Linking land-use intensification, plant communities and ecosystem processes in lowland Bolivia

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This research was conducted under the auspices of the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE & RC)

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Geovana Carreño-Rocabado

Thesis
submitted in fulfilment of the requirements for the degree of doctor
at Wageningen University
by the authority of the Rector Magnificus
Prof. Dr. M. J. Kropff,
in the presence of the
Thesis Committee appointed by the Academic Board
to be defended in public
on Monday 13 May 2013
at 4 p.m. in the Aula.

Geovana Carreño-Rocabado
Linking land-use intensification, plant communities, and ecosystem processes in lowland Bolivia,
172 pages

PHD thesis, Wageningen University, Wageningen, NL (2013)
With references, with summaries in English, Spanish and Dutch

ISBN:978-94-6173-533-1

A mis dos grandes amores Jeroen e Inat
A mi familia, mis heroes y grandes luchadores de la vida:
Eduardo, Martha, Crystian, Deysi y Camilita

Dedico también esta tesis de manera especial a los ayudantes de campo, la gente local que conoce tanto de la historia natural y de la biodiversidad. Gracias a ellos decenas de tesis de licenciatura, maestrías y doctorados han sido realizada. Espero que los títulos y el conocimiento que ellos han ayudado a adquirir también resulten en beneficios concretos para ellos y sus familias.

MUCHAS GRACIAS

Abstract

Land-use intensification (LUI) is one of the main global drivers of biodiversity loss with negative impact on ecosystem processes and the services that societies derive from the ecosystems. The effect of LUI on ecosystem processes can be direct through changes in environmental conditions and indirect through changes in plant community. In this dissertation I explored the mechanisms through which land-use intensification affects plant community assembly and ecosystem processes in the Bolivian lowland tropics. Specifically I evaluated: 1) how plant communities respond to LUI via plant *response* traits, 2) the effects of plant communities on decomposition via their *effect* traits, and 3) the relative importance of direct and indirect pathways in explaining LUI effects on ecosystem processes.

I used two gradients of LUI, a long gradient, including five common and contrasting land use types (mature forest, logged forest, secondary forest, agricultural land, and pastureland), and a short gradient of disturbance intensity represented by four experimental treatments in managed forest (unlogged forest, and forest subject to one of three levels of logging intensity and application of silvicultural treatments). Plant community response and effect were evaluated based on species diversity and functional properties. I measured for the most dominant species 12 functional traits and 14 litter traits.

