{-3} for dry bulk density (Page et al., 2011). For plots in swamp areas over alluvial soils, we assigned a value of 116.4 Mg ha^{-1} for soil carbon density (0−20 cm; Paoli et al., 2006).

We used Fisher's α as an indicator to characterize TAD. Fisher's α, a parametric index, is relatively independent of sample size and insensitive to the presence of rare species (Colwell, 2009; Parmentier et al., 2011). For details about sampling strategy, indices computation, and plot structural and compositional features, see Appendix A. Field estimates of ACD and tree diversity were compared with existing maps (Saatchi et al. (2011) and Baccini et al. (2012) for ACD; Wieder et al. (2014) for SCD; Slik et al. (2009), Raes et al. (2009); and Raes et al. (2013) for TAD; see Appendix B for details).

3.2.3 Potential explanatory variables to be tested for model building

We chose potential explanatory variables that are commonly used in the literature for this type of modeling and for which spatial data were available over the study area (Table 3.1). We worked at a 250 m grid cell resolution, which is the spatial resolution of MODIS MOD13Q1 (vegetation indices) and MOD44B (vegetation continuous fields) products. These products have been used widely for spatialization of various ground-measured vegetation-related response variables (e.g. see Nagler et al., 2007; Saatchi et al., 2008). All geographical information was projected using a Universal Transverse Mercator projection (zone 49 N, WSG 84 datum).

The MODIS MOD13Q1-derived vegetation indices (EVI and NDVI) have a temporal resolution of 16 days (23 images/year). We gathered images from 2011, 2012 and 2013 to cover the entire fieldwork period. For both EVI and NDVI, we computed a maximum, mean and standard deviation for each grid cell over the 3-year period (i.e. 3 × 23 = 69 images). The MODIS MOD44B-derived vegetation continuous fields (percent tree cover, percent non-tree vegetation and percent non vegetation) have a temporal resolution of one year. We gathered images from 2011–2013 and computed the average value for each of the three vegetation continuous fields.

Digital elevation data from the NASA Shuttle Radar Topographic Mission were obtained at a 90 m resolution (Jarvis et al., 2008) and further resampled to 250 m. Slope was computed from original data and subsequently resampled to match the designated study resolution.

Table 3.1. Description of the 20 potential explanatory variables tested for ACD, SCD and TAD model building.

Data origin	Source	Code	Description	Unit	Spatial resolution	Range over study area	Range over plot network	Example reference
MODIS	[1]	EVIMAX	Maximum EVI [b]	ind [d]	250 m	0.1617 – 1.0000	0.5549 – 0.9316	Parmentier et al. (2011)
	[1]	EVIMEAN	Mean EVI	ind	250 m	0.0298 – 0.6459	0.3567 – 0.5518	Parmentier et al. (2011)
	[1]	EVISD	Standard deviation EVI	ind	250 m	0.0447 – 0.2090	0.0727 – 0.1349	
	[1]	NDVIMAX	Maximum NDVI [c]	ind	250 m	0.3417 – 0.9995	0.8868 – 0.9984	Parmentier et al. (2011)
	[1]	NDVIMEAN	Mean NDVI	ind	250 m	0.0471 – 0.8810	0.6221 – 0.8391	Parmentier et al. (2011)
	[1]	NDVISD	Standard deviation NDVI	ind	250 m	0.0460 – 0.3106	0.0850 – 0.2197	Oindo and Skidmore (2002)
	[1]	PNTV	Percent non tree vegetation	%	250 m	0 – 78	6 – 40	Asner et al. (2014)
	[1]	PNV	Percent non vegetation	%	250 m	1 – 62	5 – 15	
	[1]	PTC	Percent tree cover	%	250 m	1 – 85	50 – 81	Hansen et al. (2003)
SRTM [a]	[2]	ALT	Altitude	m	90 m → 250 m	13 – 1,955	40 – 865	Marshall et al. (2012)
	[2]	SLOPE	Slope	%	90 m → 250 m	0.0 – 48.5	0.1 – 16.3	Marshall et al. (2012)
WordClim	[3]	TEMPE	Mean annual temperature	°C	1000 m → 250 m	17.2 – 26.8	22.5 – 26.6	Parmentier et al. (2011)
	[3]	TEMPERANGE	Temperature range	°C	1000 m → 250 m	8.5 – 10.0	9.1 – 9.9	Slik et al. (2010)
	[3]	TEMPESEAS	Temperature seasonality	°C	1000 m → 250 m	1.3 – 4.3	1.9 – 3.5	Slik et al. (2010)
	[3]	PRECIP	Mean annual precipitation	mm	1000 m → 250 m	2,346 – 4,286	2,818 – 4,149	Parmentier et al. (2011)
	[3]	PRECIPRANGE	Precipitation range	mm	1000 m → 250 m	129 – 352	190 – 270	Slik et al. (2010)
	[3]	PRECIPSEAS	Precipitation seasonality	mm	1000 m → 250 m	15 – 128	16 – 38	Slik et al. (2010)
Governmental	[4]	LANDALLOC	Land allocation	cat [e]	nr	Area for other uses Conversion forest Limited production forest National park Production forest Watershed Protection forest	Area for other uses Limited production forest National park Watershed protection forest	Van der Laan et al. (2014)
	[5]	MINDIST2	Minimum distance to disturbance source (either road, river or village)	m	nr	0 – 57,695	0 – 3,579	Van der Laan et al. (2014)
	[6]	SOIL	Soil group	cat	nr	Alluvial Peat Sedimentary Volcanic	Alluvial Peat Sedimentary Volcanic	Slik et al. (2009)

[a] SRTM = Shuttle Radar Topographic Mission [b] EVI = Enhanced Vegetation Index; [c] NDVI = Normalized Difference Vegetation Index; [d] ind = index, theoretically varying from 0 to 1; [e] cat = categorical variable

Source: [1] Available at https://mrtweb.cr.usgs.gov/; [2] Available at http://srtm.csi.cgiar.org/; [3] Available at http://www.worldclim.org/; [4] Ministry of Forestry; [5] Bakosurtanal (National Coordinator for Survey and Mapping Agency); [5] Balittanah (Indonesian Soil Research Institute)

We also used WorldClim dataset, which provides interpolated estimates of various bioclimatic variables for the 1950−2000 period with a 30 arc-second resolution (~1km resolution at the equator; see Hijmans et al., 2005), and from which we extracted mean annual temperature, temperature seasonality, temperature range, mean annual precipitation, precipitation seasonality and precipitation range (all resampled to match our 250 m resolution).

Using ArcGis 10, we computed euclidean distances from three potential disturbance sources: roads (including logging roads), rivers and villages. A raster of minimum distance to potential disturbance source was created by selecting the minimum value between the three potential disturbance sources for each grid cell. Land allocation (i.e. the designated use of an area, e.g. production forest or national park) and soil data were also considered potential explanatory variables (obtained from the Ministry of Forestry and the Indonesian Soil Research Institute, respectively; see Table 3.1 for respective classes).

3.2.4 Explanatory variable selection and model building

We used "random forest" (a machine learning algorithm; see Breiman et al., 1984) for explanatory variable selection and response variable modeling. Random forests are collections of decision trees, each trained on a bootstrap sample of a full set of observations. Model accuracy is then evaluated for each tree using observations that had been left out of the corresponding bootstrap sample (Breiman et al., 1984). This modelling technique has already been used to predict aboveground biomass (e.g. Baccini et al., 2012) and tree alpha diversity (e.g. Parmentier et al., 2011).

In case several measurement plots belonged to the same 250 m grid cell, mean response variable values were computed. Sample size was reduced from 120 individual plots to 65 composite sample sites, these constituting our "full set of observations". For each response variable, we grew a random forest of 1000 trees with the 20 potential explanatory variables. We then selected variables based on variable minimal depth and importance value (information available as model outputs; see Ishwaran and Kogalur, 2015). In addition, we eliminated the variables that showed unexplainable partial dependence behavior or whose distribution in observations was not representative of the entire study area. Details about random forest regression algorithm and explanatory variable selection are given in Appendix C.

Once explanatory variables were selected, new 1000-tree random forests were grown for each response variable and their performances in predicting dataset response values recorded. Random forests were finally used to predict response values over the whole study area. Because our measurements focused on tree-dominated vegetation lower than 900 masl, we excluded grid cells with either: (1) water, (2) non-forest vegetation (MODIS percent tree cover < 50%; following Waring et al., 2006), or (3) altitude > 900 m. After mask application, 391,523 grid cells remained. Maps of ACD, SCD and TAD that were obtained from

predictions of our models were compared with existing maps of carbon (both ACD and SCD) and tree diversity (see Appendix D for details).

3.2.5 Correlations, spatial congruence and potential threat analysis

Correlations between pairs of response variables or between our predictions and those from existing maps were assessed using Pearson's product-moment correlation. Spatial autocorrelation was accounted for using a modified version of the test (Dutilleul, 1993). A correlation was classified as weak, moderate or strong when absolute Pearson's *r* values were between 0.20–0.39, 0.40–0.59 and 0.60–0.79, respectively.

Spatial congruence between hotspots of response variables (defined for each response variable as the 10% of grid cells with the highest values) was evaluated using the proportion of grid cells that were hotspots for both response variables X and Y (this proportion varied between 0% and 10%, and was 1% for two random distributions). The level of spatial congruence was used to infer the potential effect of conservation prioritization (i.e. spatial targeting of conservation measures to hotspots of a given response variable) on non-target response variables. Prioritizing hotspots of the response variable X for conservation was declared beneficial, neutral or detrimental to the non-target response variable Y when spatial congruence was higher, similar or lower than that found between two random distributions (i.e. 1%).

To assess the potential threats to hotspots of response variables, we classified hotspot grid cells according to the land allocation under which they are situated, and recorded whether the corresponding areas were included in logging, mining or plantation concessions (concession data obtained from the Ministry of Forestry).

All statistical analyses were done using R (R Core Team, 2014). Most frequently used R packages include 'vegan' (Oksanen et al., 2015), 'raster' (Hijmans, 2015), 'randomForest' (Liaw and Wiener, 2002) and 'randomForestSRC' (Ishwaran and Kogalur, 2015).

3.3 Results

3.3.1 Response variable predictions over the study area

Altitude was a key explanatory variable for all response variables, whereas mean annual temperature and temperature seasonality were only important in explaining TAD (Figure 3.1, Table 3.2). The percentage of variance explained by the models ranged from 60%–80% depending on response variable. Application of these models over the study area revealed differences in the broad pattern of response variable distribution, with high spatial variability for ACD, and the highest values for TAD and SCD in the outer and inner part of the study area, respectively (Figure 3.2).

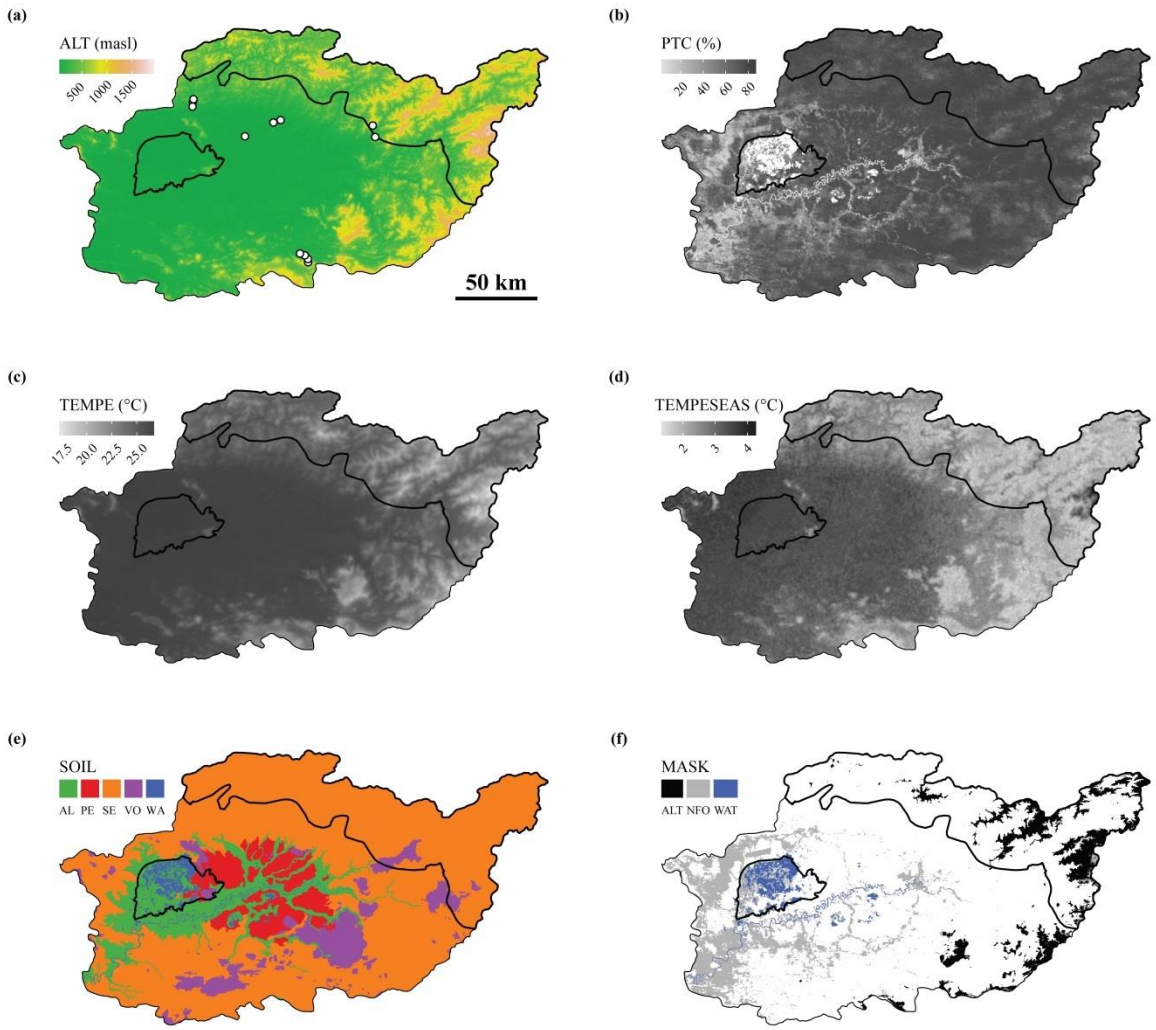

Figure 3.1. Spatial representation of explanatory variables selected for response variable prediction: (a) altitude, (b) percent tree cover, (c) mean annual temperature, (d) temperature seasonality and (e) soil type (AL = alluvial; PE = peat; SE = sedimentary; VO = volcanic; WA = water). Areas depicted in (f) are those where masks were applied (ALT = altitude > 900 m; NFO = non-forest area; WAT = water). Areas where field surveys were conducted are indicated by white dots in (a). The two national parks present in Kapuas Hulu (Betung Kerihun and Danau Sentarum, N-E and W part of the study area, respectively) are also displayed.

Table 3.2. Selected explanatory variables and random forest performance. 1000-tree random forests were grown for each response variable. The number of variables tried at each split was consistently 1 (default value: total number of explanatory variables/3).

Response variable	Explanatory variables	MSR [a]	RMSR [b]	Variance explained (%)
ACD	PTC + ALT	2302.4	48.0	75.7
SCD	SOIL + ALT	455.7	21.3	63.6
TAD	ALT + TEMPESEAS + TEMPE + PTC	110.8	10.5	77.9

[a] MSR = mean of squared residuals; [b] RMSR = root mean of squared residuals

We found moderate positive correlations between our predictions of ACD and those of existing maps, with evidence of a saturation effect from both existing maps (i.e. none to few of their predicted values exceeded a threshold of about 175 Mg ha^{-1}; Figure 3.3a–b). Correlation was strong and positive between our predictions of SCD and the top 30 cm soil carbon values in the Harmonized World Soil Database despite the limited number of unique values of the latter (Figure 3.3c). Comparisons of our predictions of TAD with three existing maps showed mixed results, with correlations varying from moderate negative to moderate positive depending on which map was used (see Figure 3.3d–f).

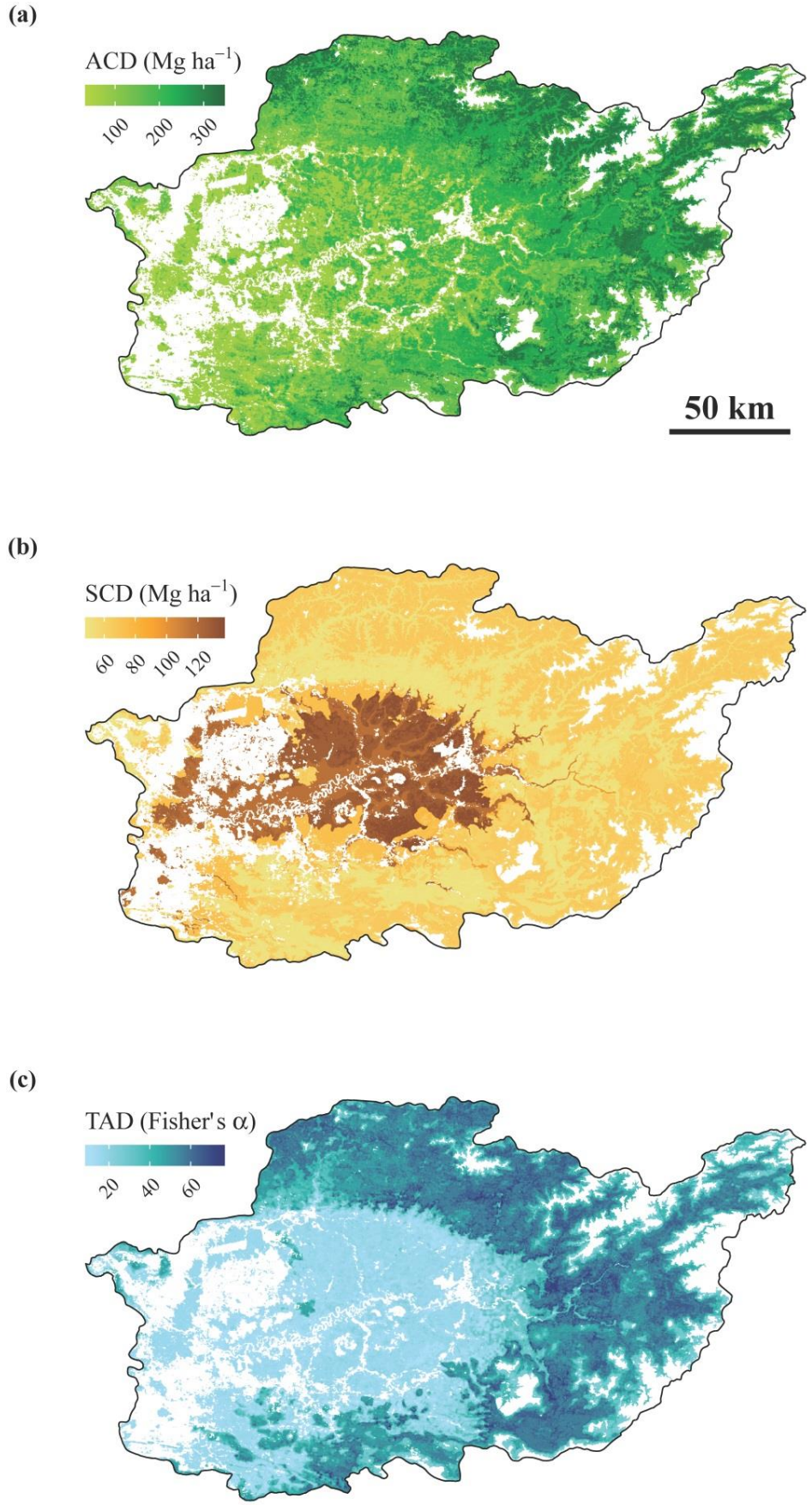

Figure 3.2. Map of predicted response variables over the study area: (a) aboveground carbon density (ACD), (b) soil carbon density (SCD), (c) tree alpha diversity (TAD, using Fisher's α). White areas correspond to areas where masks were applied.

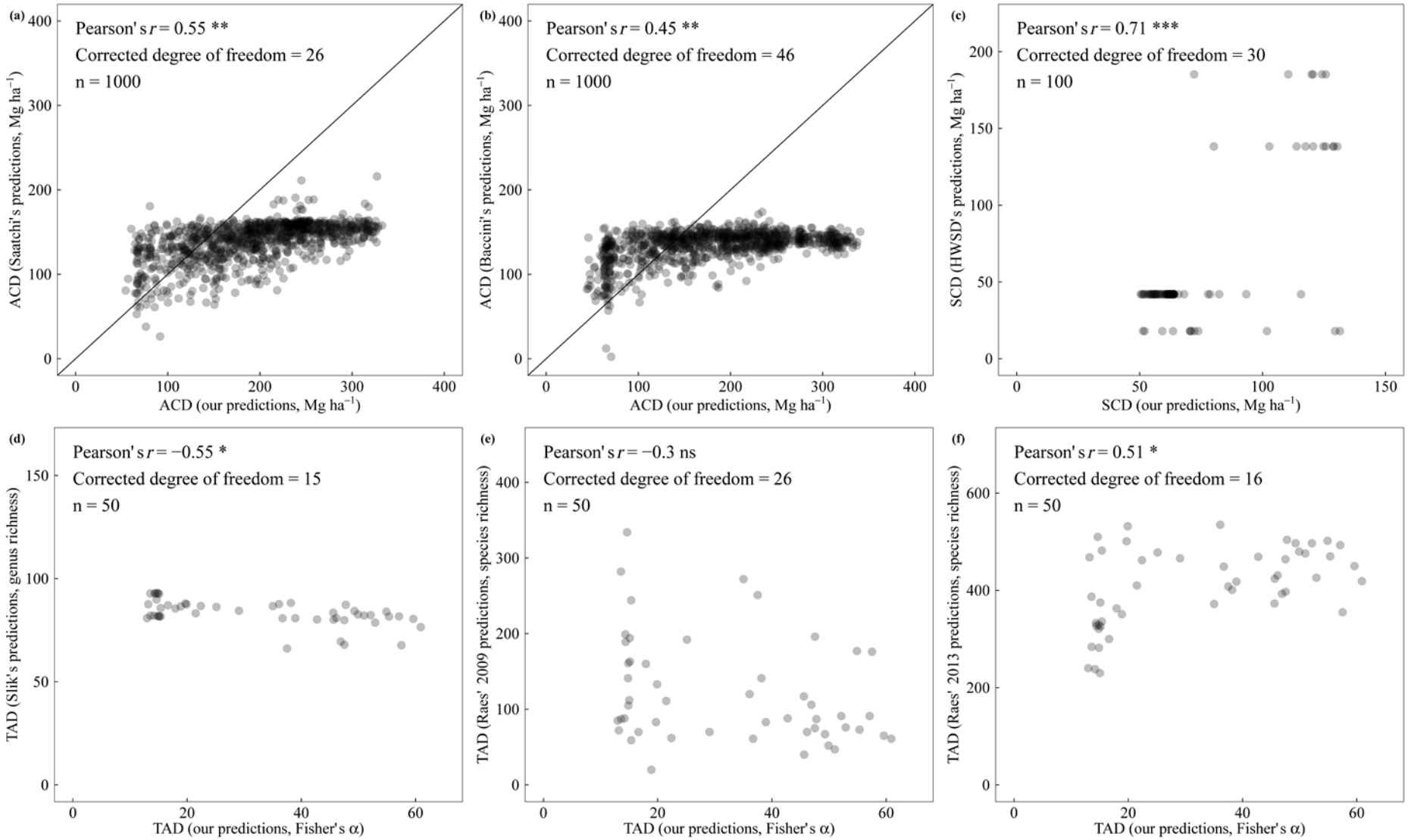

Figure 3.3. Comparison of our predictions with existing maps of (a) ACD (Saatchi et al., 2011); (b) ACD (Baccini et al., 2012); (c) SCD (Wieder et al., 2014); (d) TAD (Slik et al., 2009); (e) TAD (Raes et al., 2009); (f) TAD (Raes et al., 2013).

3.3.2 Response variable correlations and hotspot spatial congruence

The strength and sign of correlations varied greatly between pairs of response variables over the study area (Table 3.3). We found a weak negative correlation between ACD and SCD, a moderate negative correlation between SCD and TAD, and a strong positive correlation between ACD and TAD.

Table 3.3. Correlation between predicted values of response variables over the study area. Analyses were performed on a random subset of response variable values (n = 39,152, i.e. 10% of total response variable distribution). Depicted values are Pearson's correlation coefficients corrected for spatial autocorrelation. Corrected degrees of freedom are shown in parentheses.

Response variable	SCD	TAD
ACD	–0.33 * (54)	0.72 *** (24)
SCD		–0.55 ** (30)

* p < 0.05; ** p < 0.01; *** p < 0.001

We found no spatial congruence between hotspots of SCD and hotspots of either ACD or TAD (Table 3.4). However, spatial congruence between hotspots of ACD and TAD was more than three times (3.8:1) higher than expected if hotspot spatial distributions were random, meaning that about a third of ACD hotspots were also hotspots of tree diversity.

Table 3.4. Spatial congruence between hotspots (i.e. top 10% grid cells) of response variables. Values (percentage of overlapping grid cells over the total number of grid cells) potentially range from 0 to 10%. Expected spatial congruence for two variables with random spatial distribution is 1%. Lower than expected spatial congruences are indicated in bold.

Response variable	SCD	TAD
ACD	**0.0%**	3.8%
SCD		**0.0%**

3.4 Discussion

3.4.1 Ecological insight about the relationship between ACD and TAD

We found a strong positive correlation between predictions of ACD and TAD over the study area. The only non-null spatial congruence was found between hotspots of ACD and TAD. Using values computed from field measurements (those from which our predictions originated), we found a linearly increasing relationship between ACD and TAD ($R^2 = 0.33$; Figure 3.4) despite high ACD variability for a given TAD value.