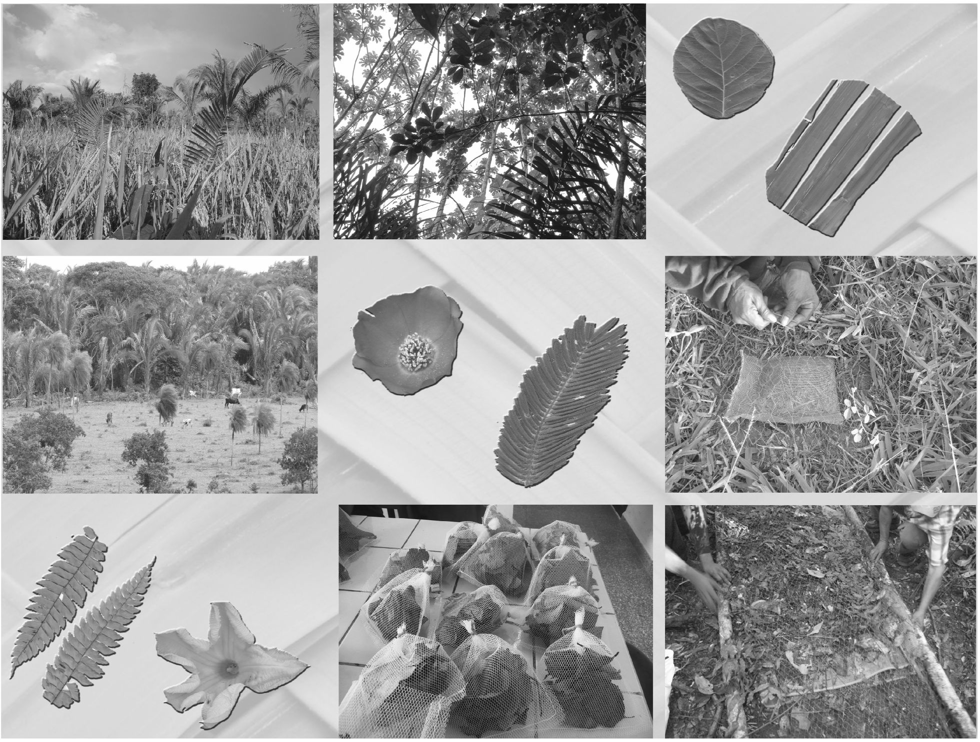
Both gradients of LUI affected functional properties of the plant communities. An increase in LUI shifted plant communities from species characterized by slow growth and slow returns on resource investment (conservative species), toward species characterized by fast growth and fast returns on resources investment (acquisitive species). However, communities with an intermediate position along the LUI gradient (i.e., secondary forests) showed dominance of conservative species mainly due to land use management (abundance of palm species due to frequent burning). Along the short gradient of LUI demographic processes mediated the changes plant communities. With and increase in disturbance caused by logging and silvicultural treatments, there was an increased recruitment of individuals with more acquisitive trait values. Moreover, the response of functional diversity differed between both LUI gradients. Whereas functional diversity decreased along the long LUI gradient, it did not change along the short LUI gradient. Communities with an intermediate position along the long LUI gradient showed higher functional diversity than communities at the extremes of the gradient. Whereas both environmental and management filters drove changes in plant communities along a long LUI gradient, changes along a short LUI gradient were mainly driven by environmental filters.

LUI affected litter decomposition through changes in environmental conditions and through changes in plant communities.

With an increase in LUI decomposition *potential* (measured as mass loss of standard litter incubated in all land use types) decreased. Since soil properties only weakly affected decomposition, other factors were probably the main drivers of the direct effects of LUI on decomposition potential. With increasing LUI the litter decomposability increased due to changes in litter quality produced by plant communities; litter from mature- and logged forest had low decomposability, litter from secondary forest had an intermediate decomposability, and litter from agricultural land and pastureland had high decomposability. Functional traits, such as leaf N concentration, specific leaf area and leaf chlorophyll content, were good and positive predictors of decomposition rate. Although experimentally litter quality explained more variation in decomposition rate across the long LUI gradient (48%) than environmental site characteristics (17%), the *actual* decomposition rate (*in-situ* decomposition of litter community into its own land use type) was site-dependent, and determined by both drivers that partlycompensated each other. Thus, litter with high decomposability (litter from pastureland) incubated in the land use type with low decomposition potential (pastureland plot) had generally a similar decomposition rate as litter with low decomposability (litter from mature forest) incubated in the land use type with high decomposition potential (mature forest plot).

Tropical ecosystems are not only very diverse in species, they are also diverse in their responses to human disturbance. I concluded that LUI has important effects on plant community properties and ecosystem processes. These effects, however, contrast with some predictions of current ecological theory. High intensification of land use does *not necessarily* lead to low plant functional diversity, and less favourable environmental conditions for decomposition do *not necessarily* lead to low decomposition rates. Instead, the multiple factors related with management decisions at local scales cause a large heterogeneity of ecosystem responses. Consequently, depending on the management decisions taken, the negative effect of LUI could be mitigated.

Contents



Agricultural field with rice and palm species, secondary forest with dominance of pioneer species (*Cecropia sp.*), pastureland surrounded by secondary forest. Litter decomposition experiment.

Chapter 1

General Introduction

Land use change as a disturbance factor

Disturbance has been defined as a sudden external factor that removes or changes plant biomass by its partial or total destruction, with effects on biodiversity and ecosystem processes (Grime 2001). Nowadays, disturbance is more related with human activities than with natural processes (MEA 2005b), to such extent that the most important direct driver of disturbance and environmental change in the past 50 years has been land-use change (Díaz et al. 1998, Díaz et al. 2006).

Land-use change is a general term for human modification of Earth's terrestrial surface. It is characterized by the arrangement, activities, and input that people undertake in a certain land-use configuration, to produce, change or maintain its productivity (MEA 2005a). The main impacts of land-use change are conversion of natural habitats for human use and management intensification of human-modified systems (Fig. 1; Foley et al. 2005, Jackson et al. 2009). Land-use change creates several types of human-modified systems (land use types), such as logged-over forest or pasturelands. These land-use changes create at the landscape scale a long gradient of land-use intensification, ranging from fragments of natural systems to highly human-modified systems. These “new systems” now occur in half of the 14 biomes of the world, with each biome experiencing a 29-50% change (MEA 2005a).

In forested areas land-use change is strongly related with deforestation (MEA 2005a). In Bolivia, for instance, deforestation represents 77% of land-cover changes because all newly established agricultural systems have been established preferentially in former forested areas. In the department of Santa Cruz, which has one of the largest forested areas in Bolivia (41% of the department area is covered by forest), deforestation rate has increased dramatically over the last 20 years. One of the most affected eco-regions has been the lowland semi-deciduous tropical moist forest. Between 2001-2004 the deforestation rate in this forest type was 400% higher than 10 years before (Killeen et al. 2007). The main systems of land-use in lowland Bolivia are intensive agriculture, shifting cultivation, cattle ranching, and timber harvesting (U.A.G.R.M and M.N.K.M 2006).

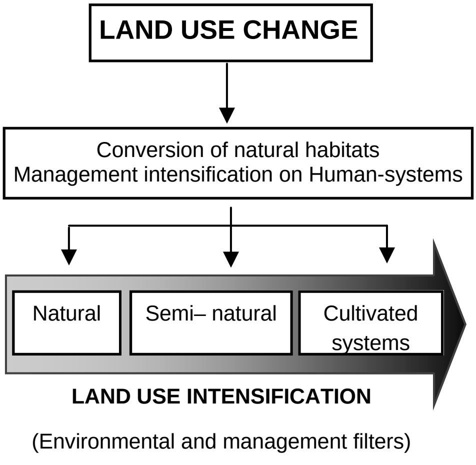


Figure 1. The two main impacts of land use change are conversion of natural habitats for human use and management intensification of human-modified systems. As a consequence of these impacts different land-use types have been created that can be arranged along a gradient of land-use intensification. Along this land-use intensification gradient both environmental and management filters influence plant community assembly.

Shifting cultivation is maybe the oldest agricultural system and consists of clearing a given area by cutting and burning the vegetation followed by a 2-7 years long period of cropping. Thereafter a long fallow period as secondary forest follows, after which the cycle starts again (Fox et al. 2000, Dixon et al. 2002).

The effects of land-use change on biodiversity and ecosystem processes can be evaluated by using a categorical approach (by comparing different land-use types), or by using a continuous approach (by arranging the different land-use types along the gradient of intensification). Both approaches were used in this dissertation.

Considerations for evaluating effects of land-use intensification

Land-use intensification (LUI) is driven by human's necessity to increase *provisioning services,* such as food and fiber. LUI, however, also diminishes the ecosystem's capability to maintain and regulate processes and services essential to maintain life (such as primary production, climatic regulation, or nutrient cycling; MEA 2005c). Therefore, an important challenge for ecologists is to understand through which mechanisms LUI affects ecosystem processes. An increased understanding and improved predictive power can then be used to inform and influence land use decisions. To assess LUI effects, three considerations should be taken into account. First, disturbance caused by LUI has to be placed out of the context of natural disturbance because its intensity not only depends on natural causes but also on human causes (White and Jentsch 2001). For instance, the intensity of natural disturbance is normally quantified in terms of the extraction of biomass or energy from an ecosystem (Grime 2001), the magnitude of disturbance, and recovery time after disturbance, whereas disturbance caused by LUI is also affected by the frequency and duration of management practices (Beare et al. 1997, Garnier et al. 2007, Jackson et al. 2009). To place the different land use types along a gradient of LUI, it is, therefore, necessary to use a multivariate approach that combines all these disturbance aspects.