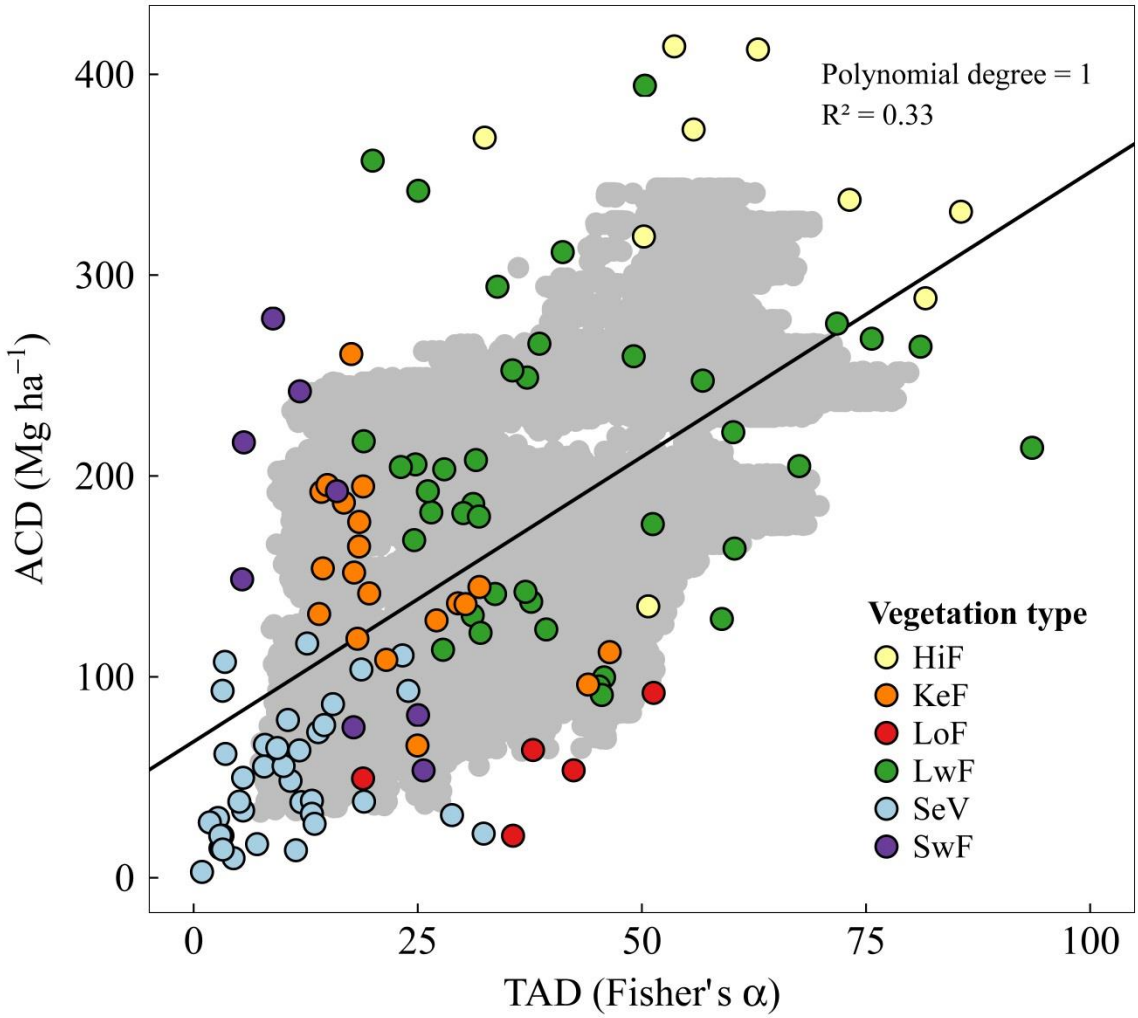

Figure 3.4. Aboveground carbon density (ACD) against tree alpha diversity (TAD, using Fisher's α). Grey dots represent model predictions (10% random selection) over the study area. Colored dots correspond to field measurements. The best-fit significant model over field measurements (selected among polynomial models with degrees 0 to 2) is also displayed. Vegetation type: HiF = hill natural forest on mineral soil; KeF = *Kerangas* forest (i.e. forest on sandstone); LoF = logged-over forest; LwF = lowland natural forest on mineral soil; SeV = secondary vegetation (either secondary regrowth or rubber gardens); SwF = swamp forest (either freshwater or peat swamp forests).

Part of that variability is inherently due to that we surveyed very different vegetation types. For example, TAD could be similar for some lowland natural forest and peat swamp plots (e.g. Fisher's $\alpha = 25$; see Figure 3.4), but ACD was much lower in the latter vegetation type. Soil nutrient content has been shown to affect spatial variations of aboveground biomass (and therefore carbon density) and tree diversity in Borneo (Cannon and Leighton, 2004; Paoli et al., 2008), with forests growing on oligotrophic soils (e.g. *Kerangas* forests on sandstone and peat swamp forests) containing lower aboveground biomass and fewer tree species than nearby forests on well-drained mineral soils (e.g. see Anderson, 1964; Brünig, 1974). While we found that TAD was limited in most nutrient-poor natural forest plots, ACD was more variable and some values reached surprisingly high levels compared to those of lowland natural forest plots on mineral soils (see Figure 3.4). This potentially originates from the relatively small size of our plots (0.04–0.2 ha).

Two – not necessarily mutually exclusive – hypotheses have gained attention in explaining how biodiversity might influence ecosystem properties such as carbon storage. The niche complementarity hypothesis states that higher levels of biodiversity lead to greater carbon storage because of increased resource use, whereas the mass ratio hypothesis holds that carbon storage is mostly driven by functional trait properties of the dominant species (Loreau and Hector, 2001). The linearly increasing relationship we found between ACD and TAD supports the niche complementarity hypothesis. Consistent with our findings, a study conducted in Panama found that species richness increased tree carbon storage (Ruiz-Jaen and Potvin, 2010). However, the study also showed that dominance was important in explaining tree carbon storage variations, thus highlighting the relevance of the mass ratio hypothesis. More work is required to test the mass ratio hypothesis with regard to our data and to weight, if necessary, the relative relevance of the two hypotheses in such a tropical forest context.

3.4.2 Potential threats over carbon and tree diversity hotspots

Considering land allocation as an indicator of potential threats to carbon and tree diversity hotspots, we found that a very high proportion of ACD and TAD hotspots were located either in watershed protection forests or national parks (Table 3.5). Very few ACD and TAD hotspots were found in concessions, which legally avoid watershed protection forests or national parks (see Appendix E for more information about concessions extent and location). Overall, provided current land allocation is maintained and the law is enforced to ensure the integrity of protected areas, ACD and TAD hotspots appear to be under low threat.

Table 3.5. Distribution (%) of response variable hotspots depending on land allocation and presence of concession. The expected repartition of hotspots of a response variable with random distribution is given for comparison. Land allocation columns are ordered from left to right along a gradient of increasing likeliness of disturbance. The sum of each row across the six land allocation types is equal to (ca.) 100%. Note that there can be more than one concession type on the same grid cell. A high proportion of SCD hotspots (compared to hotspots of other response variables) are situated in areas that are (most) likely to be disturbed.

	Land allocation						Concessions		
Hotspot of response variable	Area for other uses	Conversion forest	Production forest	Limited production forest	Watershed protection forest	National park	Logging	Mining	Plantation
Random distribution	24	23	5	1	17	30	10	11	17
ACD	< 1	0	< 1	5	25	69	< 1	1	< 1
SCD	28	7	12	46	1	6	36	17	19
TAD	1	0	< 1	13	38	48	2	3	< 1

In contrast, we found that a worryingly high proportion of SCD hotspots were located in areas under disturbance-prone land allocation ("area for other uses" and "limited production forest") and overlapped logging, mining and/or plantation concessions (Table 3.5). This raises concerns about the extent to which soil carbon stocks are secured in the study area. The vast majority of SCD hotspots were situated in peatlands. For almost 4 years now, there has been a moratorium on the issuance of new licenses for logging and conversion to other land uses in natural forests and peatlands. Whether the moratorium is effective in reducing the deforestation rate is highly debated (Busch et al., 2015; Sloan et al., 2012). Nevertheless, the concessions we consider here were granted prior to 2012, and designated areas are therefore susceptible to being legally selectively logged and/or cleared at any time.

We did not rank concession types according to their impacts on ecosystems but do acknowledge that all activities are not equally damaging. There is a general consensus about the deleterious effect on biodiversity and ES of forest conversion – especially in peatlands – to monocrop plantations (e.g. see Koh and Wilcove, 2008; Savilaakso et al., 2014). In comparison, logged-over forests have been shown to maintain relatively high levels of services (Putz et al., 2012) provided harvesting techniques that reduce the negative impact of logging on biodiversity and ES (e.g. 'reduced-impact logging' techniques) are used (Edwards et al., 2014).

3.4.3 Implications for conservation and development

Strong positive correlations between ES do not necessarily imply high spatial congruence between their respective hotspots, and vice versa (Chan et al., 2006). Yet, in our case, we found a strong positive correlation between ACD and TAD, and an above-than-expected-by-chance spatial congruence of hotspots. Prioritizing hotspots of one of ACD or TAD for conservation would therefore be beneficial to the other (Table 3.4). However, either type of prioritization would be detrimental to SCD, as would be SCD hotspot targeting for non-target response variables.

The spatial variations in total carbon stocks (i.e. carbon stored in aboveground biomass, belowground biomass, dead wood, litter and soil organic carbon) are mainly determined by variations in soil organic carbon, with stocks in peat forests largely outperforming those of forests on mineral soils (Page et al., 2011; Paoli et al., 2010). If REDD+ projects only try to maximize total carbon stock protection (i.e. focus on peatlands), additional gains for biodiversity conservation appear limited. We stress that REDD+ projects should target hotspots of ACD, which would also benefit TAD. In our case, preferential areas for REDD+ project development are in conservation areas or watershed protection forests. Yet, directing REDD+ funds toward conservation areas such as national parks is still controversial because of the seemingly lack of additionality (Macdonald et al., 2011). Until the institutional framework is clarified, targeting high-ACD watershed protection forests that are adjacent to national parks for REDD+ project development could be a first step in hindering the general trend of national park isolation that has been increasing for the last few decades (DeFries et al., 2005).

SCD hotspot protection, on the other hand, could be achieved through the strict enforcement of the current moratorium that has been praised, despite other caveats, as succeeding in peatland protection (Edwards et al., 2012; Sloan et al., 2012). Re-evaluation of permits delivered prior to 2012, especially for mining and plantations that would lead to permanent conversion of peatlands, could provide further benefits to SCD hotspot protection. If old concessions on peatlands were re-allocated, logged-over forests on mineral soils should undoubtedly be spared and allowed to recover as they provide ES similar to those of natural forests (Labrière et al., 2015; Meijaard and Sheil, 2007). Development of plantation concessions should be directed to highly degraded lowland areas on mineral soils. Some plantation concessions (e.g. timber plantations) could even lead to ecological benefits beyond economic ones (Lamb et al., 2005). Plantations of the exotic species *Acacia mangium* have, for example, been used successfully to restore natural vegetation in degraded *Imperata cylindrica* grasslands (Kuusipalo et al., 1995).

The future role of oil palm plantations (the vast majority of plantation concessions granted before 2012) in the development of Kapuas Hulu cannot be overlooked. As the extent of oil palm plantations is predicted to triple in Kalimantan by 2020 (Carlson et al., 2013), it is essential that oil palm establishment is carefully planned and plantations well managed, two conditions necessary for plantations to provide not only goods but also services to a certain extent (Sayer et al., 2012). Plantations developed only on highly degraded lands and incorporated within a matrix of land uses related to the traditional swidden system (that produce more services than oil palm plantations; see e.g. Labrière et al., 2015) could allow for development in Kapuas Hulu that would not be detrimental to carbon and biodiversity conservation. However, sound development options will be limited due to the peculiar biophysical characteristics of the area (steep slopes and peats in the outer and inner parts of the study area, respectively) that restrict the range of potential non-harmful human activities.

3.4.4 Limitations of our predictions and those from existing maps

Despite the fact that we used the best available data, the main limitations of our predictions arise from: (1) the still restricted size of our measurement dataset, and (2) the reliability of explanatory variable data. We tried to sample at least 2 ha per main vegetation type while an inventory of 4–6 ha would for instance be recommended to assess biomass of the lowland and hill dipterocarp forests of Indonesia with an error margin not higher than 6–8% (Laumonier et al., 2010). More vegetation and soil sampling will be required to challenge our predictions and gain a better knowledge of carbon and tree species distribution over the study area. Our predictions also depend on the reliability of explanatory variable data. WorldClim data, for example, are obtained by interpolating measurements collected over a vast network of weather stations worldwide. Yet, the density of weather stations was extremely low in our study area and over Borneo more generally (Hijmans et al., 2005).

Correlations between our predictions and existing maps were highly variable. While moderate positive correlations were found between our ACD predictions and those from Saatchi et al.

(2011) and Baccini et al. (2012), we found a clear saturation of their predictions (see Figure 3.3). This might be due to poor performance of GLAS (the Geoscience Laser Altimeter System) height estimation in hilly terrain with slope over 10–15° (about a third of our study area; Hilbert and Schmullius, 2012), asymptotical saturation of NDVI values in high biomass regions (Huete et al., 2002) and limited field sampling in Southeast Asian tropical forests that are structurally different from those of America and Africa (Slik et al., 2013).

While moderate negative correlations were found between our predictions of TAD and those from Slik et al. (2009) and Raes et al. (2009), more recent predictions from Raes et al. (2013) are better aligned with ours. Species distribution models used in Raes (2013) were obtained from a larger database of collection records and did not suffer from partial distribution modelling (Raes, 2012), as in earlier predictions.

3.5 Conclusion

Mapping the distribution of biodiversity and ecosystem services is crucial to guide decision making on land-use planning. Using field measurements and easily accessible explanatory variables, we were able to predict aboveground carbon density, soil carbon density and tree alpha diversity (response variables) over a mostly forested area of northern Borneo. Analyses of the correlations between response variables, and the spatial congruence of and potential threats to their respective hotspots, enabled us to discuss implications of carbon and tree diversity spatial distributions for conservation and development. We stress that prioritizing hotspots of aboveground carbon – and not total carbon – for conservation through financial mechanisms such as REDD+ would be beneficial for tree diversity conservation in the study area. The protection of the large carbon pool in peat soils should be achieved by conservation regulations, which the current moratorium on peat conversion in Indonesia is a first step toward. Re-allocating plantation concessions on highly degraded areas could help achieve economic development (and also ecosystem restoration in the case of timber plantations) in Kapuas Hulu without imperiling carbon and biodiversity conservation.

We believe that our approach can be used to predict the spatial distribution of other important ecosystem services in Kapuas Hulu (e.g. water flow regulation) or be transposed in other areas for the purpose of reaching an integrated ecosystem service based approach for land-use planning (Daily and Matson, 2008).

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3.7 Appendices

Appendix A: Sampling strategy, and plot structural and compositional features

The stratified sampling of the vegetation was based on a vegetation map built from Landsat and Spot images (Laumonier et al., 2013). Supervised classification coupled with photo-interpretation led to a 30-m resolution map depicting ca. 40 different classes of vegetation (e.g. logged-over lowland forest) and land uses (e.g. settlement). We surveyed the main vegetation types of the study area: (1) lowland forest, (2) logged-over lowland forest, (3) lowland secondary regrowth, (4) smallholder rubber gardens, (5) lowland forest on sandstone (i.e. lowland *Kerangas* forest), (6) hill forest, (7) hill forest on sandstone (i.e. hill *Kerangas* forest), (8) freshwater swamp forest, (9) mixed peat swamp forest, (10) deep peat swamp forest, and (11) riparian secondary regrowth.

For lowland secondary regrowth and smallholder rubber gardens, plots of 20 × 20 m were randomly selected across the landscape to capture the variability of vegetation structure and composition inherent to such vegetation/land-use types. For the other vegetation types, plots of 100 × 20 m were mostly used, usually at a distance of 100 m from each other. When bigger plots were selected (e.g. location KL.BK, Table A.1), they were subsequently subdivided into strips of 100 × 20 m for the sake of comparison.

Leaf samples were collected at least once for each vernacular name (consistently given by the same group of highly knowledgeable local people using the Iban language) for lowland secondary regrowth and rubber gardens, and in a semi-systematic way for the other vegetation types (i.e. at least once per sampling site for a few very common and easily identifiable species, and for each tree otherwise).

For each plot, we computed different indices to characterize TAD: species richness, S_{100}, and Fisher's α (see Table A.1). Species richness is the simplest measure of species diversity and represents the number of species found in the plot. Because species richness cannot be used to compare plots with different sampling area, we computed S_{100}, that is the expected number of species found in a sample of a hundred randomly chosen individuals (Hurlbert, 1971). S_{100} was computed using the ‘rarefy’ function of the ‘vegan’ R package (Oksanen et al., 2015). Yet, because some plots did not reach 100 individuals (see Table A.1), we had to model rarefaction curves to extrapolate S_{100} values. We tested two different functions, sqrt(x) and log(1+x), and selected the former because of better fit (Fig. A.1). Consequently, for plots with $n < 100$ individuals, S_{100} is the value of the model using the sqrt(x) function extrapolated for $n = 100$.

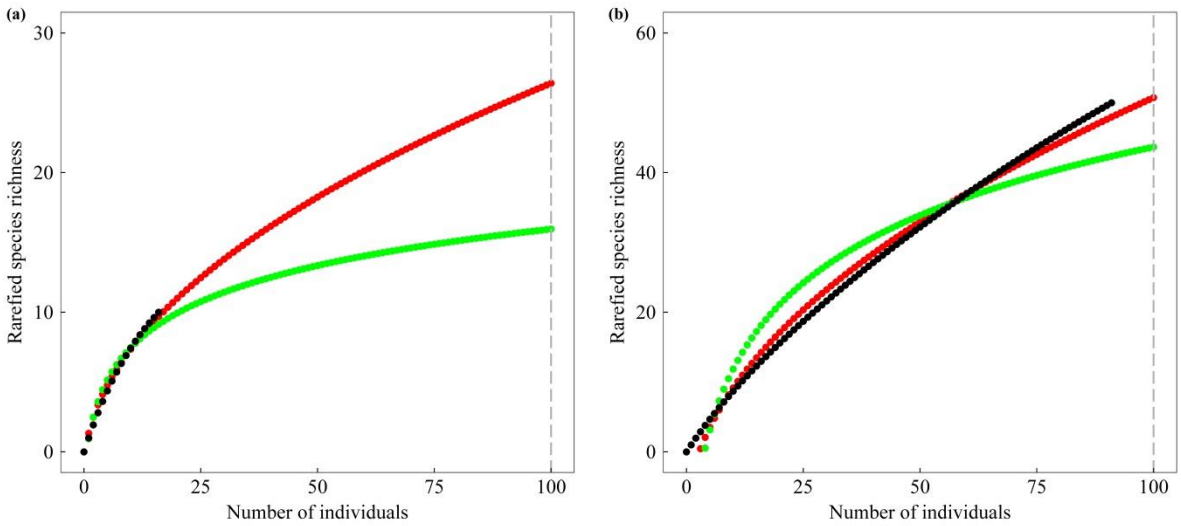

Fig. A.1 Examples of S_{100} computation for two sampling plots with n < 100 individuals. The model using the sqrt(x) function (red dots) better fits the rarefaction curve (black dots) compared to the model using the log(1+x) function (green dots).

After having conducted modeling and subsequent analysis with both S_{100} and Fisher's α, we decided to use only Fisher's α because correlations between TAD and either ACD or SCD, and spatial congruence of their respective hotspots were very similar whichever the indicator used (S_{100} and Fisher's α were very strongly correlated; Pearson's r = 0.98, $p < 0.001$), and because Fisher's α measures did not suffer potential bias due to the aforementioned computation technique.

Table A.1 Information on plot structure and diversity features. One plot was consistently discarded in ACD-related analyses because of outlier behavior (see grey-tinted line; ACD = 710 Mg ha^{-1}).

Plot ID	X_coord	Y_coord	Vegetation condition [a] and type [b]	Area	ACD (Mg ha^{-1})	Tree number	Tree density (ha^{-1})	DBH (cm)	Height (m)	WSG (g cm^{-3})	Species richness	S_{100}	Fisher's α
KL.SR 1	640522.2	127291.4	RuG_low	0.04	29.9	22	550	17.6	10.7	0.483	6	12.7	2.7
KL.SR 3	640527.9	127461.1	RuG_low	0.04	14.7	28	700	13.1	10.8	0.399	7	13.5	3.0
KL.SR 4	640533.6	127483.4	RuG_low	0.04	37.7	18	450	18.1	12.1	0.493	11	26.5	12.0
KL.SR 5	640792.7	127749.8	RuG_low	0.04	9.8	17	425	13.8	9.4	0.452	7	18.0	4.5
KL.SR 6	639219.8	127014.4	RuG_low	0.04	27.6	27	675	15.5	11.9	0.464	5	9.2	1.8
KL.SR 7	639189.1	127004.8	RuG_low	0.04	33.6	35	875	14.8	11.3	0.479	11	18.9	5.5
KL.SR 8	640355.8	127411.2	RuG_low	0.04	66.2	20	500	19.4	11.7	0.501	10	24.1	8.0
KL.SR 9	640422.6	127344.4	RuG_low	0.04	61.7	22	550	20.4	12.1	0.488	7	15.5	3.5
KL.SR 10	640450.9	127738.2	RuG_low	0.04	38.4	11	275	23.8	12.7	0.548	8	24.3	13.2
KL.SR 11	640631.3	127753.7	RuG_low	0.04	72.6	27	675	22.1	12.7	0.538	15	30.3	13.9
KL.SR 12	640622.2	127688.9	RuG_low	0.04	63.5	34	850	18.9	11.8	0.512	16	28.4	11.8
KL.SR 13	640409.2	127576.9	RuG_low	0.04	86.5	16	400	29.8	12.9	0.453	11	28.6	15.5
KL.SR 14	640397.2	127588.4	RuG_low	0.04	49.8	18	450	21.5	12.7	0.497	8	20.1	5.5
KL.SR 15	640999.5	127471.1	RuG_low	0.04	55.4	24	600	20.7	12.3	0.552	11	23.5	7.9
KL.SR 16	641092.5	127564.9	RuG_low	0.04	48.3	22	550	21.4	13.0	0.498	12	26.5	10.8
KL.SR 17	640263.1	128179.2	RuG_low	0.04	31.9	11	275	23.1	12.9	0.516	8	24.3	13.2
KL.SR 18	640071.7	128248.7	RuG_low	0.04	55.7	20	500	22.0	14.3	0.492	11	25.3	10.0
KL.SR 21	640592.1	127500.4	SeR_low	0.04	16.8	22	550	14.1	11.0	0.455	10	22.2	7.1
KL.SR 22	640560.6	127223.7	SeR_low	0.04	26.9	17	425	17.2	9.8	0.496	11	27.6	13.5
KL.SR 23	640627.8	127517.6	SeR_low	0.04	21.0	12	300	14.7	9.5	0.467	5	14.7	3.2
KL.SR 24	640726.0	127939.0	SeR_low	0.04	21.0	41	1025	14.0	10.9	0.332	8	12.7	3.0
KL.SR 25	640703.7	127946.2	SeR_low	0.04	14.1	35	875	12.7	9.8	0.369	8	14.0	3.2
KL.SR 26	640485.0	127110.0	SeR_low	0.04	64.7	21	525	20.0	11.1	0.524	11	25.1	9.3
KL.SR 27	640378.2	127070.3	SeR_low	0.04	31.3	25	625	16.8	10.9	0.529	18	37.6	28.8
KL.SR 28	639835.6	127086.7	SeR_low	0.04	13.8	16	400	15.1	11.1	0.489	10	26.4	11.4
KL.SR 29	639617.4	127015.6	SeR_low	0.04	103.8	23	575	23.0	12.7	0.515	15	33.1	18.7
KL.SR 30	639523.4	127050.8	SeR_low	0.04	22.1	16	400	16.0	12.9	0.589	13	33.4	32.4
KL.SR 31	639936.6	127121.8	SeR_low	0.04	116.7	20	500	25.5	13.1	0.586	12	27.7	12.7
KL.SR 32	639873.5	127059.3	SeR_low	0.04	76.1	21	525	21.4	13.3	0.541	13	29.1	14.6

Plot ID	X_coord	Y_coord	Vegetation condition [a] and type [b]	Area	ACD (Mg ha^{-1})	Tree number	Tree density (ha^{-1})	DBH (cm)	Height (m)	WSG (g cm^{-3})	Species richness	S_{100}	Fisher's α
KL.SR 33	640692.5	128118.7	SeR_low	0.04	37.9	39	975	15.6	11.4	0.464	11	17.5	5.1
KL.SR 34	640898.2	128537.1	SeR_low	0.04	93.1	29	725	23.4	11.3	0.568	19	37.6	23.9
KL.SR 35	641023.4	127403.8	SeR_low	0.04	38.0	30	750	16.5	10.4	0.573	18	33.9	19.0
KL.SR 36	640647.3	127206.6	SeR_low	0.04	110.7	23	575	26.8	13.6	0.591	16	35.3	23.3
KL.SR 44	640765.8	128856.4	SeR_low	0.04	3.0	7	175	10.7	10.1	0.535	2	7.4	0.9
KL.SR 47	640762.0	128992.8	SeR_low	0.04	107.5	16	400	26.7	21.5	0.493	6	15.2	3.5
KL.LR 1	640745.6	130090.4	LoF_low	0.20	63.7	124	620	20.1	11.1	0.552	55	48.2	37.9
KL.LR 2	640268.6	130293.3	LoF_low	0.20	49.5	115	575	18.8	13.1	0.512	37	33.9	18.9
KL.LR 3	640033.1	130994.7	LoF_low	0.20	21.0	151	755	13.2	10.9	0.485	59	45.5	35.6
KL.LR 4	640147.4	131207.4	LoF_low	0.20	92.1	170	850	18.9	13.5	0.558	75	56.0	51.3
KL.LR 5	640191.0	131491.5	LoF_low	0.20	53.5	145	725	18.2	12.0	0.538	63	49.7	42.4
KL.BK 1	639923.4	130079.3	NaF_low	0.20	130.7	157	785	20.1	19.2	0.599	56	44.7	31.1
KL.BK 2	639900.2	130063.4	NaF_low	0.20	168.1	135	675	21.8	19.5	0.587	46	39.7	24.6
KL.BK 3	639858.6	130035.6	NaF_low	0.20	99.8	124	620	19.6	19.0	0.568	60	52.3	45.8
KL.BK 4	639880.0	130049.0	NaF_low	0.20	141.3	139	695	19.7	18.5	0.599	55	46.3	33.6
KL.BK 5	639945.5	130096.3	NaF_low	0.20	95.3	141	705	19.1	17.0	0.588	64	54.1	45.2
KL.BK 6	639798.2	130127.6	NaF_low	0.20	203.4	172	860	21.6	20.4	0.605	55	43.4	28.0
KL.BK 7	639820.0	130140.2	NaF_low	0.20	186.1	145	725	22.8	20.2	0.575	54	45.2	31.2
KL.BK 8	639837.2	130155.4	NaF_low	0.20	137.5	163	815	20.3	18.1	0.588	63	47.5	37.7
KL.BK 9	639861.7	130171.3	NaF_low	0.20	122.0	164	820	19.3	17.9	0.594	58	44.7	32.0
KL.BK 10	639883.5	130187.2	NaF_low	0.20	113.6	166	830	18.9	17.5	0.565	54	40.3	27.8
KL.BK 11	639734.1	130220.9	NaF_low	0.20	217.3	174	870	24.1	20.6	0.560	44	33.9	19.0
KL.BK 12	639759.8	130232.1	NaF_low	0.20	205.8	186	930	20.9	20.0	0.608	53	37.5	24.7
KL.BK 13	639775.7	130245.4	NaF_low	0.20	142.4	166	830	20.0	19.4	0.587	63	49.0	37.0
KL.BK 14	639796.9	130259.9	NaF_low	0.20	181.6	151	755	21.8	18.1	0.613	54	43.3	30.1
KL.BK 15	639820.7	130278.4	NaF_low	0.20	182.0	155	775	21.4	19.3	0.593	51	43.1	26.5
KL.BK 16	639673.9	130312.2	NaF_low	0.20	204.5	146	730	23.0	19.7	0.581	46	38.3	23.1
KL.BK 17	639697.0	130324.1	NaF_low	0.20	192.5	151	755	22.4	20.1	0.615	50	41.1	26.1
KL.BK 18	639714.2	130338.6	NaF_low	0.20	249.0	135	675	25.1	19.6	0.587	57	48.5	37.2
KL.BK 19	639735.4	130351.9	NaF_low	0.20	208.0	138	690	22.5	19.5	0.599	53	44.3	31.5
KL.BK 20	639757.9	130369.1	NaF_low	0.20	265.9	149	745	24.0	20.4	0.593	61	48.5	38.6
ND.BP 1	705149.4	37293.3	NaF_low	0.20	357.1	152	760	26.5	23.1	0.676	43	32.6	20.0

Plot ID	X_coord	Y_coord	Vegetation condition [a] and type [b]	Area	ACD (Mg ha^{-1})	Tree number	Tree density (ha^{-1})	DBH (cm)	Height (m)	WSG (g cm^{-3})	Species richness	S_{100}	Fisher's α
ND.BP 2	705181.9	37276.1	NaF_low	0.20	179.9	95	475	25.1	22.0	0.619	44	44.9	31.8
ND.BP 3	705240.9	37305.8	NaF_low	0.20	252.6	87	435	26.9	24.9	0.588	44	46.0	35.6
ND.BP 4	705273.5	37284.8	NaF_low	0.20	176.1	131	655	20.1	19.0	0.597	65	54.7	51.2
ND.BP 5	705269.6	37335.6	NaF_low	0.20	259.7	121	605	22.7	20.8	0.548	61	53.8	49.1
ND.BP 6	705304.7	37316.2	NaF_low	0.20	394.4	109	545	28.0	24.1	0.583	58	55.0	50.3
ND.BP 7	705153.7	37427.0	NaF_low	0.20	311.5	108	540	26.7	25.8	0.599	53	50.4	41.2
ND.BP 8	705174.8	37473.1	NaF_low	0.20	342.0	120	600	23.6	22.4	0.557	44	40.1	25.1
ND.BP 9	705190.2	37504.8	NaF_low	0.20	294.3	110	550	24.5	21.1	0.557	49	46.0	33.9
ND.BP 10	705208.5	37539.7	NaF_low	0.20	91.1	91	455	21.2	18.5	0.518	50	50.8	45.5
NH.BK 1	749547.4	115440.8	NaF_low	0.20	128.9	107	535	22.1	16.0	0.579	61	58.0	58.9
NH.BK 2	749455.8	115342.7	NaF_low	0.20	221.8	120	600	23.2	16.9	0.598	66	58.6	60.2
NH.BK 3	749495.8	115190.5	NaF_low	0.20	123.7	112	560	21.2	16.7	0.612	53	48.6	39.3
NH.BK 4	749712.6	115109.2	NaF_low	0.20	205.0	181	905	21.7	17.4	0.600	88	61.8	67.5
NH.BK 5	749774.5	114950.5	NaF_low	0.20	163.9	129	645	20.8	19.8	0.600	69	58.1	60.3
NH.BK 6	751041.1	108433.2	NaF_low	0.20	275.9	144	720	23.8	17.5	0.612	79	61.7	71.8
NH.BK 7	750941.9	108282.4	NaF_low	0.20	247.5	145	725	23.4	18.8	0.605	72	56.3	56.8
NH.BK 8	750628.4	107881.0	NaF_low	0.20	264.4	168	840	24.2	19.4	0.584	91	62.6	81.1
NH.BK 9	751012.0	107762.0	NaF_low	0.20	268.4	154	770	23.0	17.8	0.611	84	62.1	75.6
NH.BK 10	750849.3	107604.6	NaF_low	0.20	214.1	162	810	22.6	16.5	0.586	94	65.8	93.5
ND.SB 1	711037.7	33829.6	NaF_hill	0.20	414.0	137	685	24.3	27.4	0.591	68	56.8	53.6
ND.SB 2	710922.4	33851.1	NaF_hill	0.20	135.2	147	735	19.8	19.5	0.568	69	55.0	50.7
ND.SB 3	710789.3	33887.9	NaF_hill	0.20	319.3	133	665	24.1	27.8	0.568	65	55.5	50.2
ND.SB 4	710666.4	33919.6	NaF_hill	0.20	288.5	118	590	24.2	26.3	0.578	73	64.7	81.6
ND.SB 5	710573.3	33943.8	NaF_hill	0.20	710.2	133	665	29.0	29.7	0.592	70	57.9	59.8
ND.SB 6	710452.7	33978.2	NaF_hill	0.20	412.5	141	705	23.4	25.9	0.564	74	59.4	63.0
ND.SB 7	710332.0	34004.1	NaF_hill	0.20	331.6	81	405	26.8	29.2	0.582	57	61.6	85.6
ND.SB 8	710233.7	34035.1	NaF_hill	0.20	372.6	133	665	23.8	26.6	0.556	68	56.4	55.8
ND.SB 9	710144.1	34066.2	NaF_hill	0.20	337.5	128	640	23.1	25.3	0.573	74	62.3	73.2
ND.SB 10	710028.5	34102.4	NaF_hill	0.20	368.5	119	595	24.1	25.3	0.537	50	45.4	32.5
ND.PP 1	708115.7	36334.0	NaF_kerL	0.20	177.2	171	855	19.5	22.1	0.589	43	34.0	18.5
ND.PP 2	708110.8	36224.0	NaF_kerL	0.20	192.2	152	760	20.0	23.4	0.591	35	29.4	14.2
ND.PP 3	708111.4	36085.6	NaF_kerL	0.20	195.6	203	1015	19.5	22.5	0.573	40	29.7	14.9

Plot ID	X_coord	Y_coord	Vegetation condition [a] and type [b]	Area	ACD (Mg ha^{-1})	Tree number	Tree density (ha^{-1})	DBH (cm)	Height (m)	WSG (g cm^{-3})	Species richness	S_{100}	Fisher's α
ND.PP 4	708109.4	35977.9	NaF_kerL	0.20	165.0	193	965	17.8	23.3	0.594	45	35.0	18.5
ND.PP 5	708107.0	35838.2	NaF_kerL	0.20	141.6	232	1160	15.7	24.9	0.599	50	34.5	19.6
ND.PP 6	707887.3	35831.9	NaF_kerL	0.20	194.8	175	875	19.6	29.6	0.599	44	33.5	18.9
ND.PP 7	707886.6	35950.5	NaF_kerL	0.20	154.0	187	935	17.7	24.4	0.609	38	29.3	14.4
ND.PP 8	707889.9	36077.6	NaF_kerL	0.20	186.8	229	1145	17.3	26.7	0.605	45	30.7	16.8
ND.PP 9	707891.5	36199.0	NaF_kerL	0.20	260.7	174	870	21.0	33.6	0.602	42	32.9	17.6
ND.PP 10	707889.9	36319.7	NaF_kerL	0.20	152.0	159	795	18.2	27.1	0.600	41	32.8	17.9
ND.BT 1	710118.2	32158.0	NaF_kerH	0.20	131.4	213	1065	18.1	18.6	0.622	39	30.9	14.0
ND.BT 2	710216.7	32224.7	NaF_kerH	0.20	128.2	212	1060	18.5	17.4	0.598	59	42.1	27.1
ND.BT 3	710329.4	32286.6	NaF_kerH	0.20	119.0	221	1105	18.4	15.7	0.620	47	33.8	18.3
ND.BT 4	710416.7	32346.9	NaF_kerH	0.20	144.8	191	955	20.5	16.7	0.615	62	43.7	31.9
ND.BT 5	710526.2	32412.0	NaF_kerH	0.20	65.9	160	800	16.8	15.0	0.620	50	39.3	25.0
ND.BT 6	710637.3	32221.5	NaF_kerH	0.20	112.4	146	730	19.7	17.6	0.623	66	52.5	46.4
ND.BT 7	710734.2	32285.0	NaF_kerH	0.20	136.7	247	1235	18.0	17.7	0.599	66	43.7	29.5
ND.BT 8	710834.2	32350.1	NaF_kerH	0.20	96.2	215	1075	17.4	16.3	0.621	78	51.6	44.0
ND.BT 9	710946.9	32407.2	NaF_kerH	0.20	136.3	189	945	20.6	18.0	0.609	60	44.0	30.3
ND.BT 10	711039.0	32461.2	NaF_kerH	0.20	108.6	170	850	19.2	17.8	0.628	47	36.6	21.5
BL.NS 1	671571.1	108900.9	NaF_fsf	0.20	53.5	141	705	18.1	12.0	0.523	48	40.3	25.6
BL.NS 2	671612.5	108802.6	NaF_fsf	0.20	81.0	167	835	19.1	13.9	0.520	51	39.3	25.0
BL.NS 3	671646.9	108690.9	NaF_fsf	0.20	75.0	141	705	20.1	13.8	0.514	39	34.3	17.8
BL.NS 4	672412.8	109856.9	SeR_rf	0.20	93.1	178	890	19.5	15.5	0.592	13	9.5	3.2
BL.NS 5	672277.3	109664.6	SeR_rf	0.20	78.6	232	1160	16.9	14.4	0.527	33	21.3	10.5
BT.NS 6	693335.6	118770.0	NaF_dpsf	0.20	216.8	401	2005	16.7	19.3	0.572	24	15.9	5.6
BT.NS 7	693246.8	119168.4	NaF_dpsf	0.20	148.6	310	1550	16.0	18.4	0.567	22	16.3	5.4
BT.NS 8	688794.8	117500.7	NaF_mpsf	0.20	278.5	110	550	28.1	23.0	0.552	23	22.2	8.9
BT.NS 9	689016.7	117421.1	NaF_mpsf	0.20	192.5	110	550	25.2	19.9	0.556	33	31.7	16.0
BT.NS 10	688947.3	117317.8	NaF_mpsf	0.20	242.2	114	570	26.9	18.8	0.555	28	27.0	11.9

[a] Vegetation condition: LoF = logged-over; NaF = natural; SeR = secondary regrowth; RuG = rubber garden

[b] Vegetation type: dpsf = deep peat swamp forest; fsf = freshwater swamp forest; hill = hill forest; kerH = hill *Kerangas* forest; kerL = lowland *Kerangas* forest; low = lowland forest; mpsf = mixed peat swamp forest; rf = riparian forest

Appendix B: Comparing ACD, SCD and TAD values computed from our field measurements with those extracted from existing maps

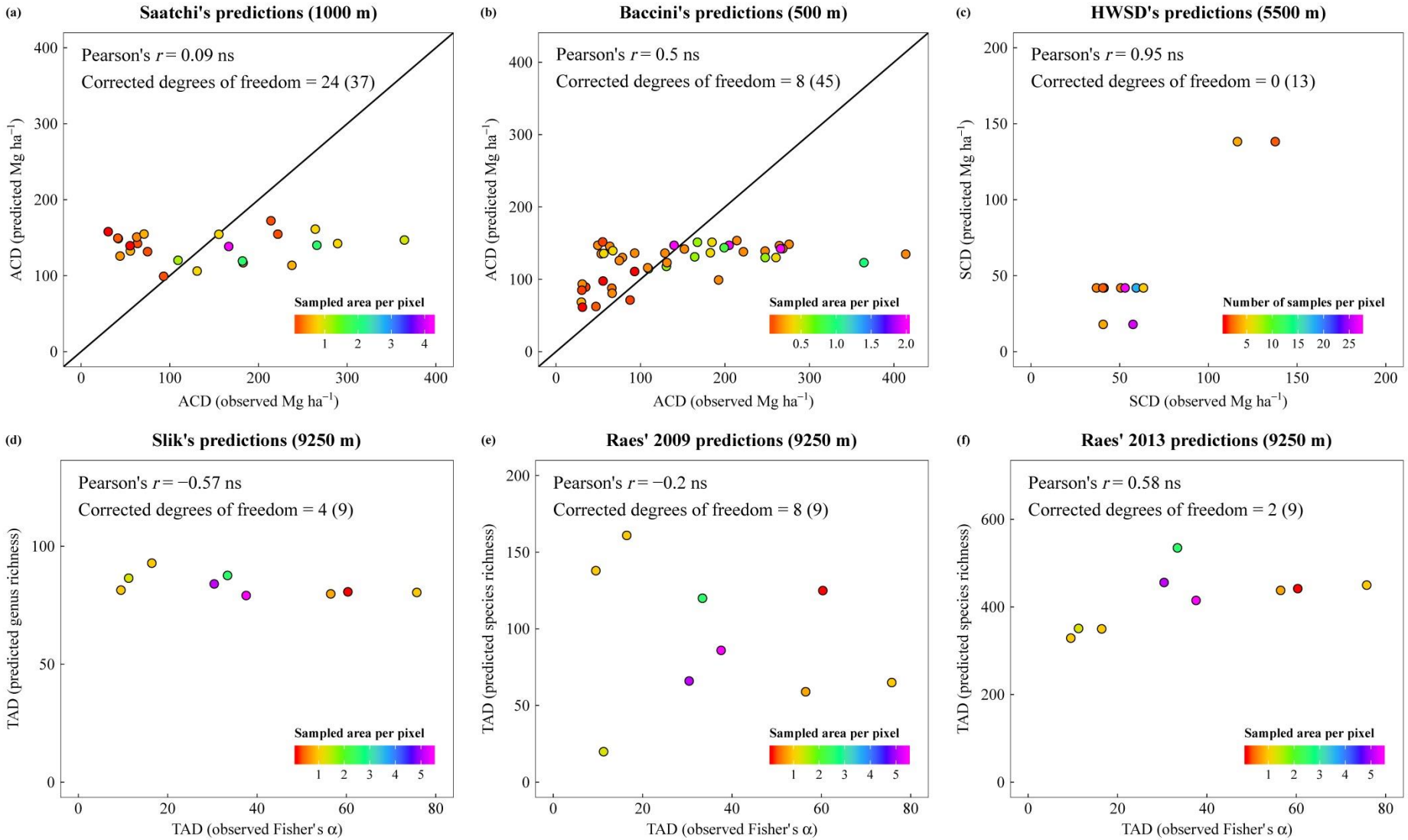

Fig. B.1 Comparison of our field measurements with existing maps of (a) ACD (Saatchi et al., 2011); (b) ACD (Baccini et al., 2012); (c) SCD (Wieder et al., 2014); (d) TAD (Slik et al., 2009); (e) TAD (Raes et al., 2009); (f) TAD (Raes et al., 2013).

Appendix C: Explanatory variable selection

A random forest is made up of a user-defined number of unpruned classification or, as in our case, regression trees (Breiman, 2001; Cutler et al., 2007). Our explanations will only focus on the use of random forests for regression. For each tree, a bootstrap sample of the dataset (ca. 63% of the response and associated explanatory variable values; replacement is allowed) is selected. For each node of any single tree, a defined number of explanatory variables – one third of the total number of explanatory variables, by default – is selected at random, and the variable providing the best split – i.e. the lowest weighted mean-squared error – is kept (Breiman et al., 1984). Each tree is fully grown, i.e. until the number of unique cases in each node does not exceed five. To test tree performance, all out-of-bag values (the remaining ca. 37% of the values that were not selected in the bootstrap sample) are then dropped down the tree and error is computed (against the mean value of node cases). For prediction, new values (i.e. explanatory variable values from a new dataset) are dropped down every tree of the forest and the average value over individual tree predictions is computed.

We ran random forests for each of the response variables (ACD and SCD, and TAD using Fisher's α) with the 20 explanatory variables. Two key features were first used to choose which variables to keep: minimal depth and importance value (see Fig. C.1–C.3). The minimal depth of a variable is the depth at which the variable first splits within a tree, relative to the root node. The smaller the minimal depth, the more predictive the variable is (Chen and Ishwaran, 2013). Variable importance (VIMP) is obtained by: (1) randomly permuting variable values in the out-of-bag dataset, (2) dropping them down the tree, (3) calculating the resulting prediction error, (4) computing the difference with the error without permutation, (5) averaging the differences over all trees (Chen and Ishwaran, 2013). The larger the VIMP of a variable, the more predictive it is (Breiman, 2001).

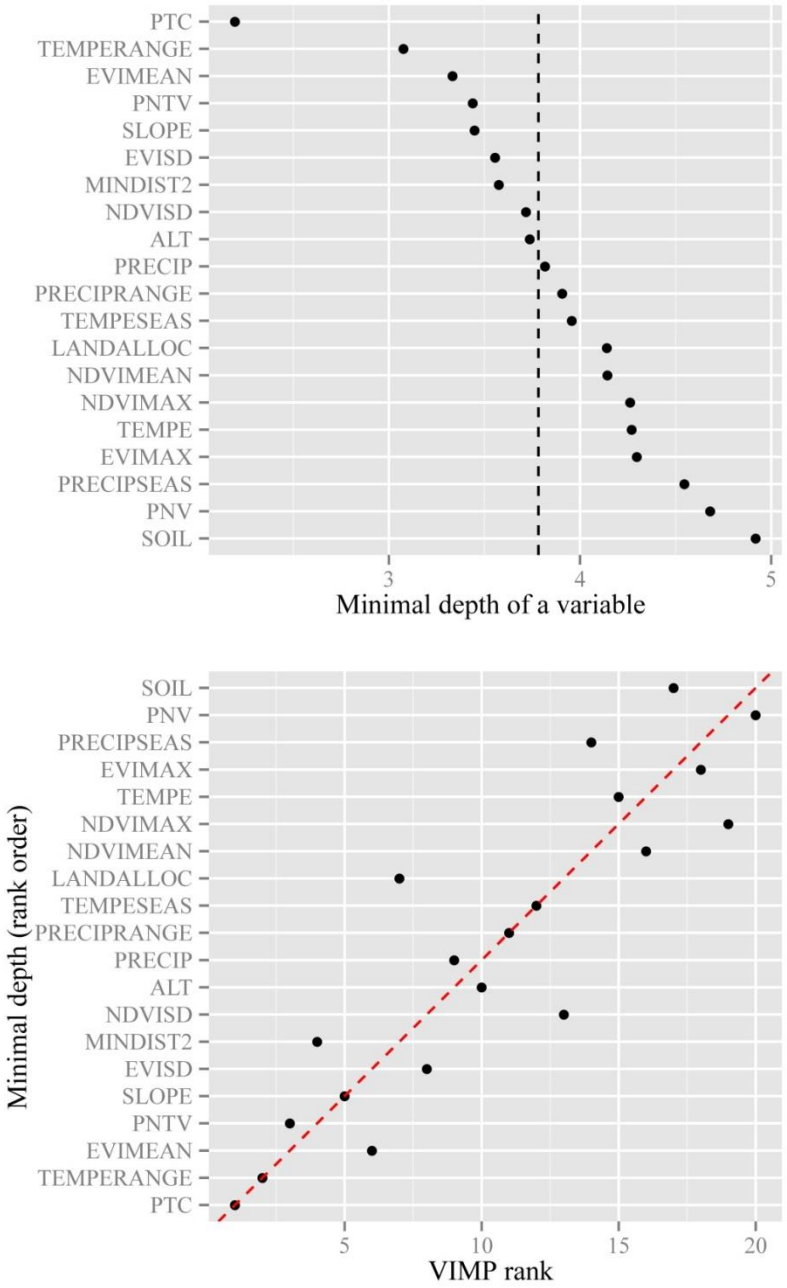

Fig. C.1 Variable selection process for ACD. Variables with minimal depth lower than the vertical dashed line in the upper panel (average minimal depth) are considered strong predictors and were preferably selected. We checked that potential variables simultaneously had a high VIMP (cf. lower panel). Abbreviations: ALT = altitude; EVIMAX = maximum Enhanced Vegetation Index (EVI); EVIMEAN = mean EVI; EVISD = standard deviation EVI; LANDALLOC = land allocation; MINDIST2 = minimum distance to disturbance source (either road, river or village); NDVIMAX = maximum Normalized Difference Vegetation Index (NDVI); NDVIMEAN = mean NDVI; NDVISD = standard deviation NDVI; PNTV = percent non tree vegetation; PNV = percent non vegetation; PRECIP = mean annual precipitation; PRECIPRANGE = precipitation range; PRECIPSEAS = precipitation seasonality; PTC = percent tree cover; SLOPE = slope; SOIL = soil group; TEMPE = mean annual temperature; TEMPERANGE = temperature range; TEMPESEAS = temperature seasonality

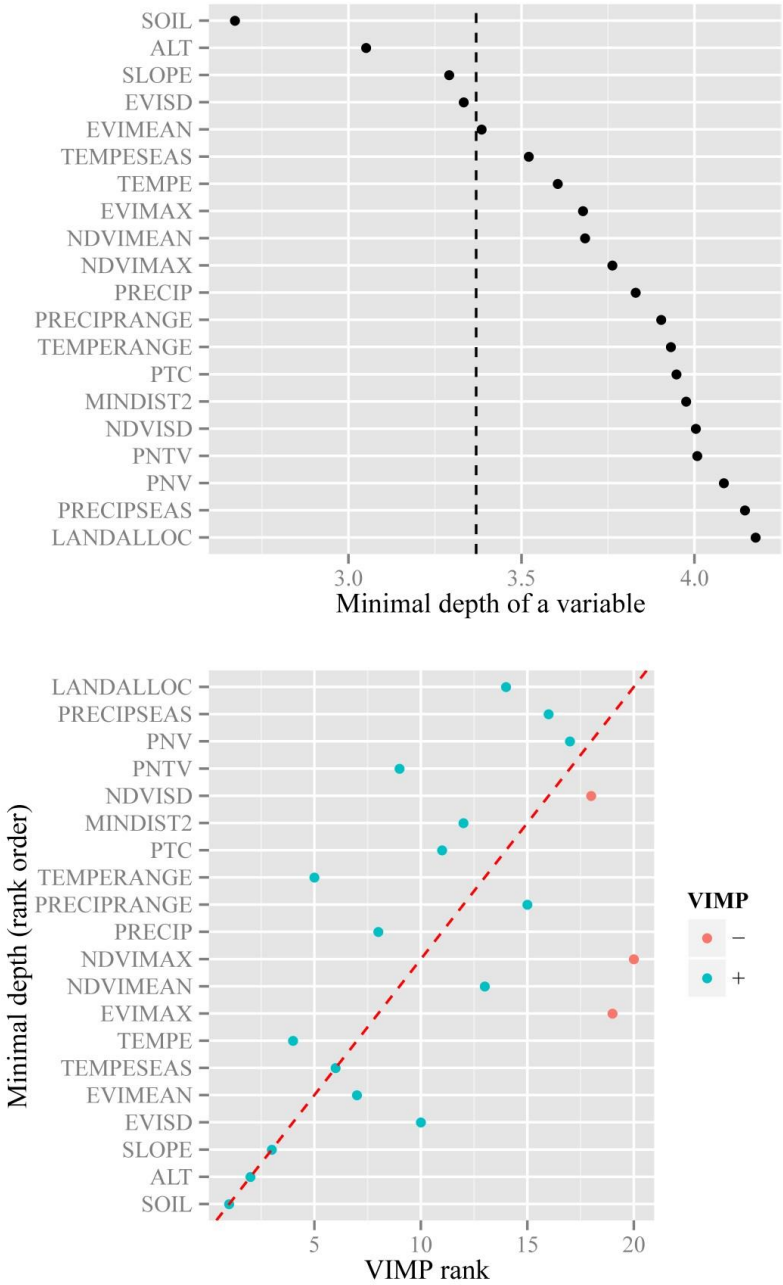

Fig. C.2 Variable selection process for SCD. Variables with minimal depth lower than the vertical dashed line in the upper panel (average minimal depth) are considered strong predictors and were preferably selected. We checked that potential variables simultaneously had a high VIMP (cf. lower panel). Note that VIMP (i.e. average difference between errors from out-of-bag predictions with and without permutation over all trees) can be negative. Abbreviations: ALT = altitude; EVIMAX = maximum Enhanced Vegetation Index (EVI); EVIMEAN = mean EVI; EVISD = standard deviation EVI; LANDALLOC = land allocation; MINDIST2 = minimum distance to disturbance source (either road, river or village); NDVIMAX = maximum Normalized Difference Vegetation Index (NDVI); NDVIMEAN = mean NDVI; NDVISD = standard deviation NDVI; PNTV = percent non tree vegetation; PNV = percent non vegetation; PRECIP = mean annual precipitation; PRECIPRANGE = precipitation range; PRECIPSEAS = precipitation seasonality; PTC = percent tree cover; SLOPE = slope; SOIL = soil group; TEMPE = mean annual temperature; TEMPERANGE = temperature range; TEMPESEAS = temperature seasonality

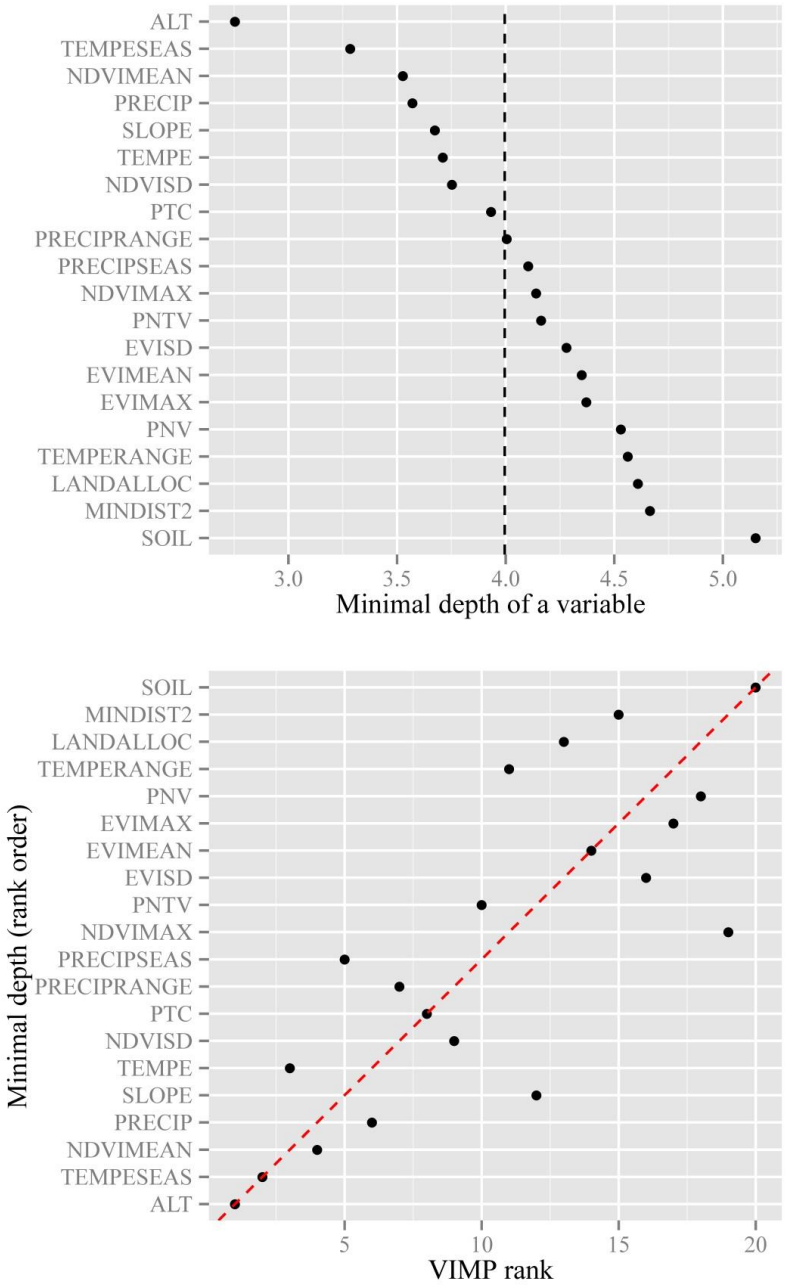

Fig. C.3 Variable selection process for Fisher's α. Variables with minimal depth lower than the vertical dashed line in the upper panel (average minimal depth) are considered strong predictors and were preferably selected. We checked that potential variables simultaneously had a high VIMP (cf. lower panel). Abbreviations: ALT = altitude; EVIMAX = maximum Enhanced Vegetation Index (EVI); EVIMEAN = mean EVI; EVISD = standard deviation EVI; LANDALLOC = land allocation; MINDIST2 = minimum distance to disturbance source (either road, river or village); NDVIMAX = maximum Normalized Difference Vegetation Index (NDVI); NDVIMEAN = mean NDVI; NDVISD = standard deviation NDVI; PNTV = percent non tree vegetation; PNV = percent non vegetation; PRECIP = mean annual precipitation; PRECIPRANGE = precipitation range; PRECIPSEAS = precipitation seasonality; PTC = percent tree cover; SLOPE = slope; SOIL = soil group; TEMPE = mean annual temperature; TEMPERANGE = temperature range; TEMPESEAS = temperature seasonality

After potential variables were selected based on their minimal depth and VIMP, they underwent a last selection step during which we checked that (1) the range of values covered by the 65 composite sample sites matched that of the whole study area, (2) partial dependence behavior was not counter-intuitive, and (3) obvious artifacts on prediction maps that used these variables were not evidenced through visual inspection. Outcomes of the selection process are displayed in Table C.1.