Second, ecosystem processes (i.e. the flow of energy and materials into an ecosystem, at local scales; Díaz and Cabido 2001, Loreau et al. 2001) depend on both biotic and abiotic components of the ecosystem. Effects of LUI on ecosystem processes can be assessed through changes in abiotic components such as soil properties and climatic variables, or through changes in plant community assembly such as species composition and/or functional diversity (Fig. 2; Chapin et al. 1997, Laliberté and Tylianakis 2012). In this dissertation I focus on plant communities as they form one of the most important elements of the biotic components, and soil properties as part of the abiotic factors. Third, it is important to consider that effects of LUI vary considerably by region, spatial scale, taxonomical group, metric used, and disturbance intensity (Gibson et al. 2011).

How to evaluate LUI effects on plant community assembly

The effects of land-use intensification on plant community assembly can be evaluated

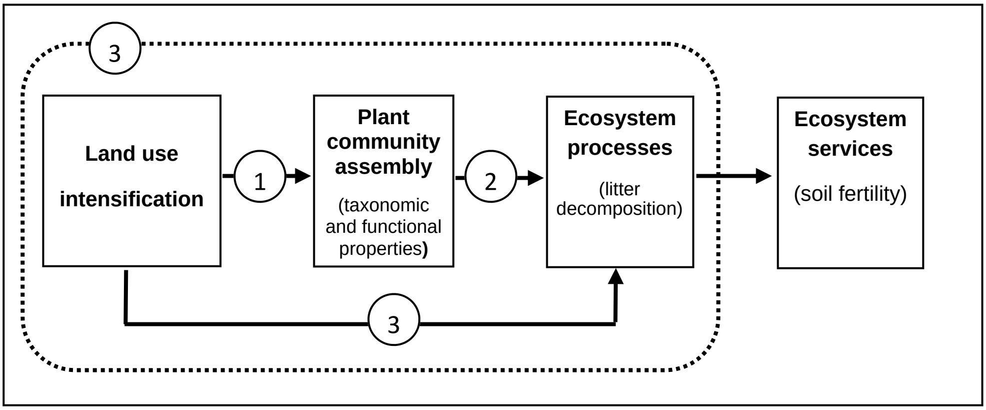


Figure 2. Conceptual framework linking the effects of land-use intensification (LUI) on plant communities, ecosystem processes and services. The numbers indicate the three objectives of this dissertation: objective (1) focuses on how plant communities respond to LUI via plant *response* traits; objective (2) evaluates the effects of plant communities on decomposition via their *effect* traits; and objective (3) analyses the relative importance of direct and indirect (via *dual* traits) pathways in explaining LUI effects on ecosystem processes.

by evaluating changes in community properties, using either a taxonomic or a functional (trait-based) approach (Ackerly and Cornwell 2007, Cornwell and Ackerly 2009, Pakeman et al. 2011). Biodiversity is one important property of communities; it is considered to be a key component to understand community assembly, ecosystem integrity and stability, and ecosystem processes (Balvanera et al. 2006, Chazdon et al. 2009, Hooper et al. 2012). Traditionally, studies that evaluated disturbance effects on biodiversity were focused on taxonomic diversity, with non-consistent responses across disturbed sites (Belaoussoff et al. 2003, Pineda et al. 2005). Studies that have used a trait-based approach show that functional diversity (i.e. the value, range, distribution, and relative abundance of functional traits; Díaz et al. 2007), rather than taxonomic diversity, is a better predictor of ecosystem processes (Hooper et al. 2002, Diaz et al. 2004, Vandewalle et al. 2010). Moreover, recent studies have indicated that not only functional diversity but also functional composition (the state of a trait in the community; Pla et al. 2012) are good indicators of community assembly (Vandewalle et al. 2010). Thus, a more complete understanding of changes in plant community assembly should evaluate both taxonomic and functional properties of the community. In this dissertation I evaluated both taxonomic and functional properties of the community, the last one in terms of functional- diversity and -composition.

Functional traits are morpho-physio-phenological characteristics of an individual that affect its performance and fitness(Violle et al. 2007). A trait-based approach can be used to obtain a mechanistic understanding of community assembly; it is based on environmental constraints (i.e. temperature, disturbances) that filter out certain function-

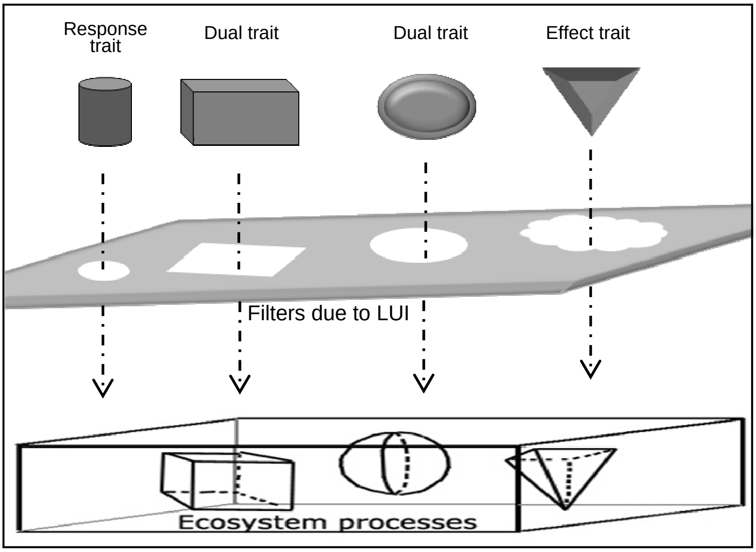


Figure 3. The analogy to evaluate the indirect effects of land-use intensification (LUI) on ecosystem processes scaling up through plant community level. LUI affects community assembly by filtering plant species based on their response-traits (shown with different geometric figures): species and their abundances will be determined by the species success “to pass through” the filters (shown with the dotted arrows). Not all traits are properly filtered out, for instance all traits smaller than a given filter will manage to pass through (triangle; modified from Shipley 2000). A given ecosystem process is determined by effect traits (shown with the empty shapes in the inferior box). Based on a response-and-effect functional framework (c.f. Suding et al. 2008) indirect effects of LUI on ecosystem processes will be determined by traits that have passed through and, that at the same time, affect a given ecosystem process. These traits meet a dual purpose, response and effect (in this dissertation called *dual* traits).

al traits, thus modifying species composition and community functional properties (Weiher et al. 1998, Shipley 2010). These traits are the *response traits.* Once the species assemblage has been modified, it is characterized by certain traits that influence ecosystem functioning. These are *effect traits* because they indicate how species affect ecosystem processes and services (Hooper et al. 2005, Diaz et al. 2011). A trait-based response-and-effect approach (cf. Suding et al. 2008) can be used to predict how land-use intensification influences ecosystem processes through changes in plant community functional properties. In this dissertation, the traits that link environmental constrains to plant community with ecosystem processes are called *dual* traits (Fig. 3). For instance leaf nitrogen concentration can be a *dual* trait, as it enhances carbon assimilation and plant growth at high irradiance (Poorter and Bongers 2006). Species vary in their importance for ecosystem processes. Dominant species make up the bulk of the community biomass, and therefore, they are also responsible for most of the ecosystem fluxes in energy and resources (Grime 1998, Garnier et al. 2004).