Table C.1 Selection/rejection of variables of highest minimum depth and importance value.

Response	Variables of highest min. depth	Selected	Rejected	
			Restricted range	PD [b] behavior
ACD	PTC [a]	X		
	TEMPERANGE			X
	EVIMEAN		X	
	PNTV		X	
	SLOPE		X	
	EVISD		X	
	MINDIST2		X	
	NDVISD		X	
	ALT	X		
SCD	SOIL	X		
	ALT	X		
	SLOPE		X	
	EVISD		X	
TAD (Fisher's α)	ALT	X		
	TEMPESEAS	X		
	NDVIMEAN			X
	PRECIP			X
	SLOPE		X	
	TEMPE	X		
	NDVISD		X	
	PTC	X		

[a] ALT = altitude; EVIMEAN = mean Enhanced Vegetation Index (EVI); EVISD = standard deviation EVI; MINDIST2 = minimum distance to disturbance source (either road, river or village); NDVIMEAN = mean Normalized Difference Vegetation Index (NDVI); NDVISD = standard deviation NDVI; PNTV = percent non tree vegetation; PRECIP = mean annual precipitation; PTC = percent tree cover; SLOPE = slope; SOIL = soil group; TEMPE = mean annual temperature; TEMPERANGE = temperature range; TEMPESEAS = temperature seasonality

[b] PD = partial dependence

Appendix D: Comparing our predicted values of ACD, SCD and TAD over the study area with those extracted from existing maps

As existing maps were systematically produced at a coarser spatial resolution, our prediction data were consistently aggregated to meet the reference resolution. Our ACD predictions were compared with previous pantropical works from Baccini et al. (2012) and Saatchi et al. (2011) at resolutions of 500 m and 1000 m, respectively. Our SCD predictions were compared with values from the regridded Harmonized World Soil Database (0–30 cm layer; Wieder et al., 2014) at a resolution of 5500 m. Our predictions of TAD (using Fisher's α) were compared with Borneo- (Raes et al., 2009; Slik et al., 2009) and Sundaland-wide (Raes et al., 2013) tree diversity estimates at a 9250 m resolution. Though methodology was different, two of these studies provided information on tree species richness (Raes et al., 2009; Raes et al., 2013). Slik et al. (2009) worked at a generic level but their study was nonetheless included for comparison on the grounds of good match between generic and species diversity patterns (Higgins and Ruokolainen, 2004). This was the case in our study area, in which we found a very strong positive correlation between species and genus richness (Pearson's $r = 0.98$, $p < 0.001$; correlation corrected for spatial autocorrelation) in our dataset. We used Pearson's correlation – corrected for spatial autocorrelation – on a given subset of randomly chosen points to compare our predictions with those from existing maps. For comparisons with predictions from Baccini et al. (2012) and Saatchi et al. (2011), we only used aggregated pixels for which all initial pixels had values. For comparison with predictions from Wieder et al. (2014), Raes et al. (2009; 2013) and Slik et al. (2009), due to much coarser resolution, we used aggregated pixels for which at least half initial pixels had values.

Appendix E: Potential threats from concessions over carbon and tree diversity hotspots

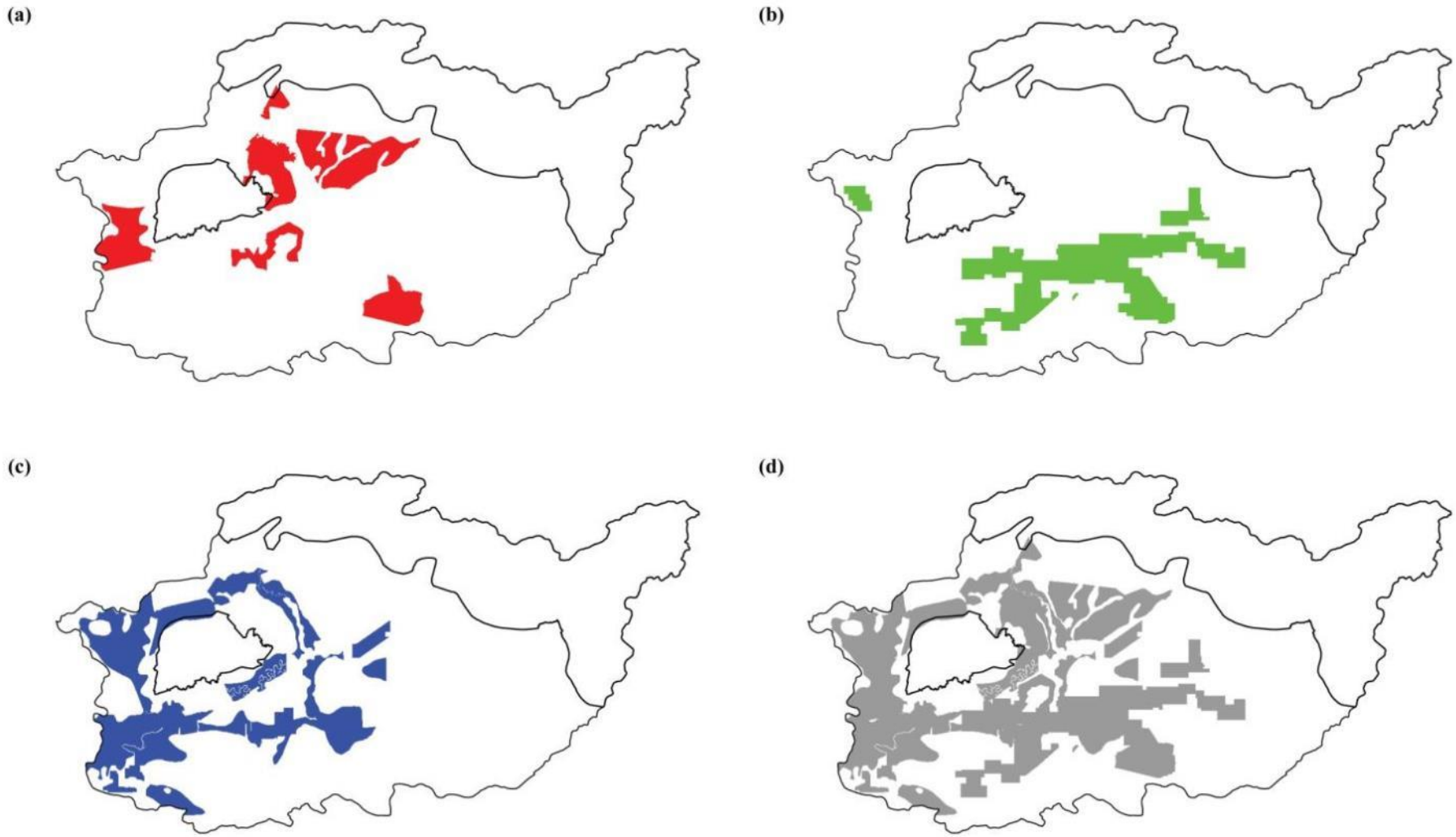

Fig. F.1 Location of concessions over the study area depending on concession type: (a) logging concessions, (b) mining concessions, (c) plantation concessions, (d) combination of the three different types of concessions. Affected areas represent ca. 2500 km², 2800 km² and 4100 km² for logging, mining and plantation concessions, respectively. Note that some areas might simultaneously be under different types of concessions. Some concessions overlapped slightly with national park borders.

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Conclusions de l'étude

A l'aide de données provenant d'inventaires botaniques et pédologiques réalisés dans différents types de végétation (forêts de plaine, forêts sur tourbe, forêts sur sable blanc, etc.) et de données facilement accessibles et disponibles sur l'ensemble de la zone d'étude (topographie, type de sol, etc.), nous avons pu élaborer des modèles régionaux de distribution de carbone (à la fois dans la biomasse aérienne et le sol) et de diversité d'espèces ligneuses (DEL). Ces modèles nous ont permis d'étudier, à l'échelle de la région, les corrélations entre carbone et DEL ainsi que la congruence spatiale de leurs « *hotspots* » respectifs. De nos résultats découlent plusieurs recommandations en termes de conservation et développement.

Voyons comment nos travaux nous permettent de nous positionner par rapport à notre hypothèse de départ qui, pour rappel, était : « Les zones d'importance pour la DEL et le carbone ne coïncident que partiellement au niveau de la zone d'étude, mais il est possible d'optimiser la protection de la DEL et du carbone (tant celui de la biomasse aérienne que du sol) en choisissant des stratégies de conservation appropriées. ».

☑ Nos résultats suggèrent que la protection des zones à hautes valeurs de carbone dans la biomasse aérienne (par le biais de mécanismes financiers comme REDD+ par exemple) pourrait également conduire à la conservation de la DEL. La protection des tourbières, zones où les stocks de carbone dans le sol sont les plus importants, nécessitera par ailleurs la mise en place de politiques de conservation adéquates dédiées, l'actuel moratoire sur la conversion des tourbières en Indonésie ne constituant qu'une première étape.

Ainsi, cette étude nous aura permis d'améliorer nos connaissances sur la distribution spatiale du carbone et de la DEL de même que leurs relations spatiales au sein de la zone d'étude. De nouvelles campagnes d'échantillonnage du sol et de la végétation mériteraient cependant d'être entreprises afin de tester la robustesse de nos prédictions, et éventuellement les améliorer.

Chapitre 4

Erosion des sols dans les tropiques humides

Contexte de l'étude

Lors de l'étude menée à l'échelle locale (voir Chapitre 2), qui visait à évaluer la diversité d'espèces ligneuses et la production de services écosystémiques (contrôle de l'érosion des sols, et atténuation du changement climatique via stockage de carbone) dans différents types d'occupation ou d'utilisation des sols, nous nous sommes rendu compte que les pertes de sol étaient très faibles (2−3 ordres de grandeurs inférieures au taux d'érosion tolérable ; Montgomery, 2007), et ce, quel que soit le type d'occupation ou d'utilisation des sols.

Parce que nos mesures étaient relativement ponctuelles, tant dans l'espace (35 parcelles de 60 m² chacune) que dans le temps (suivi sur 2 ans), il nous était difficile de juger de leur représentativité. Nous avons de plus constaté le manque, dans la littérature, d'une synthèse quantitative portant sur l'érosion des sols dans les tropiques humides et l'influence du couvert végétal dans son contrôle (mais pour une synthèse qualitative, voir El-Swaify *et al.*, 1982).

Ainsi, afin de combler une lacune de connaissances et pouvoir mettre nos mesures de terrain en perspective, nous avons choisi de conduire une revue systématique de la littérature. Nous avons suivi les recommandations de la « *Collaboration for Environmental Evidence* » (2013) pour mener à bien notre revue (Figure 4.1).

Figure 4.1. Etapes-clés de la revue systématique (*Collaboration for Environmental Evidence*, 2013)

Après avoir contrôlé analytiquement les effets de la « méthode » (type de dispositif de mesure, type de pluie, etc.) et du « contexte » (longueur de pente, pas de temps, etc.), nous avons utilisé les mesures corrigées de pertes de sol (plus de 3600) pour étudier quantitativement l'influence du couvert végétal dans le contrôle de l'érosion des sols.

Nous voulions tester l'hypothèse suivante :
« Le SE de contrôle de l'érosion des sols est fourni dès lors que le couvert végétal est suffisamment développé. »

L'hypothèse corollaire également testée étant qu'aucun type d'occupation ou d'utilisation des sols n'est en soi propice à l'érosion, mais qu'un même type d'utilisation des sols (par exemple, l'agriculture) peut conduire à des pertes de sol importantes ou bien très faibles en fonction de la gestion des sols et de la végétation.

Soil erosion in the humid tropics: A systematic quantitative review

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Résumé

Les sols sains fournissent un large éventail de services écosystémiques. Mais l'érosion des sols (l'une des composantes de la dégradation des terres) menace la fourniture durable de ces services dans le monde entier, et plus encore au niveau des tropiques humides où les risques d'érosion sont importants du fait des fortes précipitations. L'Evaluation des écosystèmes pour le Millénaire a mis en avant l'impact de mauvais choix de gestion et d'utilisation des sols dans l'augmentation de la dégradation des terres. Nous avons fait l'hypothèse que l'utilisation des sols a une influence limitée sur l'érosion des sols dès lors que le couvert végétal est suffisamment développé ou que de bonnes pratiques de gestion sont mises en œuvre. Nous avons réalisé une revue systématique de la littérature afin d'étudier l'influence de la gestion des sols et de la végétation sur le contrôle de l'érosion dans les tropiques humides. Plus de 3600 mesures de pertes de sol provenant de 55 références et couvrant 21 pays ont été compilées. L'analyse quantitative des données collectées a révélé que l'érosion des sols dans les tropiques humides est très nettement concentrée dans l'espace (au niveau des éléments de sol nu présents dans le paysage) et dans le temps (par exemple, durant la rotation des cultures). Aucune utilisation des sols n'est intrinsèquement sujette à l'érosion, mais la création dans le paysage d'éléments de sol nu liés à certaines utilisations des sols (par exemple les sentiers de débardage et chemins d'exploitation forestière) devrait être évitée autant que possible. La mise en œuvre de bonnes pratiques de gestion des sols et de la végétation (par exemple, semis selon les courbes de niveau, culture sans labour, et utilisation de bandes enherbées) peut permettre jusqu'à 99% de réduction des pertes de sol. Gestionnaires de ressources naturelles et décideurs publics peuvent ainsi aider à faire réduire les pertes de sol à large échelle en promouvant une gestion avisée des éléments de paysage particulièrement sujets à l'érosion et en mettant en valeur l'utilisation de pratiques n'entrainant que peu d'érosion, deux stratégies ne nécessitant que peu de moyens financiers et techniques.

Mots-clés

Services écosystémiques
Revue systématique
Analyse quantitative
Paysage
Utilisation des sols
Type d'utilisation des sols
Pratiques de gestion

Points-clés

• Nous avons analysé le contrôle de l’érosion des sols au niveau des tropiques humides.
• Plus de 3600 mesures de pertes de sol ont été compilées.
• Qu’importe l’utilisation des sols, la plupart des pertes de sol proviennent d’éléments de sol nu présents dans le paysage.
• Le contrôle de l’érosion des sols est fourni dès lors que le couvert végétal est suffisamment développé.
• La mise en place de pratiques de conservation peut permettre jusqu’à 99% de réduction des pertes de sol.

Abstract

Healthy soils provide a wide range of ecosystem services. But soil erosion (one component of land degradation) jeopardizes the sustainable delivery of these services worldwide, and particularly in the humid tropics where erosion potential is high due to heavy rainfall. The Millennium Ecosystem Assessment pointed out the role of poor land-use and management choices in increasing land degradation. We hypothesized that land use has a limited influence on soil erosion provided vegetation cover is developed enough or good management practices are implemented. We systematically reviewed the literature to study how soil and vegetation management influence soil erosion control in the humid tropics. More than 3600 measurements of soil loss from 55 references covering 21 countries were compiled. Quantitative analysis of the collected data revealed that soil erosion in the humid tropics is dramatically concentrated in space (over landscape elements of bare soil) and time (e.g. during crop rotation). No land use is erosion-prone per se, but creation of bare soil elements in the landscape through particular land uses and other human activities (e.g. skid trails and logging roads) should be avoided as much as possible. Implementation of sound practices of soil and vegetation management (e.g. contour planting, no-till farming and use of vegetative buffer strips) can reduce erosion by up to 99%. With limited financial and technical means, natural resource managers and policy makers can therefore help decrease soil loss at a large scale by promoting wise management of highly erosion-prone landscape elements and enhancing the use of low-erosion-inducing practices.

Keywords

Ecosystem services
Systematic review
Quantitative analysis
Landscape
Land use
Land-use type
Management practices

Highlights

• We analyzed soil erosion control in the humid tropics.
• More than 3600 measurements of soil loss were compiled.
• Whatever the land use, most soil losses come from landscape elements of bare soil.
• Soil erosion control is provided whenever vegetation is developed enough.
• Conservation practices can reduce soil loss by up to 99%.

4.1 Introduction

The ecosystem service of soil erosion control, for the delivery of which vegetation cover plays an important role, has been degrading worldwide (Millennium Ecosystem Assessment, 2005). As this regulating service is lost, soil formation can no longer compensate for soil loss due to an increase in erosion, which depletes soil resources and the ecosystem services they support (Lal, 2003; Morgan, 2005). The Millennium Ecosystem Assessment (2005) identified unwise land-use choices and harmful crop or soil management practices as the major drivers of increasing soil erosion. Soil erosion has multiple on- and off-site consequences such as decreasing crop yields, increasing atmospheric CO_2 concentration, decreasing water quality (turbidity and particle-born pollutants), sedimentation of reservoirs, and disturbed hydrological regimes such as increased flood risk due to riverbed filling and stream plugging (Chomitz and Kumari, 1998; Lal, 2003; Millennium Ecosystem Assessment, 2005; Morgan, 2005; Locatelli *et al.*, 2011).

Research on factors influencing soil loss has resulted in widely used models, such as the RUSLE (Revised Universal Soil Loss Equation). This model was built from plot data of experiments carried out in the United States and predicts soil loss from climatic (rainfall erosivity), edaphic (soil erodibility) and topographic (slope length and slope steepness) factors, as well as soil and vegetation management practices (Wischmeier and Smith, 1978; Renard *et al.*, 1997). Management of soil and vegetation has long been recognized as the most efficient and effective way to influence the extent of soil loss, and therefore soil erosion control (Goujon, 1968).

The humid tropics are rich in carbon and biodiversity and attract major attention because of the rapid loss of rainforests (Strassburg *et al.*, 2010; Saatchi *et al.*, 2011; Tropek *et al.*, 2014). Because of the large amount and high intensity of rainfall in the humid tropics, soil erosion can potentially reach dramatic levels in this region (El-Swaify *et al.*, 1982; Lal, 1990). Tropical ecosystems with healthy soils can support multiple ecosystem services (e.g. water regulation, climate regulation through carbon storage and biodiversity support) and support local livelihoods. A better understanding of soil erosion control in the humid tropics is therefore vital (Locatelli *et al.*, 2014).

Theoretically, empirical models of erosion prediction should only be applied under conditions and for purposes similar to those of their development (e.g. predicting erosion from croplands in the United States for the RUSLE). Adapting an empirical model to out-of-range conditions would require parameter calibration, which can consume both time and resources (Nearing *et al.*, 1994). While some studies have adapted temperate model factors to their own geographical contexts (e.g. Streck and Cogo, 2003 for surface soil consolidation and Diodato *et al.*, 2013 for rainfall erosivity), others have directly applied models developed for a temperate context to predict soil erosion in the humid tropics (e.g. Angima *et al.*, 2003; Hoyos, 2005).

Yet there is little consensus about the direct applicability of models such as RUSLE (and its predecessors) to a tropical context. Despite over- and under-estimation of soil loss depending on the cropping phase, Almas and Jamal (2000) found the RUSLE model to correctly predict the overall soil loss from a banana-pineapple intercropping system in Malaysia. On the other hand, Cohen *et al.* (2005) showed that erosion risk prediction was poorly achieved by the USLE (Universal Soil Loss Equation) in a watershed of western Kenya, and called for ground surveys to properly calibrate the USLE and similar empirical models.

In the face of this lack of agreement, studies that directly measure soil loss are of great interest as they can help shed light on the influence of vegetation and soil management on soil erosion control. Synthesizing and analyzing available data from multiple sources is necessary given the diversity of study contexts and the impossibility of drawing general conclusions from a single study.

Such syntheses are available for some regions of the world. Focusing on Europe and the Mediterranean, Maetens *et al.* (2012) reviewed data from 227 stations and 1056 soil erosion plots to analyze the effect of land use on erosion and runoff. They found that (semi-)natural vegetation produced lower erosion (< 1 Mg/ha/yr) than vegetation directly influenced by human activities (e.g. croplands and vineyards; 6–20 Mg/ha/yr). Montgomery (2007) also compiled erosion data from globally distributed studies (some in the humid tropics) and showed that conventional agriculture, i.e. with tillage, produced 10 to 100 times more soil loss than conservation agriculture, i.e. with no-tillage, but conditions were highly variable. For example, plots under conventional agriculture were more erosion-prone (with maximum slope of 37° and maximum annual precipitation of 5600 mm/yr) than those of plots under conservation agriculture (17° and 2000 mm/yr). Selecting erosion measurements available for the two agriculture types under the same conditions substantially reduced the sample.

No synthesis (to our knowledge) has been done so far for the humid tropics. The purpose of this study was therefore to quantitatively analyze available data (collected via systematic review of the literature) on soil erosion in the humid tropics to study how soil and vegetation management influence soil erosion control in this region. Effects of the measurement protocol (method, duration and area) and context (rainfall, slope length, slope steepness and soil erodibility) were controlled for to keep a consistent dataset and focus on the influence of soil and vegetation management on soil erosion.

The underlying hypothesis is that land use has a limited influence on soil erosion provided vegetation cover is developed enough or good management practices are implemented. This hypothesis was previously conclusively tested in a few single studies on ecosystems such as rangelands (e.g. Snelder and Bryan, 1995; Chartier and Rostagno, 2006), but never systematically nor for the humid tropics. This study aims to contribute to the scientific understanding of the relationship between soil erosion and vegetation/soil management in the humid tropics, to help clarify the applicability of widely used models such as the RUSLE, and to provide to stakeholders involved in natural resource management and protection a synthesis on soil erosion control and its sound management.

4.2 Materials and Methods

4.2.1 Materials

We searched for studies of erosion in the humid tropics, defined for the purpose of this review as the "Af" (tropical rainforest climate) and "Am" (tropical monsoon climate) Köppen climatic classes (Köppen, 1936; Peel *et al.*, 2007). Queries were built on the conjunction of elements from three thematic clusters: "scope" AND "outcome" AND "measurement". The "scope" cluster corresponded to: tropic* OR region (list of broadly defined relevant regions, e.g. Africa) OR specific country (all countries under either Af or Am climate were considered, e.g. Brazil). The "outcome" cluster encompassed the following terms: soil erosion, water erosion, soil loss, soil depletion, land degradation, sedimentation, sediment production and siltation. The "measurement" cluster included keywords defining methodological approaches and measurement methods such as "runoff plot" and "sediment trap". In order to select studies with homogeneous land use, we excluded measures at the catchment scale. Additionally, to avoid bias in the analysis of reported measurements, indirect measures and estimates (e.g. the use of ^{137}Cs as a tracer—see Sidle *et al.*, 2006) were not considered. As suggested by the Collaboration for Environmental Evidence (2013), a variety of peer-reviewed and grey literature sources were searched. Details about queries and sources are available in Appendix A. Queries were carried out during the second half of April 2013 in English, French and Spanish.

Searches led to 5183 references after removing duplicates. After irrelevant references were removed, based on information in article titles and abstracts about topic, geographical scope and erosion measurement method, the database shrank to 114 references. Finally, after screening the full texts of those references, we kept 55 of them (more details are available in Appendix B). For each reference, we retrieved data on soil loss (expressed as quantity of soil mass per unit of area) in one or more cases. A case was defined as one erosion measurement, characterized by an associated measurement method (profile meter, root exposition, sediment trap, unbounded plot or runoff plot, all with natural rainfall, and runoff plot with simulated rainfall), area and duration, topographical features (slope length and steepness), rainfall, and land-use type and subtype (see definitions in Table 4.1). For each case, building on the classification proposed by Moench (1991), vegetation cover was also described by the presence or absence of four layers: high (≥ 4 m), intermediate (at least 1 m but < 4 m), low (at least 0.1 m but < 1 m) and ground (< 0.1 m).

Table 4.1. Land-use types and subtypes

Land-use type	Land-use subtype	Definitions
Bare		Land has been opened and kept bare for various reasons (includes pre-sowing and post-harvesting cropland and skid trails).
	Tilled	High-disturbance soil management techniques (e.g. ploughing and raking) are used.
	Untilled	Low-disturbance soil management techniques (e.g. slash and burn and weeding with a knife) are used.
Cropland		Crops are sown and harvested within a single agricultural year, sometimes more than once (excludes perennial crops).
	Crop, non-established, without conservation practices	Crop was recently planted and crop cover is not developed; no conservation techniques are practiced.
	Crop, established, without conservation practices	Crop cover is developed; no conservation techniques are practiced.
	Crop with vegetation-related conservation practices	Crop cover may or may not be fully developed. Vegetation-related conservation techniques (e.g. hedgerows, intercropping and mulching) are practiced.
	Crop with vegetation- and soil-related conservation practices	Crop cover may or may not be fully developed. Both vegetation-related (e.g. hedgerows, intercropping and mulching) and soil-related (e.g. no-till farming and contour planting) conservation techniques are practiced.
Grassland		Vegetation is dominated by grasses (includes open grasslands and pastures).
	Pasture	Land is used for grazing and managed through agricultural practices such as seeding, irrigation and use of fertilizer.
	Open grassland	Land is unmanaged and has no trees or shrubs.
Shrubland		Vegetation is dominated by shrubs but can also include grasses, herbs and geophytes.
	Open shrubland	A transitional plant community occurs temporarily as the result of a disturbance such as logging or fire.
Tree-dominated agrosystem		Planted vegetation is dominated by trees, including perennial tree crops such as rubber, fruit and nut trees.
	Tree plantation	A group of planted trees is grown in the form of an agricultural crop, usually with the aim of harvesting wood.
	Tree crop without contact cover	A permanent crop has been planted; it has no contact cover (such as grass or cover crops) underneath.
	Tree crop with contact cover	A permanent crop has been planted and has contact cover (such as grass or cover crops) underneath.
	Simple agroforest	One woody perennial species is planted with one annual crop.
	Complex agroforest	Multiple species of woody perennials, often with natural vegetation regrowth, are planted (usually intercropped) with annual crops.

Land-use type	Land-use subtype	Definitions
Forest		Ground is covered with natural vegetation dominated by trees (excludes tree plantations).
	Secondary forest	Forest has regenerated naturally after clear-cutting, burning or other land-clearing activities and contains vegetation in early successional stages.
	Old-growth forest	Forest is ecologically mature, containing trees of various sizes and species (the last stage in forest succession).
	Logged-over forest	Forest has been logged-over.
	Degraded forest	Forest has been degraded by human activities other than logging or by a naturally occurring event such as a fire or severe storm.