Species have been classified along a fast-slow continuum from acquisitive to conservative species (Diaz et al. 2004), based on traits that maximize the acquisition of resources or maximize the conservation of resources (Grime 1974, Wright et al. 2005). This continuum is referred to as the leaf economic spectrum (Wright et al. 2004), or plant economics spectrum (Freschet et al. 2012)In forests the continuum ranges from fast-growing shade-intolerant pioneer tree species with high specific leaf area, high leaf nitrogen concentrations, high photosynthetic - and respiration rates, soft wood and leaves, and short leaf lifespan, to slow-growing shade-tolerant species characterized by the opposite suite of traits (Poorter and Bongers 2006). The conservative-acquisitive trade-off can also broadly be applied to contrasting floras, environments, and growth forms. It can be a good indicator of human disturbance intensity on both species assembly and ecosystem processes (Diaz et al. 2004, Garnier et al. 2007). Additionally, this species resource use strategy has been one of the basis for species domestication. For instance, many annual crops have more acquisitive traits to obtain high productivity in short time (Sponchiado et al. 1989).

Metrics to measure community functional properties

Community functional properties can be described using metrics that quantify the central tendency, the dispersion, and the distribution of functional traits within a species assemblage or community (Weiher et al. 1998, Kraft et al. 2008, Shipley 2010). Community-weighted mean (CWM) describes the central tendency of trait values in the community. It expresses the dominant attribute of the community (Shipley 2010) and its functional composition (Pla et al. 2012). The CWM of effect traits indicates, in line with the mass ratio hypothesis (Grime 1998), how communities affect ecosystem processes (Diaz et al. 2007). Trait dispersion and trait distribution describe the *variation* of trait values in the community; therefore, they represent the functional diversity (Cornwell and Ackerly 2009, Pla et al. 2012). Functional diversity can be described using multivariate indices (e.g., functional richness, functional dispersion and functional evenness; Villeger et al. 2008) that are based on a number of traits, or by single-trait metrics that describe the dispersion and distribution of single-traits. Thus, the coefficient of variation describes the *dispersion* of traits in the community (with as additional advantage that all traits are compared at a similar standardized scale), whereas the kurtosis describes the *distribution* (i.e., peakedness) of traits in the community (Magurran and McGill 2011).

Environmental and management filters as drivers of LUI effects on community plant properties

Changes in community functional properties in response to LUI are mainly driven by environmental- and management constraints (Fig. 4). Environmental factors act at local scales by changing resource availability (i.e., light or water) or abiotic conditions (temperature, relative humidity) that influence plant performance through *response traits.* For instance, higher light availability after logging increases the growth rate of

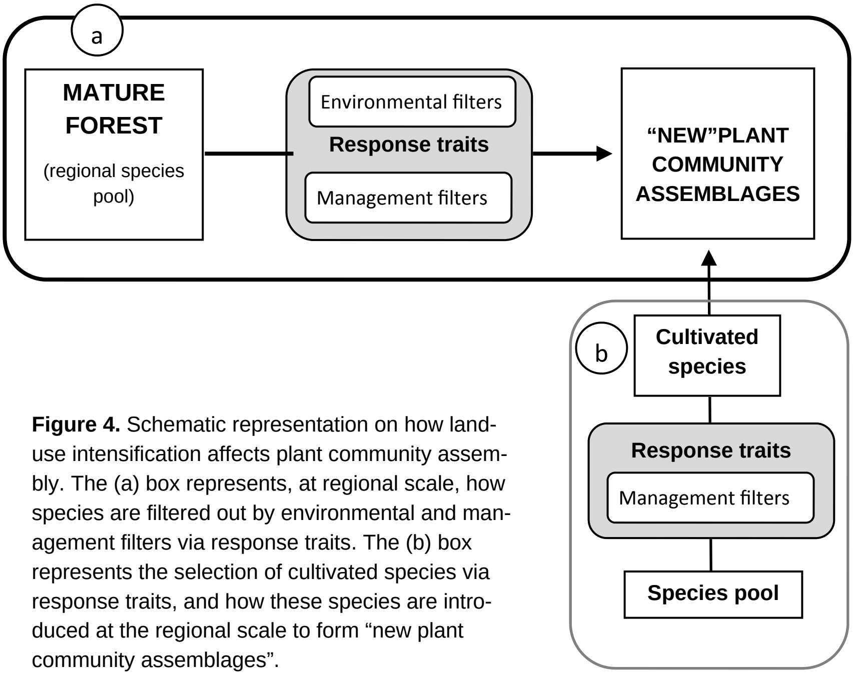


Figure 4. Schematic representation on how land-use intensification affects plant community assembly. The (a) box represents, at regional scale, how species are filtered out by environmental and management filters via response traits. The (b) box represents the selection of cultivated species via response traits, and how these species are introduced at the regional scale to form "new plant community assemblages".

woody pioneer species (Peña-Claros et al. 2008a). In this dissertation these constraints are referred to as *"environmental filters"*. Constraints related to management act at two scales: a) at global scales, as part of the processes of plant domestication that select plant species based on *response traits* such as plant and inflorescence structure (Doebley et al. 2006), and b) at local scales by introducing non-native species into the local species pool and enhancing plant performance of domesticated species at the cost of non-domesticated species. In this dissertation these constraints are referred to as *"management filters"* (Fig. 4).

The relative importance of environmental and management filters in community assembly will depend on the type of system and the gradient of intensification, with positive correlation between intensification and the influence of the management filter. For instance, changes in species assemblages across areas differing in logging intensities may be better explained as the result of environmental filters rather than management filters, while in a comparison with forest plantations the management filters may dominate . Little is known about these differences because most studies on LUI effects have focused on natural assemblages established on agricultural land in different stages of abandonment (Quétier et al. 2007a, Quétier et al. 2007b). Less studies have focused on novel human-assembled plant communities in cultivated systems (but see Vandewalle et al. 2010, Pakeman 2011). Studies that consider both natural and cultivated systems can provide information on the extent of diversity loss on the remaining diversity, and on how cultivated systems function compared to natural systems. For instance, Garnier et al. (2007) analysed the functional response of vegetation comparing various types of land use change occurring in marginal agro-ecosystems. They found that an increase in LUI results in communities dominated by plants with productive, acquisitive leaf traits. Further, since LUI is directly related with social actors, studying both natural and cultivated systems simultaneously makes it easier to link ecological and social components, and to communicate to a non-scientific-community about LUI effects on species assembly and ecosystem processes (Diaz et al. 2011).

LUI effects on decomposition

Decomposition of organic matter is a key process in biogeochemical ecosystem processes. It releases carbon and nutrients from organic material; therefore, it is directly linked to soil fertility (Wood et al. 2009), nutrient uptake by plants (Scherer-Lorenzen 2008), primary production (Bengtsson 1998, Mack and D'Antonio 2003), and CO_2 release (Cornwell et al. 2008). Because of these links, decomposition has often been used as an excellent example to understand and predict the consequences of LUI on ecosystem services (Sommerville et al. 2004, Quétier et al. 2007b). A wide range of decomposition rates among coexisting species is a characteristic found in natural ecosystems worldwide. Litter quality, climate, nutrient availability, communities of soil organisms, and site-specific factors determines either rates or patterns of decay (Lavelle et al. 1993, Björn and McClaugherty 2008). The decomposition capacity of a species has a phylogenetic origin and can be consider an intrinsic trait of the species (Cornwell et al. 2008).

LUI results in land use types that differ largely in environmental conditions and species composition, and therefore, in their litter quality (Foley et al. 2005, Garnier et al. 2007, Jackson et al. 2009). Plant litter quality involves anatomical, mechanical and chemical litter properties. LUI effects on litter decomposition can be either directly, through changes in soil properties or climatic variables, or indirectly through changes in plant community assemblages and their *effects traits* (Fig. 3). To establish the link between community traits and ecosystem processes, it is necessary to determine which litter and fresh leaf traits are better predictors of litter decomposition rate. The positive association between litter quality and its decomposability is related with the content of labile (leaf N and P) and recalcitrant (cellulose, lignin and polyphenols) components. Important predictors of litter decomposability are nitrogen-, phosphorus-, tannins-, and lignin concentration, and C:N, and lignin:N ratios of the litter (Tian et al. 1995, Parsons and Congdon 2008, Bakker et al. 2011, Onoda et al. 2011, Makkonen et al. 2012).