The final data set consisted of 3649 measurements from 55 references covering 21 countries in the humid tropics (Figure 4.2, Table 4.2). Most references originated from peer-reviewed journals (n = 44) and used runoff plots to quantify soil loss (n = 48). Publication years ranged from 1973 to 2012, with half of the references published before 1997 (Figure 4.3a). The number of cases per study was highly variable, and the six references with the most cases contributed half the total number of cases in the final data set (Figure 4.3b, Table 4.2). Study length ranged from two days (studies under simulated rainfall) to 17 years (Figure 4.3c). References generally reported erosion values per rainfall event, per year or for the duration of the study (Figure 4.3d). Most references assessed one to three land-use types (Figure 4.3e), of which bare soils and croplands were the most studied (Figure 4.3f).

Rainfall erosivity and soil erodibility were assessed for each case. An indicator of rainfall erosivity *sensu* Renard *et al.* (1997) could not be obtained or computed for most cases because monthly data were not available or because measurement duration was too short to apply an annual erosivity index. We thus used total rainfall as an indicator of rainfall erosivity based on the finding by Maetens *et al.* (2012) that soil loss does not correlate better with erosivity indices than with total rainfall.

For soil erodibility, we combined different indices because of the diverse ways soils were described in the studies. For each case, we calculated three soil erodibility indices from soil texture and organic matter data with an empirical table and two different equations (Stewart *et al.*, 1975; Sharpley and Williams, 1990; Torri *et al.*, 1997). If soil data were not available in a study, we extracted them from the ISRIC global soil dataset (resolution of 1 km) using measurement coordinates (ISRIC – World Soil Information, 2013). For each index, soils were split into low-, medium- and high-erodibility classes of equal sizes. A soil was then classified as highly erodible if it was considered highly erodible by at least two of the three indices, low if it was considered low by at least two indices and medium otherwise (more details are available in Appendix C).

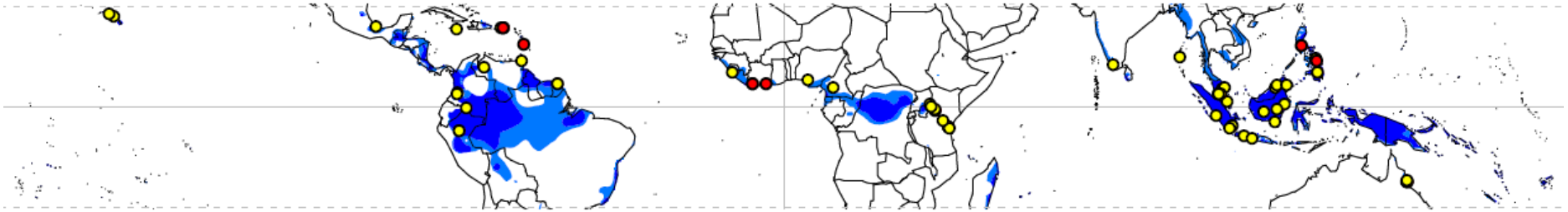

Figure 4.2. Location of study sites (n = 61). Some dots represent several references, and some references contribute more than one dot. Red dots show locations provided by the six references with the most cases. Af (tropical rainforest) climate ranges are displayed in dark blue and Am (tropical monsoon) climate ranges in light blue.

Table 4.2. Contributing references by geographical location. References from Southeast Asia and Northeast Australia (n = 29) made up more than half of all references (n = 55). The 30 references with the fewest cases provided about 10% of all cases (n = 3649). The 6 references with the most cases are printed in bold.

Reference	Country	Source type	Method	Rainfall type	Soil data [a]	Land-use type(s) [b]	Cases	Case time frame(s)	Study length
Africa (n = 11)									
Ambassa-Kiki and Nill (1999)	Cameroon	journal article	runoff plot	natural	ST + OM	3 (B, C, T)	3	study	2 years
Boye and Albrecht (2004)	Kenya	project report	runoff plot	simulation	ST + OM	1 (B)	10	rainfall event	2 days
Collinet (1983)	Côte d'Ivoire	project report	runoff plot	natural	none	2 (C, F)	24	year, study	3 years
Collinet (1988)	**Côte d'Ivoire**	**PhD thesis**	**runoff plot**	**simulation**	**none**	**2 (B, C)**	**189**	**rainfall event**	**2 months**
Defersha and Melesse (2012)	Kenya	journal article	runoff plot	natural	ST + OM	3 (B, C, G)	87	rainfall event, month	1 month
Kamara (1986)	Sierra Leone	journal article	runoff plot	natural	ST + OM	2 (B, C)	14	month	2 years
Lundgren (1980)	Tanzania	journal article	runoff plot	natural	ST + OM	2 (F, T)	33	year, study	2 years
Ngatunga *et al.* (1984)	Tanzania	journal article	runoff plot	natural	ST + OM	3 (B, C, G)	36	season, year	1 year
Odemerho and Avwunudiogba (1993)	Nigeria	journal article	runoff plot	natural	ST	2 (C, G)	126	rainfall event, study	5 months
Roose (1973)	**Côte d'Ivoire**	**PhD thesis**	**runoff plot**	**natural**	**none**	**5 (B, C, F, G, T)**	**431**	**rainfall event, day, month, season, year**	**17 years**
Våje *et al.* (2005)	Tanzania	journal article	runoff plot	natural	ST + OM	2 (B, C)	10	rainfall event, season	2 years
America & North Pacific Ocean (n = 10)									
Alegre and Cassel (1996)	Peru	journal article	runoff plot	natural	OM	3 (B, C, F)	4	study	52 months
Alegre and Rao (1996)	Peru	journal article	runoff plot	natural	OM	3 (B, C, F)	50	season, year, study	5 years
Bellanger *et al.* (2004)	Venezuela	journal article	runoff plot	natural	ST + OM	3 (B, C, T)	41	rainfall event, week, season	5 months
Dangler and El-Swaify (1976)	USA (Hawaii)	journal article	runoff plot	simulation	none	1 (B)	16	rainfall event	1.75 years
Francisco-Nicolas *et al.* (2006)	Mexico	journal article	runoff plot	natural	OM	1 (C)	18	year, study	8 years
Fritsch and Sarrailh (1986)	France (French Guiana)	journal article	runoff plot	natural	none	2 (B, F)	38	month, season, year, study	32 months
McGregor (1980)	Colombia	journal article	runoff plot	natural	ST	3 (C, F, G)	7	study	8 week
Ruppenthal *et al.* (1997)	Colombia	journal article	runoff plot	natural	none	2 (B, C)	32	season	2 years
Sarrailh (1981)	France (French Guiana)	project report	runoff plot	natural	none	2 (F, G)	50	month, season, year, study	20 months
Wan and El-Swaify (1999)	USA (Hawaii)	journal article	runoff plot	simulation	ST + OM	2 (B, C)	6	rainfall event	2 days

Reference	Country	Source type	Method	Rainfall type	Soil data [a]	Land-use type(s) [b]	Cases	Case time frame(s)	Study length
SE Asia & NE Australia (n = 29)									
Afandi *et al.* (2002a)	Indonesia	journal article	runoff plot	natural	ST + OM	1 (T)	54	month	3.5 years
Afandi *et al.* (2002b)	Indonesia	journal article	sediment trap	natural	ST + OM	4 (C, F, G, T)	77	month, study	11 months
Almas and Jamal (2000)	Malaysia	journal article	runoff plot	natural	none	3 (B, C, T)	52	season	9 months
Baharuddin *et al.* (1995)	Malaysia	journal article	runoff plot	natural	none	3 (B, F, G)	90	month, year	2 years
Bons (1990)	Indonesia	conference proceedings	runoff plot	natural	none	2 (S, T)	2	year, study	26 months
Chatterjea (1998)	Singapore	journal article	runoff plot	natural	none	2 (B, G)	30	rainfall event	1.3 years
Comia *et al.* (1994)	Philippines	journal article	runoff plot	natural	ST + OM	1 (C)	16	year, study	3 years
Daño and Siapno (1992)	Philippines	conference proceedings	runoff plot	natural	none	1 (T)	22	year, study	2 years
Hartanto *et al.* (2003)	Indonesia	journal article	runoff plot	natural	none	2 (B, F)	135	rainfall event, season	2.5 months
Hashim *et al.* (1995)	Malaysia	journal article	runoff plot	natural	ST + OM	2 (B, T)	152	rainfall event, season, study	1.5 years
Jaafar *et al.* (2011)	Malaysia	journal article	runoff plot	natural	ST + OM	1 (F)	6	year	1 year
Leigh (1982)	Malaysia	journal article	sediment trap	natural	ST	1 (F)	11	year	1 year
Malmer (1996)	Malaysia	journal article	unbounded plot	natural	none	2 (B, F)	3	year, study	1 year
Moehansyah *et al.* (2004)	Indonesia	journal article	runoff plot	natural	ST	3 (C, G, T)	156	rainfall event, season, study	8 months
Moench (1991)	India	journal article	runoff plot	natural	OM	1 (T)	21	study	9 months
Pandey and Chaudhari (2010)	India	journal article	runoff plot	natural	ST	3 (C, F, T)	44	year, study	3 years
Paningbatan et al. (1995)	**Philippines**	**journal article**	**runoff plot**	**natural**	**ST + OM**	**1 (C)**	**168**	**rainfall event, season**	**3 years**
Poudel *et al.* (1999)	Philippines	journal article	runoff plot	natural	ST + OM	1 (C)	35	season, study	2.5 years
Poudel *et al.* (2000)	Philippines	journal article	runoff plot	natural	OM	1 (C)	12	year	2.5 years
Presbitero (2003)	**Philippines**	**PhD thesis**	**runoff plot**	**natural**	**OM**	**2 (B, C)**	**433**	**rainfall event**	**2.5 years**
Prove *et al.* (1995)	Australia	journal article	profile meter	natural	none	1 (C)	14	year	6 years
Ross and Dykes (1996)	Brunei	book chapter	runoff plot	natural	ST	1 (F)	24	month	8 months
Shimokawa (1988)	Indonesia	book chapter	root exposition	natural	none	1 (F)	21	year	1 year
Siebert and Belsky (1990)	Indonesia	journal article	runoff plot	natural	ST + OM	1 (C)	3	season	9 months
Sinun *et al.* (1992)	Malaysia	journal article	runoff plot	natural	none	3 (B, F, G)	78	month, year	1 year
Sudarmadji (2001)	Indonesia	conference proceedings	runoff plot	natural	ST	1 (F)	3	study	4 months
Syed Abdullah and Al-Toum (2000)	Malaysia	journal article	sediment trap	natural	ST + OM	1 (F)	12	year	1 year

Reference	Country	Source type	Method	Rainfall type	Soil data [a]	Land-use type(s) [b]	Cases	Case time frame(s)	Study length
van der Linden (1980)	Indonesia	journal article	runoff plot	natural	ST + OM	3 (B, C, G)	88	rainfall event, study	3 months
Verbist *et al.* (2010)	Indonesia	journal article	runoff plot	natural	ST + OM	2 (F, T)	18	year	4 years
Caribbean islands (n = 5)									
Khamsouk (2001)	**France (Martinique)**	**PhD thesis**	**runoff plot**	**natural, simulation**	**ST + OM**	**3 (B, C, T)**	**429**	**rainfall event**	**1.5 years**
Larsen et al. (1999)	**USA (Puerto Rico)**	**journal article**	**unbounded plot**	**natural**	**ST**	**3 (B, G, S)**	**177**	**month, season, year**	**3.75 years**
McDonald *et al.* (2002)	Jamaica	journal article	runoff plot	natural	ST + OM	3 (B, C, F)	24	year, study	5 years
Mohammed and Gumbs (1982)	Trinidad and Tobago	journal article	runoff plot	natural	ST + OM	2 (B, C)	6	rainfall event, season	3 months
Ramos Santana *et al.* (2003)	USA (Puerto Rico)	journal article	runoff plot	natural	none	3 (B, G, T)	8	month	1 month

[a] ST = soil texture; OM = organic matter
[b] B = bare; C = cropland; G = grassland; F = forest; S = shrubland; T = tree-dominated agrosystem

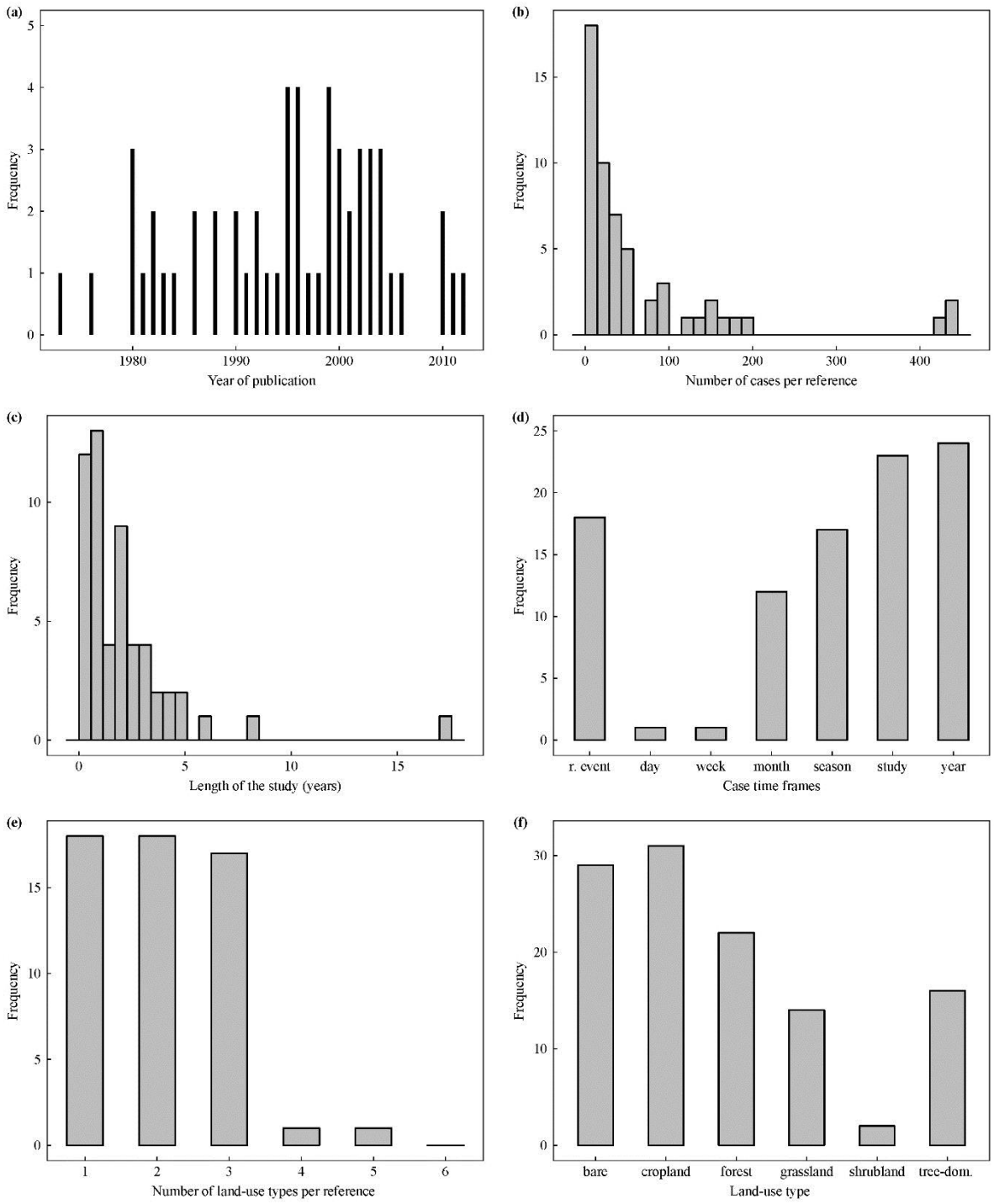

Figure 4.3. Frequency distribution of (a) year of publication of the contributing references (n = 55), (b) number of cases per reference (total cases = 3649), (c) length of the study, (d) case time frames, (e) number of land-use types investigated per reference, (f) land-use types investigated. Total for (d) >55 because some references provide data on more than one time frame; total for (f) >55 because most references reported on more than one land use. R. event = rainfall event; tree-dom. = tree-dominated agrosystem.

4.2.2 Data analysis

All data transformation and statistical analysis were done using R (R Core Team, 2013). Due to highly skewed distributions, all continuous variables (erosion, duration, area, rainfall, slope length and slope steepness) were $\log_{10}$-transformed to normalize their distribution. If not specified, further mention of values of these variables will refer to their $\log_{10}$-transformed values. Because null values cannot be $\log_{10}$-transformed, each null value of measured soil loss (664 values, expressed in g after transforming values reported in other units in the papers) was replaced by a random value taken from a uniform distribution in the range of 0.001 to 1 g, an interval arbitrarily chosen in which 1 g represents a measurement detection threshold (Chiappetta *et al.*, 2004). After substituting the null values, measured soil loss (g) was converted into soil loss per unit of area and per year ($g/m^2/yr$). Replicating the substitution process 10 times, we checked that the randomness of the data replacement did not affect the subsequent results.

In order to analyse the effect of soil or vegetation management on soil erosion, we controlled first for the effect of the measurement protocol (method, duration and area) (Hair *et al.*, 2006). Annual soil loss values obtained from extrapolation of measures taken over a single rain event are likely to be larger than values from measures over one year, and soil loss values per unit of area are probably higher in small plots than in larger areas because of sediment deposition (Boix-Fayos *et al.*, 2006). We used only the two quantitative descriptors of measurement protocol (area and duration), as they were good proxies for method (60% correct determination, jackknifed classification following discriminant function analysis). We transformed the $\log_{10}$ values of soil loss and context variables (rainfall, soil erodibility, slope length and slope steepness) into the residuals resulting from a linear regression against duration, area and the interaction between the two variables (all three significant at $p < 0.001$; Table D1). Residuals were further adjusted to correspond to a reference protocol of measurements over one year and 100 m^2 (this value corresponding to the order of magnitude of the median area).

We then controlled for the effect of context on soil loss by calculating the residuals of a general linear model relating soil loss to context (values of rainfall, slope length and slope steepness, after factoring out the effects of protocol, as well as soil erodibility classes). All the context variables had a significant effect on soil loss ($p < 0.05$; Table D2). The residuals were adjusted to a "reference scenario" with the median values for annual rainfall (exclusively from cases where rainfall was measured for one year or more), slope length, slope steepness (back-transformed values being 2444 mm, 16.4 m and 16.5%, respectively), and a soil erodibility of class "medium".

All subsequent statistical analyses (ANOVA and Tukey's HSD) used these $\log_{10}$-transformed soil loss values, corrected for the effect of the measurement protocol and context and scaled to correspond to a reference scenario. We tested for differences (at $p < 0.001$) in soil loss depending on (1) land-use type, (2) land-use subtype and (3) the number and (4) nature of

layers constituting the vegetation cover. As six references provided half the total number of cases, we tested whether they had a dominant effect on the overall results. To do so, we reanalysed the data after removing these references one by one, but no significant changes in the results and no changes in the findings were observed.

4.3 Results

Soil loss was maximum on bare soils and strikingly exceeded that of all other land-use types (Figure 4.4). Minimum soil loss was found in forests. Croplands had the second highest soil loss value among land-use types. Mean soil loss values for grasslands and shrublands were about half that of croplands. The ratio (of geometric means in the natural scale) shrank to 1:3 for mean soil loss between tree-dominated agrosystems and croplands. The erosion rate in forests was ca. one-tenth and one-150th than that of croplands and bare soils, respectively. The ratio of soil loss values between two consecutive land uses (sorted by decreasing mean soil loss) was much higher between bare soils and croplands (ca. 20:1) than between other land-use types (ratios below 3:1).

Soil loss differed significantly between subtypes of land uses within the same type. Soil loss was minimum for tree crops with contact cover (e.g. grass or cover crop) and maximum on tilled bare soils, with a ratio of 1:1200 between the two values (Figure 4.5). Among bare soils, soil loss was 40% higher with tillage than without (the latter still had a high absolute value of soil loss). Among croplands, recently planted crops without vegetation-related conservation practices (e.g. hedgerows, mulching or intercropping) had erosion rates similar to those of bare soils (either tilled or not), whereas well-established crops on similar lands reduced soil loss by 89% on average. Vegetation-related conservation practices reduced soil loss by 93% in recently planted cropland but did not reduce soil loss significantly in land with established crops. Simultaneous soil- and vegetation-related conservation practices (e.g. no-till farming and hedgerows) decreased soil loss in croplands (up to 99% compared to no conservation practices in land with recently planted crops).

Among tree-dominated agrosystems, tree crops with contact cover faced 99% less soil loss on average than tree crops without contact cover. Simple agroforests had greater soil loss than complex ones (3:1 ratio); however, the difference was not significant. Among the five least erosion-prone land-use subtypes, three were of forest type (old-growth, secondary, and logged-over forests).

The number of layers constituting the vegetation cover had a significant impact on soil loss. Soil loss was maximal without any layer and minimal with four layers. Soil loss was one-tenth as much with one layer as without, and one-70th as much with two layers as without (Figure 4.6). The 90% reduction in soil loss between one and two layers was also significant. Conversely, no significant difference in mean soil loss was found between two and four layers.

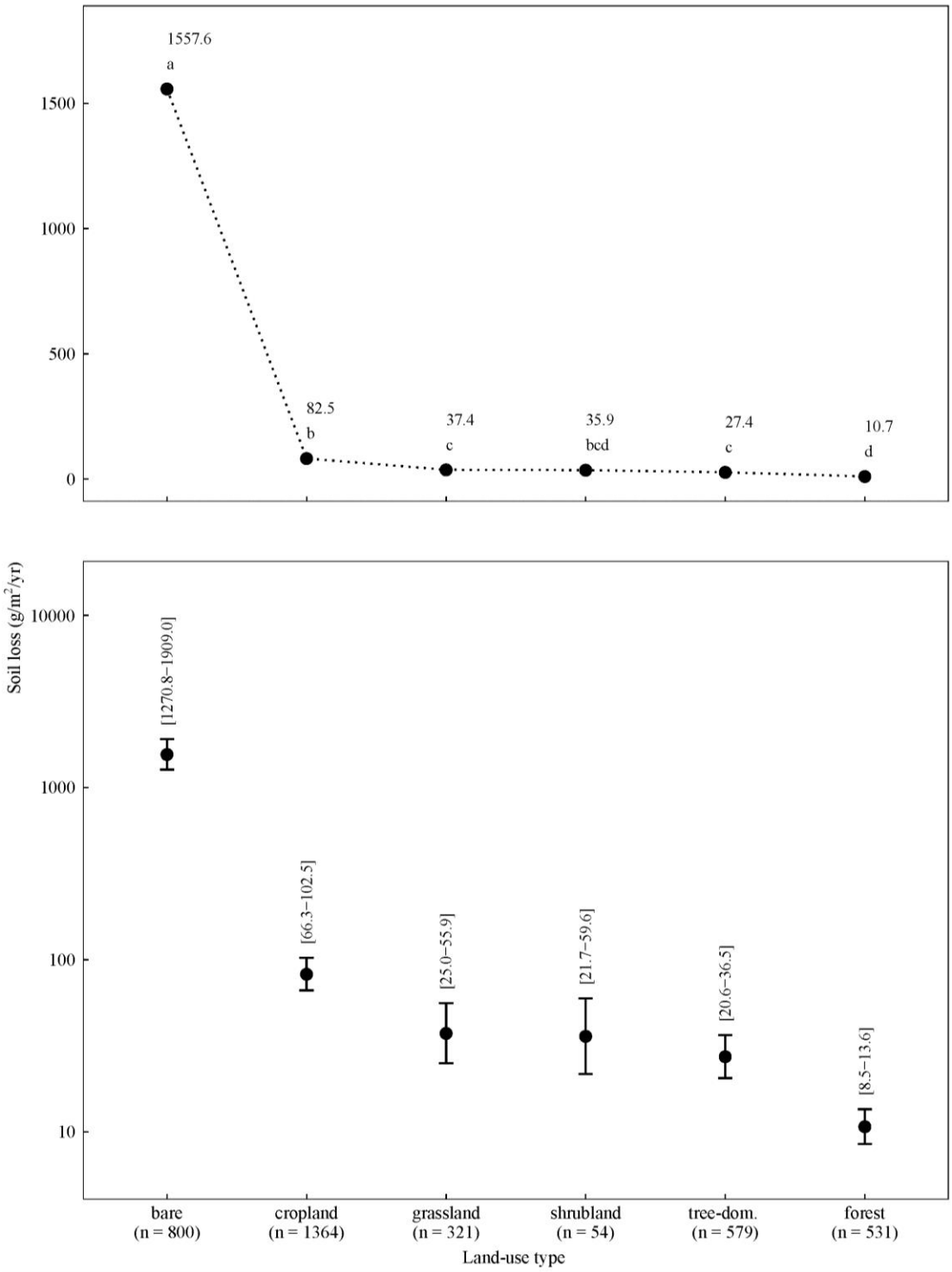

Figure 4.4. Impact of land-use type on soil loss under reference scenario (significant difference at $p < 0.001$). Geometric means along with 95% confidence intervals on the natural scale are plotted on a $\log_{10}$ scale for the sake of readability (bottom panel). Log_{10}-transformed mean soil loss values with the same letter are not significantly different (Tukey's HSD, $p < 0.01$). Geometric means are also plotted on the natural scale to highlight the loss of soil erosion control from cropland to bare land (top panel). Tree-dom. = tree-dominated agrosystem.

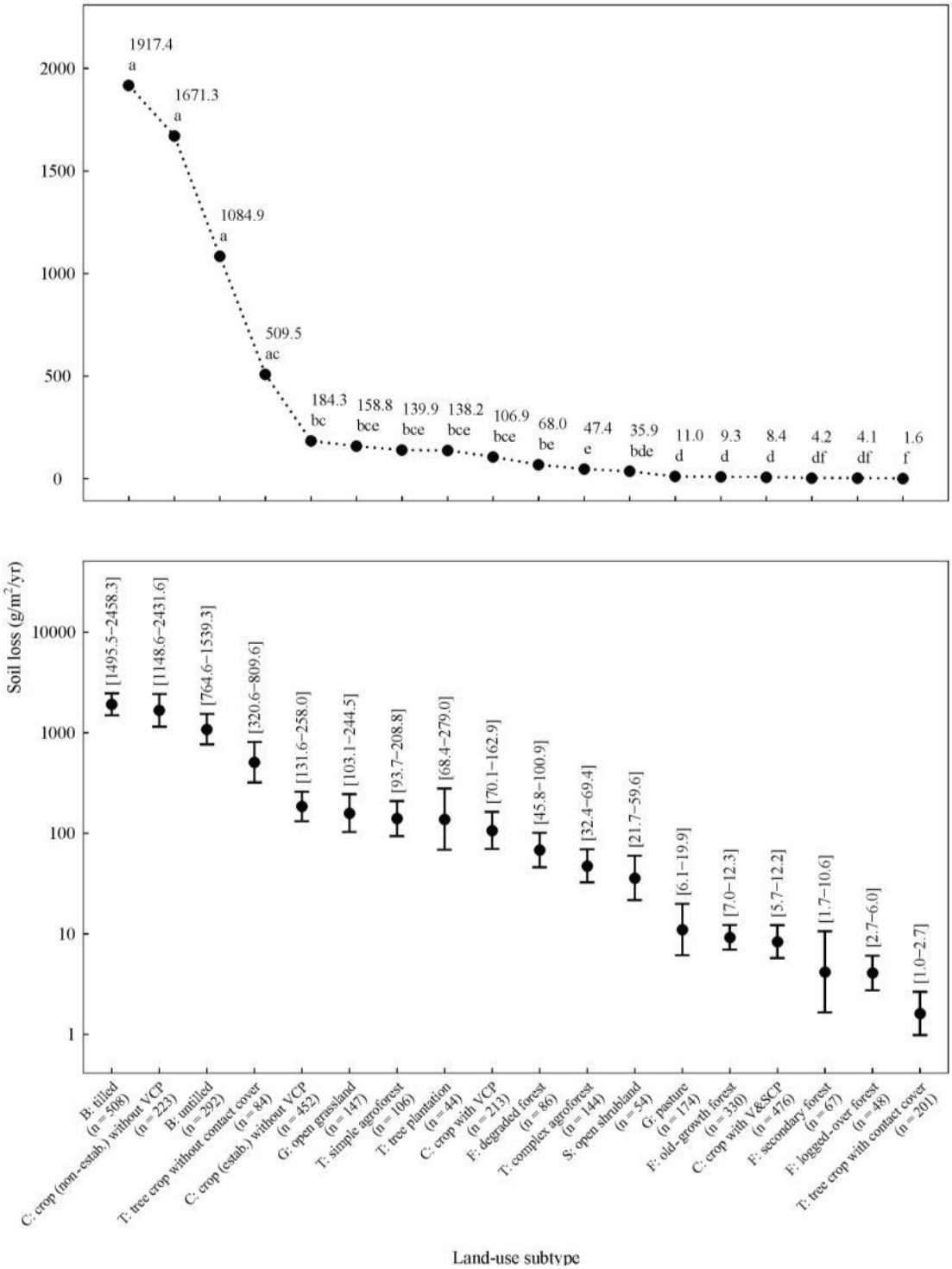

Figure 4.5. Impact of land-use subtype on soil loss under reference scenario (significant difference at $p < 0.001$). Geometric means along with 95% confidence intervals on the natural scale are plotted on a $\log_{10}$ scale for the sake of readability (bottom panel). Log_{10}-transformed mean soil loss values with the same letter are not significantly different (Tukey's HSD, $p < 0.01$). Geometric means are also plotted on the natural scale to highlight the loss of soil erosion control from tree crops with contact cover to tilled bare soils (top panel). B = bare; C = cropland; G = grassland; F = forest; S = shrubland; T = tree-dominated agrosystem; estab. = established; VCP = vegetation-related conservation practice(s); V&SCP = vegetation- and soil-related conservation practice(s).

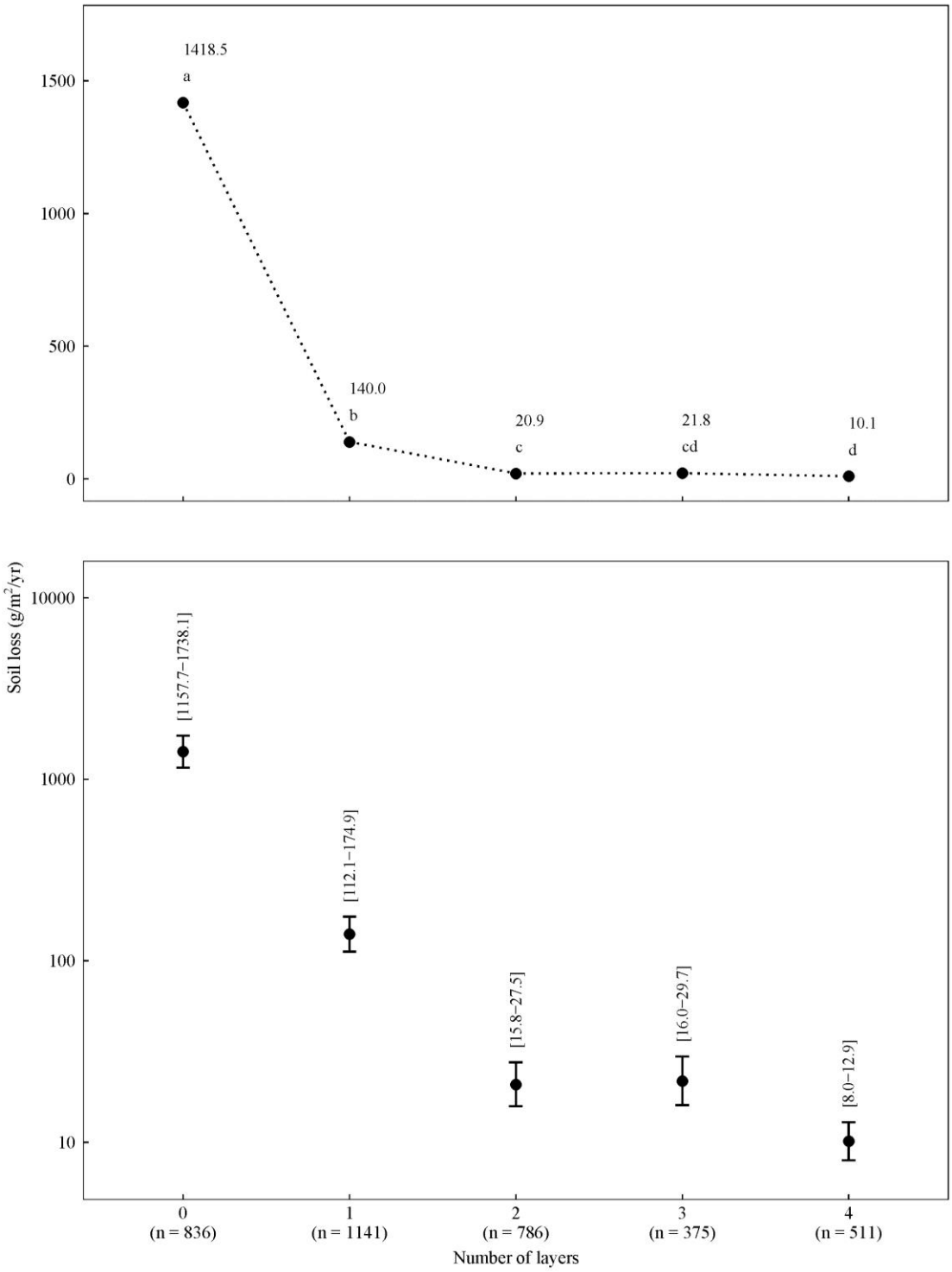

Figure 4.6. Impact of the number of vegetation layers on soil loss under reference scenario (significant difference at $p < 0.001$). Geometric means along with 95% confidence intervals on the natural scale are plotted on a $\log_{10}$ scale for the sake of readability (bottom panel). Log_{10}-transformed mean soil loss values with the same letter are not significantly different (Tukey's HSD, $p < 0.01$). Geometric means are also plotted on the natural scale to highlight the loss of soil erosion control from one layer of vegetation to none (top panel).

The type of layers constituting the vegetation cover had a significant impact on soil loss. The presence of high, intermediary, low and ground layers influenced soil loss significantly and differently (Table 4.3): soil loss under a unique layer of high vegetation (≥ 4 m) was twice that occurring on bare soils, whereas other layers decreased soil loss compared to bare soils by a factor of 5, 8 and 5 for intermediary, low and ground layers respectively, and a factor of 200 for a combination of the three layers.

Table 4.3. Coefficients of the generalized linear model regression of annual soil loss ($\log_{10}$-transformed values) against presence/absence of high (≥ 4 m), intermediate (1 m ≤ height < 4 m), low (0.1 m ≤ height < 1 m) and ground (< 0.1 m) vegetation layers.

	Estimate	Standard error	p
Intercept (bare)	2.97	0.044	***
High	0.22	0.071	**
Intermediary	−0.66	0.054	***
Low	−0.91	0.058	***
Ground	−0.71	0.068	***
Adjusted R^2: 0.204			
Number of observations: 3649			

** $p < 0.01$; *** $p < 0.001$

4.4 Discussion

4.4.1 Soil erosion is concentrated in space and time

Soil erosion control can abruptly be lost when vegetation cover is not developed enough and/or when poor soil and vegetation management practices are implemented (Figures 4.3–4.5). While we found the ratio of soil loss values between bare soils and croplands to be ca. 20:1 in the humid tropics, the ratio ranged from 2:1 to 10:1 in Europe and the Mediterranean (Cerdan *et al.*, 2010; Maetens *et al.*, 2012). This suggests that soil erosion control is still provided in the humid tropics to a certain extent for crop- and grass-dominated land uses but is alarmingly depleted in bare soils, with dramatic consequences on soil loss. The 2-order-of-magnitude difference in soil loss between one and zero vegetation layer also suggests that some vegetation cover is necessary for soil erosion control to be provided. Consequently, bare soils should be avoided at all times.

The abrupt loss of soil erosion control depicted in Figures 4.3–4.5 suggests that, in most land uses, erosion is concentrated spatially (over bare soil, e.g. logging roads or non-protected crop fields between rotations) and temporally (e.g. before vegetation is fully established). Soil loss was lowest in plots under tree crops with contact cover, but such crops might not be totally erosion-neutral. Similarly, the fact that soil loss in logged-over forests is not different from that in old-growth forests should not lead to the delusive conclusion that logging does not increase soil erosion. Bare soil elements exclusively related to logging and farming (e.g. roads and trails) contribute to disproportionately increase the overall erosion rate of such activities (e.g. Rijsdijk, 2005; Gómez-Delgado, 2010). Much attention should therefore be given to managing these elements (e.g. through water diversion, use of vegetative buffer strips and trail consolidation) so as to reduce the overall impact of such activities.

Attention must also be given to temporal transitions between land uses, for example when establishing crops or plantations. Although this finding has been reported before (Sarrailh, 1981; Baharuddin *et al.*, 1995; Anderson and Macdonald, 1998; Bruijnzeel *et al.*, 1998; Rijsdijk, 2005; Defersha and Melesse, 2012), our study brings a strong quantitative endorsement to it because of the number of studies and cases taken into consideration.

Studies investigating the consequences of land-use changes for soil erosion often used a synchronic approach (comparing different land uses in different plots to infer the consequences of a conversion, in a single plot, from one land use to the other). Unlike a diachronic approach measuring soil loss before, during and after land use change (e.g. Fritsch and Sarrailh, 1986; Malmer, 1996), a synchronic approach does not record the transition (e.g. through clear-cutting or tillage) from one land use to the other. This transition appears to be critical for understanding the consequences of land-use changes for soil loss in the humid tropics, where vegetation regrowth is rapid but most of the annual soil loss is potentially caused by a limited number of extreme rainfall events (e.g. Poudel *et al.*, 1999; Defersha and Melesse, 2012). Comparing synchronic and diachronic approaches for soil carbon

sequestration assessment, Costa Junior *et al.* (2013) found that results depended on the selected approach, and recommended use of the diachronic approach whenever possible. Because of intrinsic variations in soil characteristics (e.g. texture) between sites under the same land use or management practice, a diachronic approach should always be preferred. On the other hand, a synchronic approach using multiple replicates makes it possible to highlight trends in the consequences of land use change or management.

In this respect, the sequence of land uses—bare untilled, cropland, open grassland, open shrubland, secondary forest and old-growth forest—can be interpreted as snapshots of different successional stages following shifting cultivation (after clearing, cultivation, and subsequent natural regeneration). This review showed that soil erosion decreased along the sequence, attesting to the recovery of soil erosion control. Martin *et al.* (2013) highlighted a similar increasing trend for carbon storage and plant diversity during post-disturbance forest recovery. This suggests a synergy (or a joint increase in multiple ecosystem services following implementation of a practice—forest regeneration in this case) between soil erosion control, carbon storage and plant diversity. But the evaluation of a wider range of ecosystem services (including e.g. water regulation) is advised so as to avoid promoting measures (e.g. afforestation) that would be detrimental for the delivery of other services.

4.4.2 What matters in soil erosion control by vegetation?

The change of slope in Figure 4.5 highlights four land uses in which soil erosion control is depleted. In addition to two situations of bare soils, recently planted croplands without vegetation-related conservation practices also provide a low level of soil erosion control. This highlights the importance of good management of croplands: vegetation-related conservation practices (such as hedgerows) can ensure that, even during inter- or early-rotation periods when crop cover is not yet developed, erosion can be prevented or minimized.

Tree crops without contact cover also provide critically low levels of soil erosion control, which is confirmed by the analysis of the effect of vegetation layers: the presence of a sole high layer increases erosion compared to bare soil. This is consistent with other studies that pointed out the role of tree canopy in modifying rainfall kinetic energy (e.g. Wiersum, 1985; Brandt, 1988; Calder, 2001). Leaves of the canopy layer help break the kinetic energy of raindrops, but secondary drops falling from the canopy (particularly from large leaves) are often larger than the raindrops and reach the ground with a higher kinetic energy than in areas without a canopy layer (Wiersum, 1985; Brandt, 1988). This results in increased soil erosion, particularly when the canopy is high and there is no understorey vegetation. Teak (*Tectonia grandis* L.f.) plantations, for example, have often been associated with high erosion rates because of lack of understorey and large tree leaves (Calder, 2001). But a recent study showed that poor vegetation and soil management rather than intrinsic teak leaf morphology was responsible for those high erosion rates (Fernández-Moya *et al.*, 2014).

Litter and understorey both help break the kinetic energy of raindrops and therefore decrease splash erosion (Brandt, 1988). Multiple layers of vegetation are necessary in plantations to minimize soil erosion, and non-compliance with sound management rules (e.g. the repeated use of fire to clear ground cover and understorey) directly and dramatically increases soil loss (Wiersum, 1984). Overall, whatever the land use, we found low and ground layers of vegetation to be essential in decreasing soil loss (Table 4.3). This is consistent with plot-derived results from northern Vietnam, which identified a critical value of understorey biomass (130 g/m²) above which soil loss was negligible (Anh *et al.*, 2014). Therefore, low and ground covers should be restored and/or maintained whatever the land use.

4.4.3 Soil erosion under human-impacted or managed vs. natural vegetation

This study also showed that the difference between "human-impacted or managed" and "natural" vegetation does not explain soil loss in the humid tropics (although intuitively one would expect lower soil erosion under natural vegetation). For example, we found that soil loss in old-growth forest is higher than in tree crops with contact cover. Soil erosion is a natural phenomenon that also occurs in old-growth forest despite its complex vegetation structure and high ground cover (mostly leaf litter or wood debris). In Tanzania, Lundgren (1980) suggested that good land management practices (e.g. mulching and no burning) accounted for lower erosion rates in agrosystems than in natural forest, even though this observation was made during normal rainfall conditions and it was impossible to predict how the human-managed system would have reacted to extreme rainfall events. In South Andaman island, Pandey and Chaudhari (2010) showed that coconut plantations with a contact cover of *Pueraria phaseoloides* had similar soil loss as nearby native evergreen forest and therefore recommended the use of contact cover in plantations for soil erosion control on the island.

Our quantitative analysis strongly supports the idea that no land use (except bare soils) is erosion-prone per se and that sound management of soil and vegetation can reduce soil erosion in managed areas to levels even lower than in areas under natural vegetation.

4.4.4 Differences in soil erosion control between tropical vs. temperate regions

Comparing the effect of land use on soil erosion in the humid tropics (this review) and in temperate regions (Renard *et al.*, 1997; Burke and Sugg, 2006), we found that changes in soil erosion control along a gradient of land uses had similar shape in both temperate and tropical areas (Figure 4.7). A difference between these climatic zones is observed in grasslands and croplands, where soil erosion control is higher in the humid tropics than suggested by the RUSLE. Our analysis shows a much more pronounced threshold effect in the relation between vegetation and soil erosion control than given by the RUSLE, which suggests that soil erosion is more concentrated in space and time in the humid tropics than elsewhere. The

difference can be explained by the more rapid development of dense vegetation protecting soil in croplands and grasslands of the humid tropics. Because of the "universal" nature of the mechanism of soil erosion, the RUSLE, an empirically-based model that integrates all the factors known to influence soil erosion (e.g. soil erodibility, rainfall erosivity), could potentially be used to predict soil erosion for any geographical context. But factors' parameters were computed from data collected exclusively in temperate regions and the direct application of the RUSLE to a tropical context would lead to soil loss misestimation especially for croplands and grasslands. Properly calibrating all RUSLE factors' parameters (especially those related to soil and vegetation management) using data acquired in a tropical context is therefore critical to achieve accurate prediction of soil erosion in the humid tropics.

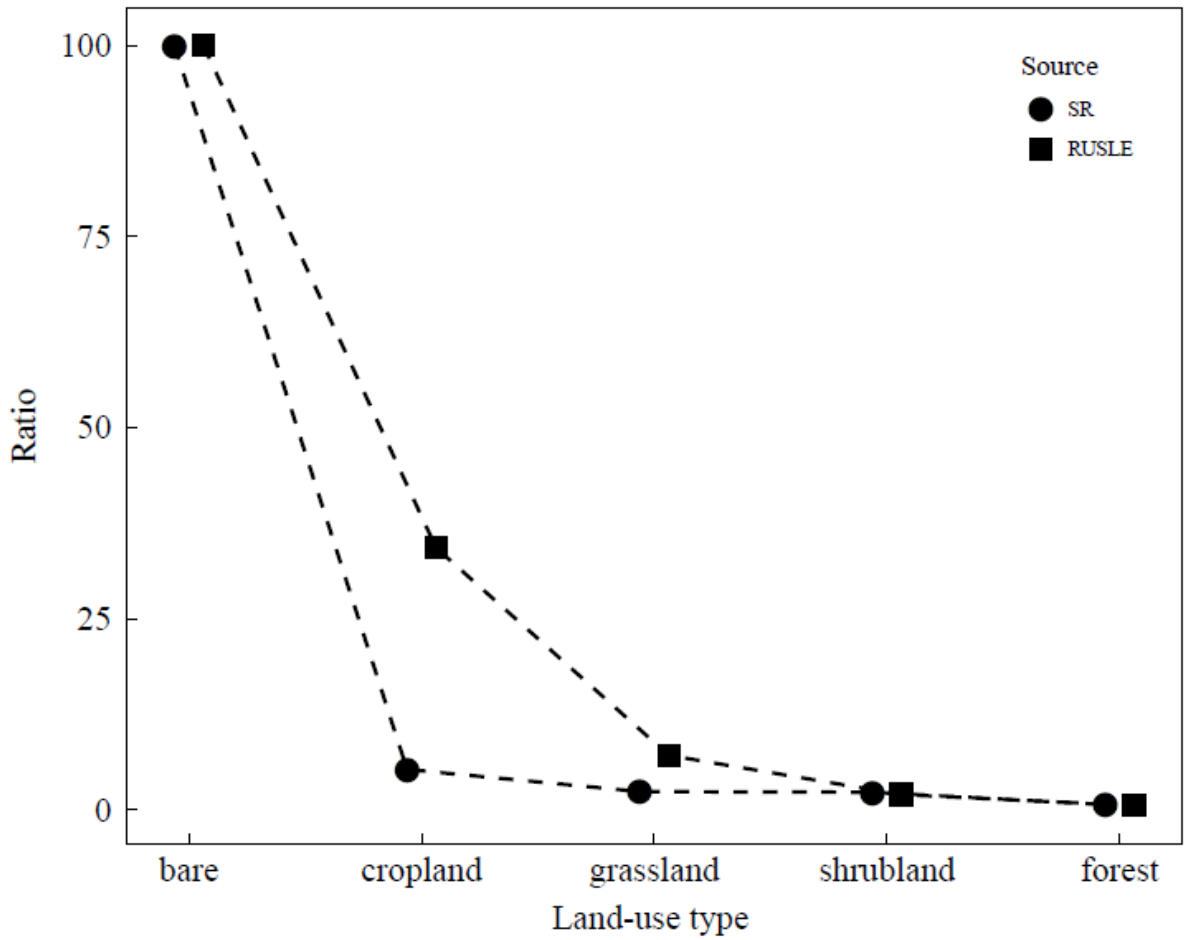

Figure 4.7. Ratio of cover-management factors for the RUSLE for 5 different land uses (reference being erosion on bare soils), and ratio of soil loss per land use to soil loss on bare soils from our systematic review (SR).

4.4.5 Limitations of the study

This analysis faced challenges related to data availability. As soils were sometimes poorly described, we had to use a global database to estimate texture and carbon content, which probably influenced the accuracy of our soil erodibility indices. The structure of the vegetation cover (e.g. number and height of layers, planting density and presence or absence of ground cover) was not always well described. For example, Sinun *et al.* (1992) studied an abandoned logging track where a sharp decrease in soil loss was recorded over time; but while soil loss was measured on a monthly basis over one year, vegetation was not described over time. Two noticeable exceptions were Khamsouk (2001) and Presbitero (2003), in which vegetation cover was regularly and systematically estimated, but with different approaches (e.g. crown cover and contact cover).

The aim of this study was to quantitatively analyse soil erosion control in the whole humid tropics, but references only covered 21 countries and some sub-regions were critically under-represented, e.g. the Brazilian part of the Amazon and the Congo basin (Figure 4.2, Table 4.2). Yet, Köppen climatic classes "Af" and "Am" are homogeneous in term of temperature, rainfall pattern and vegetation type (Köppen, 1936), which supports the applicability of this study's findings to under-represented sub-regions. Research should nevertheless be carried out in the Amazon and the Congo basin to document the effect of local human activities (e.g. small- and large-scale agriculture, fuelwood collection and industrial logging) on soil erosion.

Because six references (from four countries) represented half the total number of cases, we tested for their dominant effect on the overall results, but no such effect was found; this further supports the relevance of this study to the whole humid tropics. Mean annual soil loss values in this study appeared to be in the line of benchmarks provided by other studies. For example, annual erosion rates ranged from 0.1 to 90 and 3 to 750 Mg/ha in humid West Africa for croplands and bare soils, respectively (Morgan, 2005), compared to 1 and 16 Mg/ha on average in our analysis. Other benchmarks are 0.03 to 6.2, 0.1 to 5.6, and 1.2 to 183 Mg/ha for old-growth forests and tree crops with and without contact cover, respectively (Wiersum, 1984), compared to 0.1, 2 and 5 Mg/ha in our analysis.

Since we used $\log_{10}$-transformed data to carry out statistical analyses, back-transforming means led to geometric means in the natural scale that are intrinsically less sensitive to extreme values (Bland and Altman, 1996). This explains the fact that our values lie in the lower part of the range.

4.5 Conclusion

Soil erosion in the humid tropics is dramatically concentrated both spatially (over bare soil) and temporally (before vegetation cover establishes), and low and ground layers of vegetation are essential in mitigating soil erosion. Because soil erosion appears more concentrated in space and time in the humid tropics than elsewhere, models developed in temperate regions should not be directly applied in the humid tropics, and thorough research should be conducted to calibrate model parameters. As a preliminary step to answer the UN call for action to reverse land degradation (UN, 2012), we stress the need to establish standard measurement procedures for soil erosion and influencing factors, to mirror what was achieved for terrestrial carbon measurement (Walker *et al.*, 2012). For improving soil and vegetation management, uncovered or unprotected soils should be avoided at all times, and low and ground layers of vegetation should be restored and/or maintained whatever the land use.

No land use (except bare soils) is erosion-prone per se and natural resource managers and policy makers need to promote sound management of soil and vegetation (e.g. contour planting, no-till farming, intercropping and use of cover crops) to reduce soil loss from erosion-prone landscape elements. Because of the relative affordability and simplicity of such management practices, substantial decrease in soil loss can be attained at the catchment or regional scale with limited financial and technical means. Since soil erosion appears to decrease during the different phases of forest regeneration, soil ecosystem services (e.g. nutrient cycling, flood regulation, water purification), the delivery of which is greater in healthier soils, might be good candidates for ecosystem services bundling with biodiversity protection and carbon storage.

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4.7 Appendices

Supporting information for

Soil erosion in the humid tropics: A systematic quantitative review

N. Labrière, B. Locatelli, Y. Laumonier, V. Freycon, M. Bernoux

Appendix A. Queries and sources
Table A1. The systematic review process

Appendix B. Exclusion criteria
Table B1. References excluded after full reading, sorted by main exclusion criteria

Appendix C. Soil erodibility indices
Table C1. Soil erodibility values depending on texture class and percentage of organic matter
Equation C1. Soil erodibility as computed by Torri *et al.* (1997)
Equation C2. Soil erodibility as computed by Sharpley and Williams (1990)
Figure C1. Classification of soils in three categories of soil erodibility
Figure C2. Final classification of soil erodibility

Appendix D. Supplementary tables
Table D1. Coefficients of the generalized linear model regressions aiming at removing the effect of the method on annual soil loss, rainfall, slope length and slope steepness
Table D2. Coefficients of the generalized linear model regressions aiming at removing the effect of the context on annual soil loss values that have already been corrected from the effect of the method using corrected values of rainfall, slope length and slope steepness and dummy variables for the categorical variable of soil erodibility

References

Appendix A. Queries and sources

Queries were built on the conjunction of elements from three thematic clusters: "geographical scope" AND "outcome" AND "on-site direct measurement". Below is an example of the query made on Web of Knowledge on 16 April 2013.

Topic = (tropic* OR (America OR Africa OR Asia OR Caribbean) OR (Anguilla OR Antigua and Barbuda OR Australia OR Bahamas OR Bangladesh OR Barbados OR Belize OR Bolivia OR Brazil OR Brunei Darussalam OR Cambodia OR Cameroon OR Central African Republic OR Christmas Island OR Cocos Islands OR Colombia OR Comoros OR Congo OR Cook Islands OR Costa Rica OR Côte d'Ivoire OR Cuba OR Democratic Republic of the Congo OR Dominica OR Dominican Republic OR Ecuador OR El Salvador OR Equatorial Guinea OR Fiji OR French Guiana OR French Polynesia OR Gabon OR Grenada OR Guadeloupe OR Guatemala OR Guinea OR Guyana OR Haiti OR Hawaii OR Honduras OR India OR Indonesia OR Jamaica OR Kenya OR Kiribati OR Laos OR Liberia OR Madagascar OR Malaysia OR Maldives OR Marshall Islands OR Martinique OR Mauritius OR Mexico OR Micronesia OR Montserrat OR Myanmar OR New Caledonia OR New Zealand OR Nicaragua OR Nigeria OR Palau OR Panama OR Papua New Guinea OR Paraguay OR Peru OR Philippines OR Puerto Rico OR Réunion OR Saint Kitts and Nevis OR Saint Lucia OR Saint Vincent and the Grenadines OR Samoa OR Sao Tome and Principe OR Seychelles OR Sierra Leone OR Singapore OR Sint Maarten OR Solomon Islands OR Sri Lanka OR Suriname OR Taiwan OR Tanzania OR Thailand OR Tokelau OR Tonga OR Trinidad and Tobago OR Turks and Caicos Islands OR Tuvalu OR Uganda OR Vanuatu OR Venezuela OR Vietnam OR Virgin Islands)) AND Topic = (soil erosion OR water erosion OR soil loss OR soil depletion OR land degradation OR sedimentation OR sediment production OR siltation) AND Topic = ("erosion plot" OR "erosion plots" OR "runoff plot" OR "runoff plots" OR "run off plot" OR "run off plots" OR "erosion bridge" OR "erosion bridges" OR "erosion pin" OR "erosion pins" OR "erosion stake" OR "erosion stakes" OR "rainfall simulator" OR "rainfall simulation" OR "sediment trap" OR "sediment traps" OR "sediment basin" OR "sediment basins" OR "silt fence" OR "silt fences" OR (t ha-1 AND measure*) OR (Mg ha-1 AND measure*))
Refined by: [excluding] Research areas = (fisheries OR oceanography OR marine freshwater biology OR paleontology OR chemistry)

This query led to 617 references.

Similar queries were made in the different sources we identified; query design was adjusted to meet different search interface requirements. Explored sources and the number of returned references are shown in Table A1. Some sources (shown in grey type in the table) did not lead to any references. Searches led to 5183 references after duplicate removal ("Before step 1" column). This initial list was refined in three successive steps: (1) removal of references found to be irrelevant based on journal title, (2) use of broad exclusion criteria (references found to be irrelevant based on article title and/or abstract, or outside the study's geographical scope, or written in a language other than English, French or Spanish) and (3) use of fine exclusion criteria (outside of tropical rainforest and tropical monsoon climate zones, or not using on-site direct measurement).

Out of the 114 references retrieved after Step 3, 55 were kept after full reading.

Table A1 Summary of the systematic review process

Source	Before step 1	After step 1	After step 2	After step 3	Kept
Databases					
Web of Knowledge	416	327	57	10	7
Scopus	422	334	81	18	7
Science Direct	839	528	76	13	8
ingentaconnect	0	0	0	0	0
BioOne	0	0	0	0	0
AGRIS FAO	49	44	4	2	1
Database platforms					
OvidSP	219	193	101	15	6
Internet databases					
Scirus	58	54	2	0	0
Google Scholar	59	55	28	11	6
Libraries					
JSTOR	984	420	25	8	3
Online Wiley	632	229	29	8	2
PLOS	0	0	0	0	0
Taylor & Francis	204	95	12	1	1
Specialist organizations or professional networks					
FAO	0	0	0	0	0
IRD (French)	1015	1011	130	12	7
IRD (English)	217	217	18	1	0
ICRAF	0	0	0	0	0
CIRAD	0	0	0	0	0
CIFOR	2	2	2	1	1
IAHS	36	36	32	7	1
Web search engines					
Google	31	29	20	7	5
Total references	**5183**	**3574**	**617**	**114**	**55**

Appendix B. Exclusion criteria after full reading

Out of the 114 references retrieved after Step 3, 59 were excluded for one or more of the following reasons:

- Aim of study: the aim of the study did not permit extraction of cases (e.g. study of runoff, no measure of soil loss)
- Artificial land cover: only artificial land covers were considered (e.g. terraces, graded roads)
- Duplicate data: data from the reference were already retrieved from another reference included in the study
- Geographical scope: did not fit with the geographical scope of the study (often too dry)
- General nature of discussion: no case could be extracted from the reference
- Insufficient data: missing data about rainfall, slope steepness, etc.
- Method: indirect and/or off-site measurement of soil loss

Table B1 References excluded after full reading, sorted by main exclusion criteria

Aim of study	Artificial land cover	Duplicate data	Geographical scope	General nature	Insufficient data	Method
Brandt (1988)	Anderson and Macdonald (1998)	Blanchart *et al.* (2004)	Alvarado Narvaez *et al.* (2011)	Chatelin (1979)	Brooks *et al.* (1994)	Ambassa-Kiki and Lal (1992)
Cervantes and Vahrson (1992)	Bruijnzeel *et al.* (1998)	Collinet (1984)	Barai *et al.* (2009)	Douglas (1999)	Chatterjea (1994)	Blanchart *et al.* (2000)
Douglas (1996)	Purwanto and Bruijnzeel (1998)	Fritsch (1992)	Hulugalle *et al.* (1994)	El-Swaify *et al.* (1982)	Douglas (2003)	Clarke and Walsh (2006)
Fritsch *et al.* (1987)	Ramos-Scharrón and MacDonald (2005)	Presbitero *et al.* (1995)	MacDonald *et al.* (2001)	El-Swaify (1990)	Greer *et al.* (1996)	Douglas *et al.* (1992)
Larose *et al.* (2004)		Presbitero *et al.* (2005)	Otero *et al.* (2011)	Lal (1980)	Hill and Peart (1998)	Douglas *et al.* (1999)
Lo *et al.* (1988)		Roose *et al.* (1999)	Ramos-Scharrón and MacDonald (2007)	Sheng (1990)	Kariaga (1999)	Jansson (1988)
Morgan *et al.* (1984)		Siebert (1990)	Ramos-Scharrón (2010)	Sidle *et al.* (2006)	Millington (1981)	Thapa *et al.* (1999)
Presbitero *et al.* (2004)		Uribe-Gomez *et al.* (2002)	Volveras *et al.* (2007)	Stadtmueller (1990)	Oruk *et al.* (2012)	Van Dijk *et al.* (2003)
Salako *et al.* (1991)					Perret *et al.* (1996)	Wallin and Harden (1996)
Sayer *et al.* (2004)					Rijsdijk (2005)	Walsh *et al.* (2006)
Van Dijk and Bruijnzeel (2004)						

Appendix C. Soil erodibility indices

We calculated soil erodibility indices based on a table (Table C1) and two equations (Equation C1 and Equation C2).

Table C1 Soil erodibility values depending on texture class and percentage of organic matter. Adapted from Stewart *et al.* (1975). Values are given in SI units (t ha hr / ha MJ mm). The values from the original paper (given in U.S. customary units) were multiplied by 0.1317 to convert them to SI units.

	Organic matter		
Texture class	**<0.5%**	**2%**	**4%**
Sand	0.007	0.004	0.003
Fine sand	0.021	0.018	0.013
Very fine sand	0.055	0.047	0.037
Loamy sand	0.016	0.013	0.011
Loamy fine sand	0.032	0.026	0.021
Loamy very fine sand	0.058	0.050	0.040
Sandy loam	0.036	0.032	0.025
Fine sandy loam	0.046	0.040	0.032
Very fine sandy loam	0.062	0.054	0.043
Loam	0.050	0.045	0.038
Silt loam	0.063	0.055	0.043
Silt	0.079	0.068	0.055
Sandy clay loam	0.036	0.033	0.028
Clay loam	0.037	0.033	0.028
Silty clay loam	0.049	0.042	0.034
Sandy clay	0.018	0.017	0.016
Silty clay	0.033	0.030	0.025
Clay		0.017–0.026	

Equation C1 Soil erodibility as computed by Torri *et al.* (1997):

$$K = 0.0293 \times (0.65 - D_G + 0.24\, D_G^2) \times \exp\left(-0.0021 \frac{OM}{f_{clay}} - 0.00037 \left(\frac{OM}{f_{clay}}\right)^2 - 4.02\, f_{clay} + 1.72\, {f_{clay}}^2\right)$$

Where $D_G = -3.5\, f_{clay} - 2.0\, f_{silt} - 0.5\, f_{sand}$

K is in SI units (t ha hr / ha MJ mm). *OM* is the percent organic matter, f_{sand} the fraction of sand (particle size of 0.05–2.0 mm), f_{silt} the fraction of silt (particle size of 0.002–0.05 mm), and f_{clay} the fraction of clay (particle size of 0.00005–0.002 mm).

Equation C2 Soil erodibility as computed by Sharpley and Williams (1990):

$$K = \frac{1}{7.593} \times \left\{0.2 + 0.3 \exp\left[-0.0256\, \%_{sand} \left(1 - \frac{\%_{silt}}{100}\right)\right]\right\} \times \left(\frac{\%_{silt}}{\%_{clay} + \%_{silt}}\right)^{0.3}$$
$$\times \left(1.0 - \frac{0.25\, OM}{OM + \exp(3.72 - 2.95\, OM)}\right) \times \left(1.0 - \frac{0.7\, SN}{SN + \exp(-5.51 + 22.9\, SN)}\right)$$

Where $SN = 1.0 - \frac{\%_{sand}}{100}$

K is also in SI units (t ha hr / ha MJ mm). OM, $\%_{sand}$, $\%_{silt}$, and $\%_{clay}$ are the percent of organic matter, sand, silt and clay respectively.

Each of the three indices was classified into low, medium and high classes with each class having (as much as possible) the same size (Figure C1).

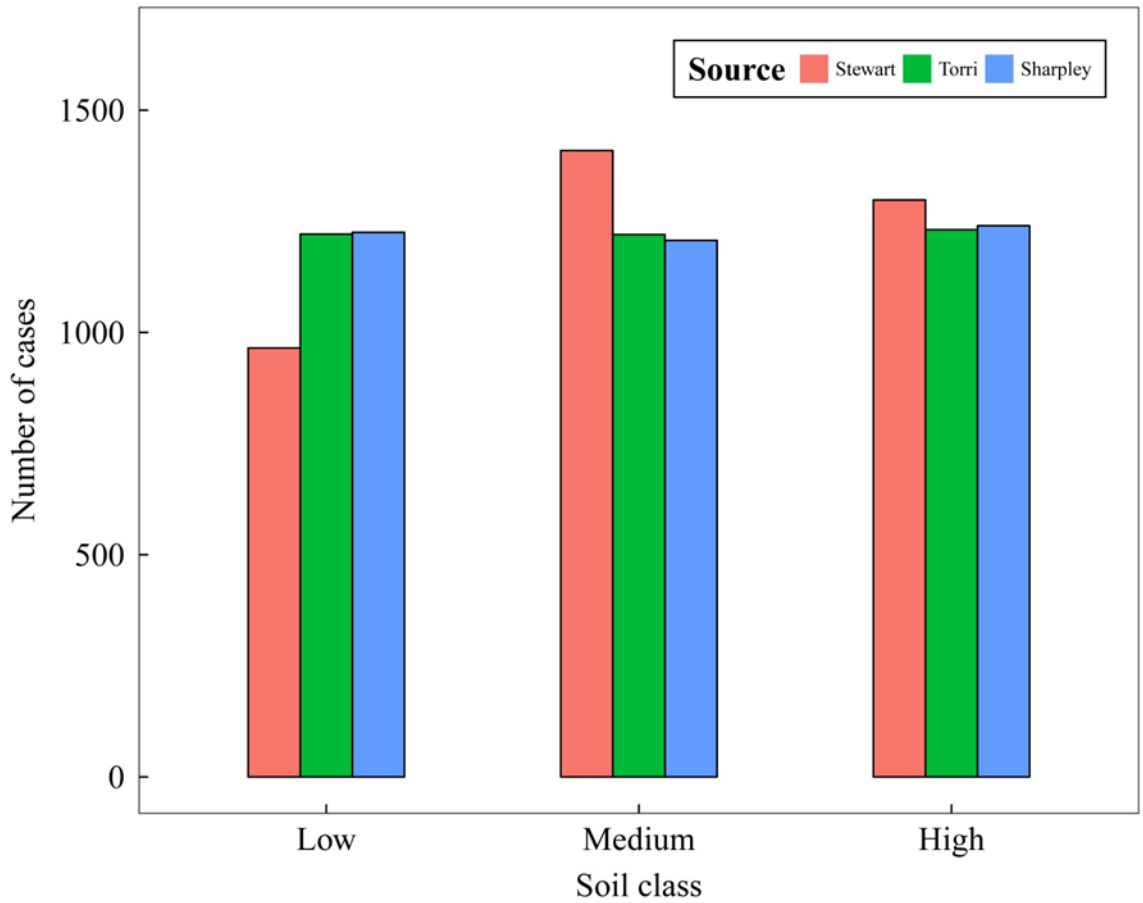

Figure C1 Classification of soils from cases in three categories of soil erodibility (low, medium, high) using values computed from three indices (Stewart *et al.*, 1975; Sharpley and Williams, 1990; Torri *et al.*, 1997).

Based on this information, a soil was classified as highly erodible if it was considered highly erodible by at least two of the three indices, low if it was considered low by at least two indices, and medium otherwise (Figure C2).

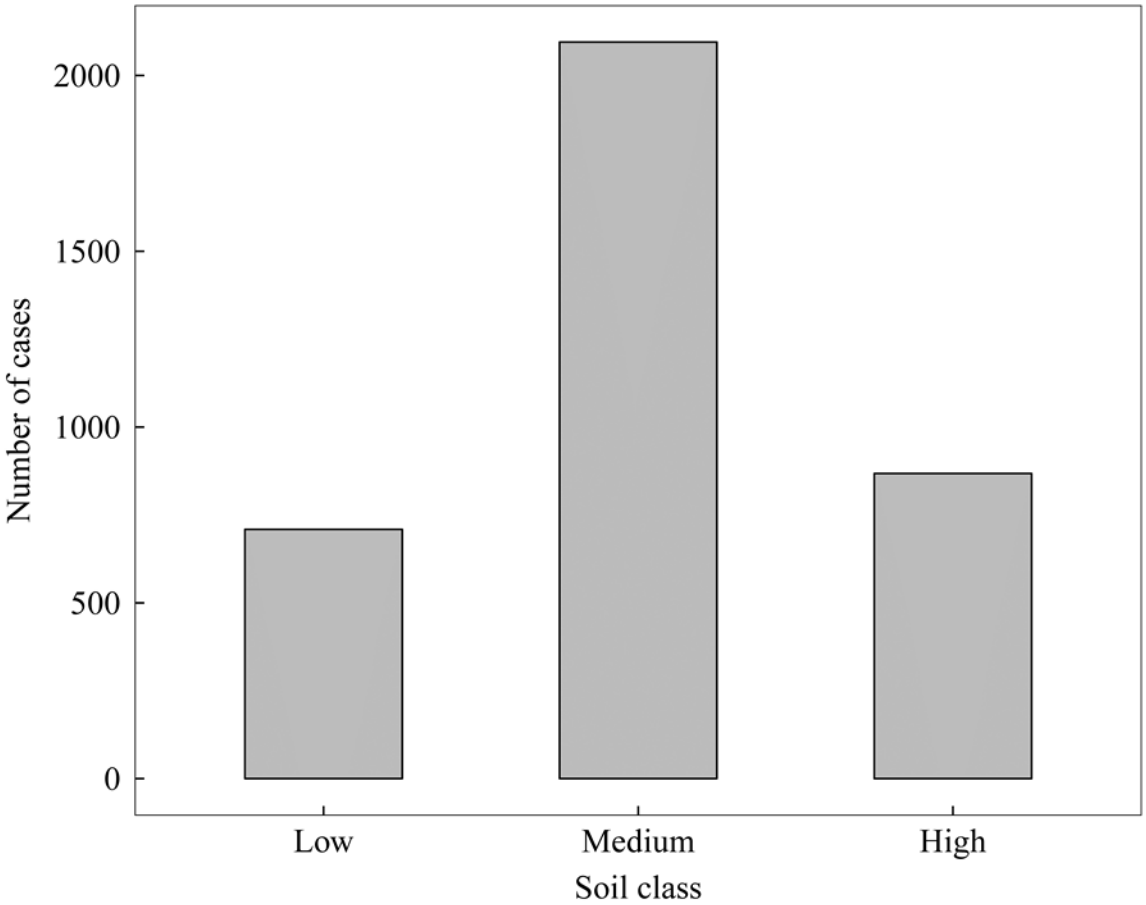

Figure C2 Final classification of soil erodibility for the 3649 cases used in this study. This classification resulted in 709, 2081 and 859 cases with soils of low, medium and high erodibility, respectively.

Appendix D. Supplementary tables

Table D1 Coefficients of the generalized linear model regressions aiming at removing the effect of the method on annual soil loss (ASL), rainfall (R), slope length (L) and slope steepness (S) values. Independent and dependent variables are log-transformed (log10); t values are shown in parentheses. Model: X ~ duration + area + duration x area.

	ASL		R		L		S	
Intercept	0.77172	***	2.66618	***	0.907039	***	1.910419	***
	(4.374)		(60.822)		(46.81)		(59.91)	
Duration	−1.0209	***	0.28848	***	0.200409	***	0.159649	***
	(−13.912)		(15.824)		(24.87)		(12.04)	
Area	0.4828	***	0.20918	***	0.176396	***	−0.34332	***
	(4.934)		(8.604)		(16.41)		(−19.41)	
Duration × area	0.26941	***	0.14342	***	−0.088304	***	−0.085643	***
	(6.609)		(14.161)		(−19.73)		(−11.62)	

*** $p < 0.001$

Table D2 Coefficients of the generalized linear model regressions aiming at removing the effect of the context on annual soil loss values that have already been corrected from the effect of the method (ASL_corrM) using corrected values of rainfall (R_corrM), slope length (L_corrM) and slope steepness (S_corrM) and dummy variables for the categorical variable of soil erodibility (three levels); t values are shown in parentheses. Model: ASL_corrM ~ SoilClass1 + SoilClass2 + R_corrM + L_corrM + S_corrM + R_corrM × L_corrM + R_corrM × S_corrM + L_corrM × S_corrM.

	ASL_corrM	
Intercept	−6.92199	***
	(−4.586)	
SoilClass1	−0.5999	***
	(−6.877)	
SoilClass2	−0.69147	***
	(−10.013)	
R_corrM	1.30016	**
	(2.908)	
L_corrM	6.70099	***
	(6.048)	
S_corrM	1.75875	*
	(2.01)	
R_corrM × L_corrM	−0.66741	*
	(−1.989)	
R_corrM × S_corrM	0.67587	***
	(3.413)	
L_corrM × S_corrM	−3.48788	***
	(−7.933)	

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

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Conclusions de l'étude

Les mesures de pertes de sol que nous avons rassemblées à la suite d'une revue systématique de la littérature (plus de 3600) nous ont permis d'analyser quantitativement le service écosystémique (SE) de contrôle de l'érosion des sols. Nous avons pu mettre en évidence que, quel que soit le type d'occupation ou d'utilisation des sols, la plupart des pertes de sol viennent d'éléments de sol nu présents dans le paysage. De même, il est apparu que le service de contrôle de l'érosion des sols est fourni dès lors que le couvert végétal est suffisamment développé.

Confrontons les hypothèses initiales à ces principaux résultats. Pour rappel, nous avions postulé que : (1') « Aucun type d'occupation ou d'utilisation des sols n'est en soi propice à l'érosion. » ; (1) « Le SE de contrôle de l'érosion des sols est fourni dès lors que le couvert végétal est suffisamment développé. ».

☑ L'exemple des champs de culture est particulièrement indiqué pour confirmer la première hypothèse. En effet, si les pertes de sol sont très importantes pour des cultures sans mesures particulières de gestion des sols ou de la végétation, les pertes sont drastiquement réduites (plus de 99% de réduction) dans le cas où des mesures appropriées sont appliquées (voir Figure 4.5).

☑ La seconde hypothèse est confirmée par le fait que l'on enregistre une baisse de 90% des pertes de sol dès lors qu'au moins une couche de végétation est présente sur zone (voir Figure 4.6). Cela dit, nous avons également démontré que toutes les couches de végétation ne contribuent pas également au contrôle de l'érosion des sols.

Dans le cadre du Chapitre 2, nous avions émis l'hypothèse que « les milieux naturels produisent plus de SE […] que les milieux perturbés par les activités anthropiques ». Si cela se vérifiait pour le service de contrôle de l'érosion des sols à l'échelle locale (voir Figure 2.8), qu'en est-il au regard des données recueillies à l'échelle des tropiques humides ?

☒ Les pertes de sol sont effectivement parmi les plus basses pour les forêts naturelles mais elles sont toutefois significativement inférieures pour les cultures arboricoles avec ajout d'un couvert en contact avec le sol.

Au vu des conclusions de cette revue systématique, les faibles valeurs de pertes de sol mesurées pour tous les types d'occupation ou d'utilisation des sols dans le Chapitre 2 (pour rappel, 2−3 ordres de grandeurs inférieures au taux d'érosion tolérable) apparaissent tout à fait cohérentes. En effet, sur toutes les parcelles, il y avait systématiquement un couvert végétal. Celui-ci était plus ou moins développé suivant le type d'occupation ou d'utilisation des sols. Notons de plus que, dans les zones les plus récemment perturbées par les activités anthropiques au début de l'étude (par exemple champs de cultures vivrières ou jeune recrû),

le développement d'un couvert végétal dense, synonyme de pertes de sol faibles, a pu survenir au cours des deux ans qu'a duré de l'étude (Figure 4.8).

Figure 4.8 Epaisseur du mat racinaire (environ 50 cm) dans un champ de cultures vivrières abandonné depuis près d'1 an et colonisé par des fougères (© Imam Basuki).

Chapitre 5

Synthèse, discussion générale et perspectives

5.1 Synthèse des travaux de thèse

5.1.1 Retour sur les objectifs et moyens mis en œuvre pour y parvenir

Pour rappel, l'objectif général de la thèse était d'aboutir à une meilleure compréhension de la distribution spatiale de la diversité d'espèces ligneuses (DEL) et de deux services écosystémiques (SE) d'intérêt dans la zone d'étude, ainsi que d'approfondir les connaissances sur les relations qui existent entre eux.

Quant aux objectifs spécifiques, ils étaient de :

- évaluer les niveaux de services écosystémiques produits par, et diversité d'espèces ligneuses abritée dans différents types d'occupation ou d'utilisation des sols au voisinage d'un village dont les moyens de subsistance sont liés à l'agriculture sur brûlis et la culture de l'hévéa (échelle locale)
- élaborer des modèles régionaux de distribution de carbone (à la fois dans la biomasse aérienne et le sol) et de diversité d'espèces ligneuses, à partir d'inventaires botaniques et pédologiques réalisés sur l'ensemble de Kapuas Hulu (échelle régionale).
- discuter de la nature des relations spatiales qui existent à l'échelle de la région entre carbone et diversité d'espèces ligneuses, et des stratégies qui pourraient conduire à la préservation de leurs « *hotspots* » (échelle régionale)
- analyser l'influence du couvert végétal dans le contrôle de l'érosion des sols dans l'ensemble des tropiques humides (échelle globale)

Afin d'atteindre nos objectifs, notre travail s'est principalement appuyé sur :

- des campagnes de terrain afin d'inventorier différents types de végétation
- la mise en place d'un dispositif de suivi de l'érosion à l'échelle du paysage
- l'utilisation d'outils de modélisation (en particulier « *random forest* ») afin de prédire les valeurs de DEL et stocks de carbone (dans la biomasse aérienne et dans le sol) à l'échelle de la zone d'étude
- une revue systématique de la littérature

Les travaux que nous avons réalisés ont été présentés sous la forme de trois articles visant des revues internationales à comité de lecture (l'un a été accepté, les deux autres sont en cours de révision). Nous nous sommes attachés durant nos travaux à appréhender la DEL et les SE à des échelles différentes : à l'échelle locale (Chapitre 2), à l'échelle régionale (Chapitre 3), et enfin à l'échelle des tropiques humides (Chapitre 4). La section suivante revient sur les principaux résultats des trois études.

5.1.2 Principaux résultats

A l'échelle locale, nous avons mesuré les stocks de carbone, la DEL et les pertes de sol dans différents types d'occupation ou d'utilisation des sols d'un paysage aux abords d'un village du nord de Bornéo dont les moyens de subsistance sont liés à l'agriculture sur brûlis et la

culture de l'hévéa. Nous avons constaté que la production de services et la DEL sont maximales en forêt naturelle, et que les forêts post-exploitation produisent des services qui sont similaires (bien qu'en quantité moindre du fait de l'exploitation) et abritent de même une importante DEL. Nous avons également remarqué que les types d'utilisation des sols liés à l'agriculture itinérante sur brûlis fournissent plus de services et abritent une diversité d'espèces ligneuses plus importante que les plantations industrielles de palmiers à huile ou d'hévéa qui se développent à Bornéo. Les résultats de cette étude plaident donc pour la protection inconditionnelle des forêts naturelles restantes, une gestion pertinente des forêts post-exploitation afin d'éviter qu'elles ne soient converties en plantations, et un soutien pour le maintien de systèmes d'agriculture et d'agroforesterie traditionnels.

A l'échelle de la région, nous avons réalisé des inventaires botaniques et pédologiques dans différents types de végétation (forêts de plaine, forêts sur tourbe, forêts sur sable blanc, etc.). Nous nous sommes servis de ces inventaires et de données facilement accessibles pour élaborer des modèles régionaux de distribution de carbone (à la fois dans la biomasse aérienne et le sol) et de DEL. Nous avons trouvé, dans la zone d'étude, une forte corrélation positive entre le carbone contenu dans la biomasse aérienne et la DEL. La corrélation devient négative lorsque l'on considère le carbone du sol car ce dernier est particulièrement élevé dans les tourbières où la diversité est faible. Si nous avons mis en évidence une importante congruence spatiale entre les zones présentant les plus hautes valeurs (« *hotspots* ») de carbone dans la biomasse aérienne et de DEL, celles entre carbone du sol et carbone de la biomasse aérienne ou DEL sont nulles. Nos résultats suggèrent que la protection des zones à hautes valeurs de carbone dans la biomasse aérienne (par le biais de mécanismes financiers comme REDD+ par exemple) pourrait également conduire à la conservation de la DEL. Nous avons par ailleurs établi que la protection des zones renfermant les plus importants stocks de carbone dans leurs sols n'était pas garantie. La majorité de celles-ci se trouve en effet au niveau de tourbières menacées de conversion en plantations de palmiers à huile, et l'actuel moratoire visant à interdire l'attribution de nouvelles concessions dans des forêts naturelles ou tourbières ne constitue qu'une première étape en vue de leur nécessaire protection.

Enfin, à l'échelle des tropiques humides, nous avons conduit une revue systématique afin de recueillir toutes les données de pertes de sol disponibles sur la zone. Il s'agissait, ce faisant, de combler un vide existant car, s'il existe plusieurs études sur la biodiversité ou les stocks de carbone au niveau des tropiques humides, aucune ne traitait jusqu'alors du service de contrôle de l'érosion des sols. Nous avons pu, par le biais de cette revue systématique, synthétiser quantitativement l'influence du couvert végétal dans le contrôle de l'érosion des sols. Nous avons montré que l'érosion des sols se concentre dans l'espace (au niveau des éléments nus d'un paysage) et dans le temps (entre deux rotations de cultures). Le service de contrôle de l'érosion des sols étant fourni dès lors que le couvert végétal est suffisamment développé, nos résultats soulignent l'importance de la mise en place de pratiques de conservation des sols simples (mise en place de haies, paillage des zones cultivées, etc.), qui permettent d'obtenir des diminutions de pertes de sol drastiques.

5.2 Discussion générale et perspectives

5.2.1 Limites du type d'occupation ou d'utilisation des sols comme indicateur de production de SE

Les relevés de terrain effectués durant nos travaux (concentrés à l'échelle d'un paysage pour le Chapitre 2, étendus à l'ensemble de la zone d'étude pour le Chapitre 3) ont souligné la variabilité des valeurs mesurées au sein d'un même type d'occupation ou d'utilisation des sols, qu'il s'agisse de pertes de sol, de densité de carbone dans la biomasse aérienne ou les sols ou encore de diversité d'espèces ligneuses (DEL). De même, la synthèse de plus de 3600 données de pertes de sol à l'échelle des tropiques humides a mis en évidence que la grandeur moyenne de pertes de sol pour un type d'occupation ou d'utilisation des sols particulier (par exemple, l'agriculture) masquait en fait des disparités importantes dès lors que l'on prend en compte la mise en œuvre de bonnes pratiques de gestion des sols et de la végétation (par exemple, agriculture avec vs. sans bonnes pratiques).

Ainsi, l'utilisation du type d'occupation ou d'utilisation des sols comme substitut (« *proxy* ») pour caractériser la DEL d'une zone ou sa production de SE possède des limites. L'approche consistant à attribuer à un type d'occupation ou d'utilisation des sols une valeur unique de production de SE ou de DEL sur la base de valeurs précédemment publiées dans la littérature (approche « *look-up table* » ; voir Tableau 5.1) n'a de sens qu'utilisée à grande échelle et faible résolution spatiale (par exemple, valeur de production d'un SE pour un pays). Car, par essence, ce type d'approche ne peut rendre compte de la variabilité des valeurs de SE et de DEL (liée à des différences d'altitude, de pente, de conditions édaphiques, d'histoire des lieux, etc.) au sein d'un paysage ou d'une région,

Malgré cette restriction d'utilisation, l'approche « *look-up table* » reste couramment utilisée en cas d'absence de données. Elle est ainsi préconisée par le Groupe d'experts intergouvernemental sur l'évolution du climat (GIEC) comme échelon 1 (« *tier 1* » ; c'est-à-dire le moins complexe, le moins demandant, mais aussi le moins précis des 3 échelons) de suivi des émissions de gaz à effet de serre (IPCC, 2006). Les pays désireux de participer au programme REDD+ doivent en effet, dans un premier temps, évaluer les stocks de carbone présents sur leurs territoires, et notamment ceux contenus dans la biomasse aérienne. Ne disposant pas de données de qualité en quantité suffisante, beaucoup de ces pays ont donc recours à l'approche « *look-up table* », avec les limites qui y sont associées. Une récente étude menée par Langner *et al.* (2014) a montré que les valeurs utilisées actuellement surestiment sans doute la biomasse des forêts tropicales et propose d'utiliser de nouvelles valeurs par défaut, tirées des cartes de biomasse de Saatchi *et al.* (2011) et Baccini *et al.* (2012).

Tableau 5.1. Différents types d'approches utilisés pour cartographier la fourniture de SE, et critères les caractérisant (d'après Martínez-Harms & Balvanera, 2012)

Criteria	Categories considered	Rationale
Availability of data sources	Primary data	Maps derived from sampling in the field (e.g., field data, surveys, or interviews or census data)
	Secondary data	Maps derived from readily available information not verified in the field (e.g., cartographical data, remote-sensed data, socioeconomic data, and mixed sources like databases like global statistics)
Types of data source	Biophysical data	Land-cover, remote-sensed, topographical, hydrological, and climate data
	Socioeconomic data	Road map, population map, photos, and census data
	Mixed Sources	Database (global statistics, e.g., Olson's global map of carbon storage and FAO reports), bibliography, surveys, and field data.
Scale	Patch	$10–10^2$ km^2
	Local	$10^2–10^3$ km^2
	Regional	$10^3–10^5$ km^2
	National	$10^5–10^6$ km^2
	Global	$>10^6$ km^2
Method	Look-up tables	Use of existing ES values from the literature to land-cover classes
	Expert knowledge	Experts rank land-cover types based on their potential to provide specific ES
	Causal relationships	Incorporate existing knowledge about how different layers of information related to ecosystem processes and the services to create a new proxy layer of the ES
	Extrapolation of primary data	Field data databases weighted by cartographical data (generally land cover)
	Regression models	Employing field data of ESs as response variables and proxies (e.g., biophysical data and other sources of information obtained from GIS) as explanatory variables

Pour autant, la restriction liée à l'échelle d'étude demeure, et une estimation des stocks de carbone à une échelle locale ou régionale (échelle à laquelle sont développés la plupart des projets REDD+) utilisant l'approche « *look-up table* » augmenterait très nettement le risque que la valeur présentée ne soit que peu représentative de la situation réelle (Langner *et al.*, 2014). De plus, cette approche ne permet pas d'étudier les relations entre SE multiples à plus fine échelle du fait de biais conséquents liés à l'utilisation du type d'occupation ou d'utilisation des sols comme « *proxy* » (Eigenbrod *et al.*, 2010).

Nous avons présenté, dans le Chapitre 3, une méthode de modélisation des stocks de carbone dans la biomasse aérienne à l'échelle régionale, à partir de données d'inventaires et de facteurs explicatifs facilement accessibles. Nous pensons que cette méthode serait particulièrement adaptée pour l'estimation des stocks de carbone de zones de projets REDD+. De plus, la méthode peut être adaptée à d'autres SE, permettant de pouvoir s'affranchir du recours à l'utilisation du type d'occupation ou d'utilisation des sols dont les limites ont été présentées pour toute échelle inférieure à celle nationale.

5.2.2 Vers une étude dynamique de la production de SE

Plusieurs fois au cours de nos travaux nous est apparue l'importance de prendre en compte la dimension temporelle dans l'évaluation de la production de SE. La considération de l'évolution dans le temps de la production de SE nous aurait permis de pouvoir aborder les synergies et trade-offs éventuels entre SE, que ce soit à l'échelle du paysage (cf. approche 2 de Figure 1.4) ou bien à l'échelle de la région (cf. approche 4 de Figure 1.4).

A l'échelle du paysage, des mesures de pertes de sol réalisées pendant près de 2 ans pour le compte de l'étude présentée dans le Chapitre 2 ont indiqué des taux annuels d'érosion très faibles (2−3 ordres de grandeurs inférieures au taux d'érosion tolérable ; Montgomery, 2007), et ce, quel que soit le type d'occupation ou d'utilisation des sols. L'étude présentée dans le Chapitre 4 (revue systématique de la littérature) a révélé que les pertes de sol étaient localisées dans l'espace et dans le temps, particulièrement pendant le laps de temps où le couvert végétal n'est pas suffisamment développé (par exemple, lors des rotations entre culture). Les résultats des Chapitres 2 et 4 mettent clairement en évidence qu'aucun type d'occupation ou d'utilisation des sols n'est intrinsèquement sujet à l'érosion, dès lors que des mesures de conservation sont mises en œuvre. Il est à penser que ce sont les transitions entre types d'occupation ou d'utilisation des sols, et non les types en eux-mêmes, qui pourraient contribuer de façon importante aux pertes de sols à l'échelle des paysages par le biais de la création d'éléments de sol nu (voir Figure 5.1 pour le cas de l'exploitation forestière). Aussi, si les mesures de pertes de sol dans les types d'occupation ou d'utilisation des sols en lien avec l'agriculture itinérante sur brûlis ou l'exploitation forestière ne permettent pas de conclure à un impact négatif de ces pratiques sur le SE de contrôle de l'érosion des sols (ceci étant à moduler du fait qu'aucune mesure n'a été effectuée au niveau des chemins d'exploitation forestière ou des glissements de terrain se produisant le long de ceux-ci), il aurait été intéressant de mettre en place des parcelles de mesure avant que les transitions n'aient lieu afin de quantifier la contribution des transitions entre types d'occupation ou d'utilisation des sols (et donc celle des activités associées) au phénomène d'érosion.

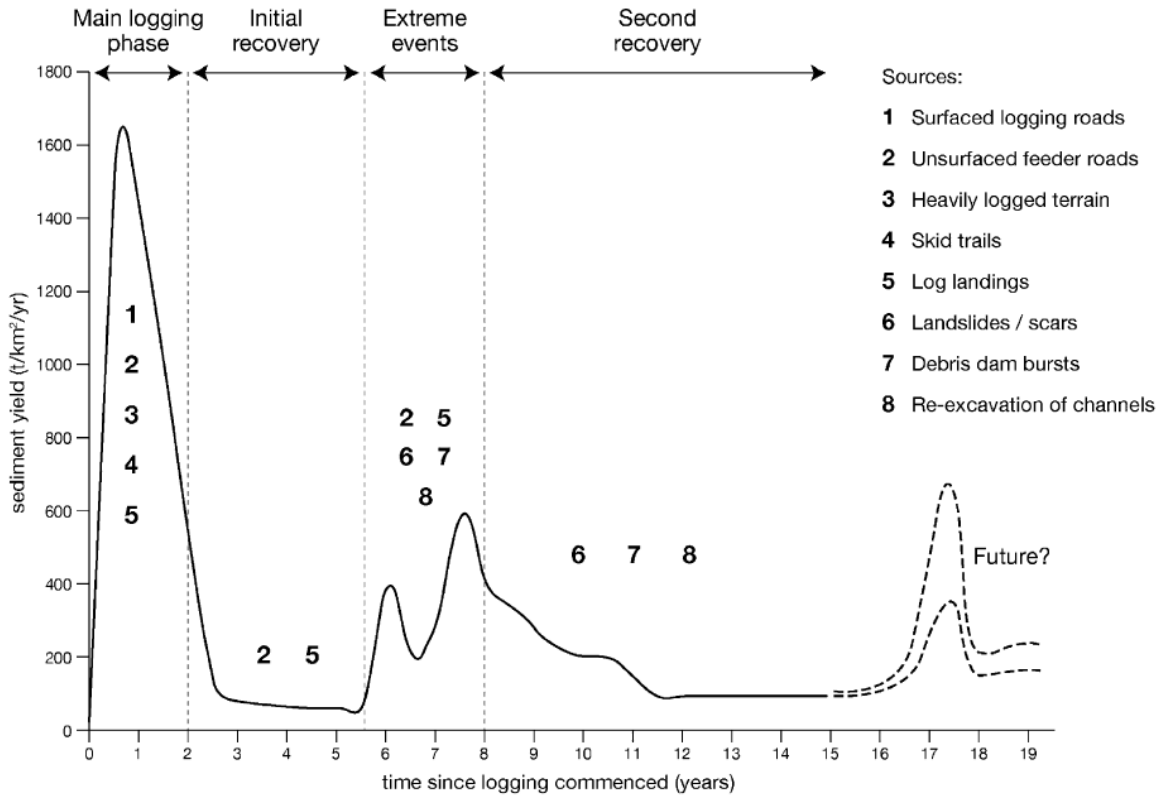

Figure 5.1. Changement des apports en sédiments et principales sources au cours du temps dans le bassin versant de Baru (forêt exploitée de façon sélective) depuis la période pré-exploitation (1988) jusque 14 après (Clarke & Walsh, 2006)

Toujours à l'échelle du paysage, il serait également particulièrement intéressant de faire un suivi à long terme de l'évolution du carbone et de la biodiversité dans les paysages toujours dominés par l'agriculture itinérante sur brûlis. Cette pratique est par essence dynamique, s'appuyant sur l'exploitation temporaire (après abattage et brûlis de la végétation présente) d'une zone avant d'y laisser la végétation se régénérer. Comprendre comment, au sein de tels paysages, les stocks de carbone et la biodiversité fluctuent avec le temps serait de première importance afin de pouvoir soutenir ces pratiques qui, selon l'étude statique présentée dans le Chapitre 2, fournissent des SE et abritent une DEL bien plus importante que des monocultures de palmiers à huile ou d'hévéas.

A l'échelle de la région, nous avons constaté lors des dernières années la conversion d'importantes étendues de forêts sur tourbe en plantations de palmiers à huile. Ces conversions entrainent des modifications dans la fourniture, sur l'ensemble de Kapuas Hulu, de SE comme l'atténuation du changement climatique via stockage de carbone dans la biomasse aérienne ou le sol. La diversité d'espèces ligneuses, et plus généralement la biodiversité, est également fortement impactée (voir par exemple Koh & Wilcove, 2008 pour une quantification des conséquences délétères de telles conversions sur la biodiversité). Dans le cadre de l'étude présentée dans le Chapitre 3, nous avons pu mettre en évidence les menaces potentielles (en termes de perturbation ou conversion futures de la végétation) qui pèsent sur les « *hotspots* » de carbone et de DEL, notamment du fait du chevauchement de ces zones avec des concessions attribuées pour l'exploitation forestière ou encore la conversion en plantations. Au-delà de cette étude qualitative, il aurait également pu être intéressant de développer différents scénarios extrêmes/souhaitables de développement (par exemple, conversion de l'ensemble des concessions pour plantations vs. réaffectation des concessions sur des zones fournissant peu de SE) afin d'en évaluer quantitativement les conséquences en termes de changements de fourniture de SE.

5.2.3 Relier composantes « fourniture » et « demande »

Au cours de nos travaux, nous nous sommes concentrés sur la composante « fourniture » des SE. Nous avons pu mettre en évidence les facteurs influençant la production de SE (notamment, le contrôle de l'érosion des sols). De plus, les différentes études que nous avons menées nous ont permis d'acquérir une meilleure connaissance de la répartition spatiale, à l'échelle de la zone d'étude, tant des stocks de carbone de la biomasse aérienne et du sol (liés au SE d'atténuation du changement climatique) que de la diversité d'espèces ligneuses.

Dans le prolongement des travaux présentés dans le cadre de cette thèse, il serait très intéressant d'approfondir la compréhension des liens entre la composante « fourniture » et la composante « demande » pour les SE étudiés et la DEL. Identifier la demande pour des SE, de façon individuelle ou par paquet (« *bundle* »), constitue une étape primordiale dans le processus de mise en place de paiements pour services environnementaux (PSE). L'idée principale autour des PSE est que des bénéficiaires externes de services environnementaux s'engagent contractuellement à payer des propriétaires terriens ou des personnes utilisant

certaines zones d'intérêt (par exemple, les zones agricoles en amont d'importantes villes) afin que ceux-ci adoptent (ou continuent d'utiliser) des usages des sols et des ressources naturelles assurant la conservation ou bien la restauration des écosystèmes et des services qu'ils fournissent à ces bénéficiaires (Wunder, 2007). Il s'agit donc, en fin de compte, d'internaliser les externalités positives au bénéfice de populations qui dans le contexte tropical, sont bien souvent particulièrement démunies.

Des données socio-économiques récoltées dans la zone d'étude (Shantiko *et al.*, 2013) ont permis d'identifier les demandes des populations locales, et de proposer différents types de PSE adaptés aux caractéristiques sociales et environnementales des sites pilotes (Fripp & Shantiko, 2014). L'étude de la composante « fourniture » (ce sur quoi se sont concentrés nos travaux) constitue une étape clé dans l'évaluation de la faisabilité des PSE, avant leur éventuelle mise en place dans la zone d'étude (voir étape 8 de la Figure 5.2).

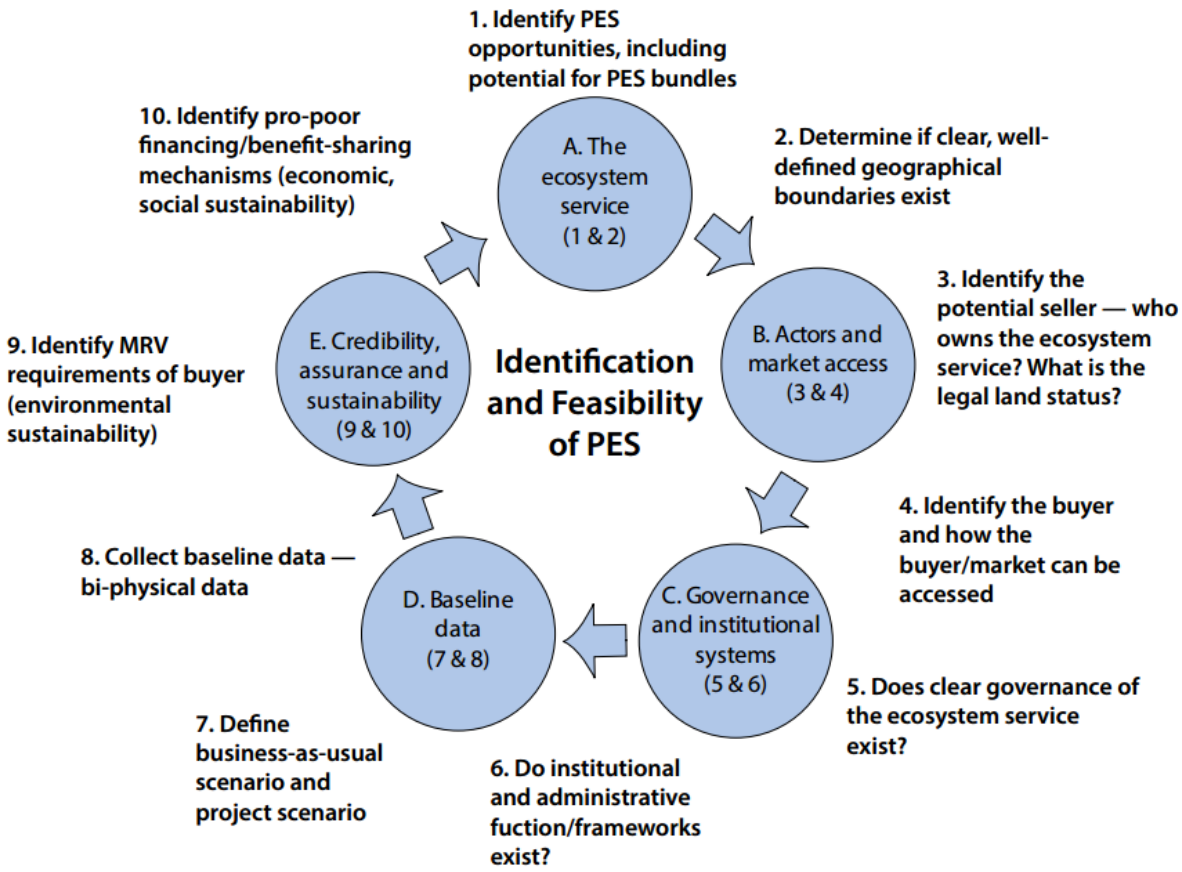

Figure 5.2. Les dix étapes-clés pour évaluer la faisabilité de PSE (Fripp & Shantiko, 2014)

5.2.4 Traits fonctionnels et production de SE

Dans le cadre de l'étude présentée dans le Chapitre 3, nous avons mis en évidence une forte corrélation positive entre stocks de carbone dans la biomasse aérienne (caractéristique en lien avec le fonctionnement des écosystèmes) et diversité d'espèces ligneuses. Si la nature des relations entre diversité des plantes et fonctionnement des écosystèmes reste controversée

(voir par exemple Loreau & Hector, 2001 pour deux hypothèses sur les liens entre biodiversité et fonctionnement des écosystèmes), un faisceau d'évidences tend à indiquer que la diversité des traits fonctionnels (caractéristiques d'un organisme telles que la taille des feuilles, celle des graines, ou encore la densité de bois) d'individus présents dans un écosystème a bien une influence sur le fonctionnement de celui-ci (Diaz & Cabido, 2001). Bien que la collecte d'informations sur les traits fonctionnels demande des moyens humains et financiers importants (Baraloto *et al.*, 2010), il serait intéressant dans l'avenir de disposer de telles données afin d'aboutir à une compréhension fine de l'influence de la diversité des traits fonctionnels sur le fonctionnement des écosystèmes (et donc les SE qu'ils produisent). Ces connaissances nous permettraient alors d'évaluer les conséquences, en termes de production de SE à l'échelle de la zone d'étude, de la perte d'espèces possédant des traits fonctionnels particuliers selon différents scénarios prenant en compte l'effet du changement climatique et/ou de pressions anthropiques directes (abattage sélectif, par exemple), à l'instar des travaux de Bunker *et al.* (2005).

Chapitre 6

Conclusion générale

A l'heure où l'avenir des dernières grandes étendues de forêts naturelles de Bornéo reste bien incertain, nos travaux avaient pour objectif d'aboutir à une meilleure compréhension de la distribution spatiale de la diversité d'espèces ligneuses (DEL) et de services écosystémiques (SE) d'intérêt dans une zone encore majoritairement couverte de forêts. L'échelle d'étude pouvant influencer la nature des relations entre SE, nous avons choisi de travailler à différentes échelles d'étude : locale (Chapitre 2), régionale (Chapitre 3) et globale (Chapitre 4). Chacune de ces études nous a permis d'émettre des suggestions en matière de gestion des ressources naturelles. Nos recommandations peuvent contribuer à aboutir à un aménagement du territoire qui, tout en permettant un développement socio-économique de la zone au bénéfice des populations locales (par exemple par le biais d'un soutien au système traditionnel d'agriculture itinérante sur brûlis dans certaines conditions, ou encore l'établissement de plantations sur des zones dégradées), ne menacerait pas la production de SE et la préservation de la DEL sur le territoire.

La production de SE et la DEL étant maximales en forêt naturelle, celles-ci devraient bénéficier d'une protection inconditionnelle dans l'état actuel de la ressource. De même, une gestion pertinente des forêts post-exploitation devrait être mise en place de sorte à éviter leur conversion en plantations industrielles. Les types d'utilisation des sols en lien avec l'agriculture itinérante sur brûlis fournissent plus de SE et comportent une DEL plus importante que les plantations industrielles de palmiers à huile ou d'hévéas qui tendent à les supplanter. Une réflexion sur les mécanismes à mettre en place afin de supporter l'agriculture traditionnelle s'impose. La possibilité d'une internalisation des externalités positives découlant de ce type de pratiques agricoles, éventuellement par le biais de paiements pour services environnementaux, devrait être étudiée plus avant.

La forte corrélation positive entre stocks de carbone dans la biomasse aérienne et DEL sur l'ensemble de la zone d'étude, et la congruence spatiale importante de leurs « *hotspots* », indiquent que la protection des stocks de carbone dans la biomasse aérienne, par l'intermédiaire de mécanismes financiers tels REDD+, pourrait être bénéfique à la conservation de la DEL. Au-delà du moratoire actuel sur la conversion de forêts sur tourbes en Indonésie, la protection des importants stocks de carbone présents dans le sol des tourbières nécessite la mise en place de régulations adéquates. Si les options de développement peuvent paraitre limitées du fait des caractéristiques biophysiques particulières de la zone d'étude (zones de fortes pentes dans les parties périphériques limitant les activités humaines telles que l'exploitation forestière, grande zone de tourbières dans la partie centrale etc.), des programmes de restauration des surfaces dégradées (faisant par exemple intervenir des plantations de bois d'œuvre), ou l'intégration dans la mosaïque paysagère complexe créée par l'agriculture itinérante sur brûlis de petites plantations familiales de palmiers à huile, demeurent des pistes de développement qui nécessiteraient d'être étudiées.

Les recommandations émises afin que soit optimalement fourni le SE de contrôle de l'érosion des sols tiennent leur force de la nature systématique de la revue (la première sur le sujet) que nous avons conduite afin d'y parvenir. L'analyse de plus de 3600 mesures de pertes de sol

provenant de 55 références et couvrant 21 pays des tropiques humides a révélé que l'érosion est très nettement concentrée dans l'espace (au niveau des éléments de sol nu présents dans le paysage) et dans le temps (par exemple, durant la rotation des cultures) dans cette partie du globe. Nous avons montré que la mise en œuvre de bonnes pratiques de gestion des sols et de la végétation (par exemple, semis selon les courbes de niveau, culture sans labour, et utilisation de bandes enherbées) pouvait permettre jusqu'à 99% de réduction des pertes de sols.

Les conclusions et recommandations provenant de l'étude réalisée à l'échelle locale valent, de fait, pour des paysages semblables de Bornéo. De même, la relation que nous avons mise en évidence à l'échelle régionale entre stocks de carbone dans la biomasse aérienne et DEL, et les recommandations qui en découlent en termes de gestion des ressources naturelles, sont propres à la zone d'étude. Cela dit, la méthode de modélisation utilisée pour prédire stocks de carbone et DEL est parfaitement transposable à d'autres SE et contextes. De même, les recommandations tirées de la revue systématique valent pour l'ensemble des tropiques humides. Ainsi, au-delà d'une meilleure compréhension de la distribution spatiale de la DEL et de SE d'intérêt pour la zone d'étude, tel qu'était défini l'objectif principal, nous pensons que nos travaux pourront contribuer à évoluer vers une approche intégrée de l'aménagement du territoire fondée sur la prise en compte des services écosystémiques.

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Résumé

D'importants changements d'occupation et d'utilisation des sols se poursuivent dans les tropiques humides, où les paysages forestiers sont particulièrement impactés. Un aménagement avisé du territoire requiert des informations sur les services écosystémiques produits dans ces paysages ainsi que sur la biodiversité qu'ils abritent. Cette thèse porte sur l'étude de la diversité d'espèces ligneuses et l'évaluation de la production de services écosystémiques (contrôle de l'érosion des sols, et atténuation du changement climatique via stockage de carbone) dans les paysages forestiers du nord de Bornéo à différentes échelles et à l'aide de données mesurées sur le terrain. A l'échelle locale, l'étude de la distribution de la diversité d'espèces ligneuses et de la production de services écosystémiques au sein de la mosaïque paysagère entourant un village traditionnel du nord de Bornéo a souligné le rôle important des forêts naturelles, des forêts post-exploitation et des jachères liées à l'agriculture itinérante sur brûlis dans la production de services et la conservation de la diversité d'espèces ligneuses. A l'échelle régionale, l'analyse des relations spatiales entre carbone et diversité d'espèces ligneuses sur une région du nord de Bornéo encore largement couverte de forêts a montré que le carbone de la biomasse aérienne et la diversité d'espèces ligneuse sont fortement positivement corrélés. Inversement, les corrélations entre carbone du sol et carbone de la biomasse aérienne ou diversité d'espèces ligneuses se sont révélées négatives. Des recommandations en matière de conservation et d'opportunités de développement ont été formulées. A l'échelle globale, l'analyse quantitative de plus de 3600 mesures de pertes de sol collectées par le biais d'une revue systématique de la littérature a révélé que l'érosion des sols dans les tropiques humides est très nettement concentrée dans l'espace (au niveau des éléments de sol nu présents dans le paysage) et dans le temps (par exemple, durant la rotation des cultures). Nous avons de plus confirmé que la mise en œuvre de bonnes pratiques de gestion des sols et de la végétation pouvait permettre jusqu'à 99% de réduction des pertes de sol. Nos travaux permettent d'avoir une meilleure compréhension de la distribution spatiale de la diversité d'espèces ligneuses et de services écosystémiques dans les paysages forestiers tropicaux encore peu étudiés, et contribueront à une approche intégrée de l'aménagement du territoire fondée sur la prise en compte des services écosystémiques, approche qui reste anecdotique dans ces régions.

Mots-clés : Services écosystémiques ; Diversité d'espèces ligneuses ; Stockage de carbone ; Contrôle de l'érosion des sols ; Utilisation des sols ; Changement d'utilisation des sols ; Relation spatiale ; Spatialisation ; Revue systématique

Abstract

While substantial changes of land use and land cover are still occurring in the humid tropics, information about the amount of ecosystem services and the extent of biodiversity respectively provided by, and hosted in tropical forested landscapes is required to help decision makers achieve sound land-use planning. Working at different scales with field measurements, we focused on tree diversity, soil erosion control, and climate change mitigation through carbon storage (in both aboveground biomass and soils). At the local scale, a study of the distribution of tree diversity and ecosystem service production over a mosaic landscape surrounding a traditional village of northern Borneo highlighted the role of natural forests, logged-over forests and land uses related to the swidden agriculture system in producing ecosystem services and hosting tree diversity. At the regional scale, an analysis of the spatial relationships between carbon and tree diversity over a still mostly forested region of northern Borneo showed that aboveground carbon and tree diversity were strongly positively correlated. Conversely, correlations between soil carbon and either aboveground carbon or tree diversity were negative. Suggestions about conservation and development opportunities were made according to these findings. At the global scale, the quantitative analysis of more than 3600 measurements of soil loss compiled through a systematic review of the literature revealed that soil erosion in the humid tropics is dramatically concentrated in space (over landscape elements of bare soil) and time (e.g. during crop rotation). Interestingly, the implementation of sound practices of soil and vegetation management was shown to help reduce erosion by up to 99%. Overall, our work allows a better understanding of the spatial distribution of ecosystem services and tree diversity in tropical forested landscapes, and might prove useful for the purpose of reaching an integrated "ecosystem service based approach" for land-use planning.

Keywords: Ecosystem services; Tree diversity; Carbon storage; Soil erosion control; Land use; Land-use change; Spatial relationship; Spatialization; Systematic review