Leaf traits sort plant species along a leaf economic spectrum, which ranges from slow-growing conservative species to fast-growing acquisitive ones (Diaz et al. 2004). This leaf economics spectrum is expected to translate into a spectrum of slow to fast decomposability (Cornelissen 1996, Cornwell et al. 2008, Bakker et al. 2011). If LUI results in a shift in plant community composition from conservative to acquisitive species (Garnier et al. 2007), then it can also be expected that LUI will lead to higher decomposition rates.

Site-specific factors, such as management practices, can also directly affect decomposition. For instance, lower pH in forest compared with agricultural land was positively associated with decomposition rate, and temperature increase after forest clearing for slash-and burn agriculture was positively associated with decomposition (Neher et al. 2003).However, although organic fertilization increased soil nitrogen along land use transitions in grassland systems, there was no effect on litter decomposition (Quétier et al. 2007b). Another important factor affected by LUI is soil biodiversity, which can decrease as a result of cultivation, removal or of plant residues (Beare et al. 1997).

Objectives and thesis outline

In this dissertation I explore the mechanisms through which land-use intensification affects plant community assembly, and ecosystem processes at local scales in the Bolivian lowland tropics. To understand the relationship between the three components (land-use intensification, plant community, and ecosystem processes) I have three general objectives:

1. To evaluate how plant communities respond to land-use intensification via plant *response*-traits (arrow 1 in Fig. 2, chapter 2 and 3)

2. To evaluate the effect of plant communities on ecosystem processes via their *effect*-traits (arrow 2 in Fig. 2, chapter 3 and 4)

3. To assess the relative importance of direct and indirect pathways in explaining LUI effects on ecosystem processes (arrow 3 and box in Fig. 2, chapter 5 and 6).

This dissertation consist of six chapters including the general introduction (chapter 1), four research chapters (chapter 2 to 5) and the general discussion (chapter 6). To evaluate how land-use intensification affects plant communities and ecosystem processes I use five contrasting land use types that represent a long gradient of LUI (mature forest, logged forest, secondary forest, agricultural land, and pastureland; Table 1), which allows to understand the role of management and environmental filters in plant community assembly and changes in ecosystem processes. I also use less contrasting land use types that represent a short gradient in LUI. They consist of mature and logged forest, and include four treatments of logging and silvicultural practices that represent a gradient of disturbance intensity (unlogged, normal, light silviculture, and intensive silviculture; Table 2).

In chapter 2 I use the long gradient of LUI to compare *how functional properties of the plant community change across these land use types* by measuring single-trait metrics of central trait tendency, trait variation, and trait distribution. I also investigate *the complementarity among these metrics to indicate differences among land use types*.

In chapter 3 I use a short LUI gradient to quantify the *effect of different intensities of disturbance due to logging and silvicultural treatments on species diversity, functional composition and functional diversity of tree*

Table 1. Description of five land use types used to evaluate the link between land-use intensification, plant communities, and ecosystem processes in low land Bolivia. The land use types have been arranged from low to high intensification based on five parameter or sources of disturbance: intensity given by the percentage of forest cover removed or remaining biomass; total events of disturbance; frequency given by the number of disturbance events (sowing, logging) per year; magnitude indicated by the percentage of deforested area in 1 km ratio; and, regeneration indicating the period since abandonment in which natural regeneration is allowed to occur. Quantification of each parameter per land use type gives a general estimation of intensification (*= 2 times every 30 years).

Land use type	Description	Parameters used to show differences in land-use intensification				
		Intensity (%)	**Total events of disturbance**	**Frequency (times/ year)**	**Magnitude (%)**	**Regeneration (years)**
Mature forest (MF)	Forest without signs of large scale of disturbance (in the current past)	0	0	0	0	>200
Intensively logged forest (LF)	Managed forest 8 year after logging using reduced-impact logging techniques plus silvicultural practices (commercial trees left as seed trees, post-harvest liberation of future crop trees, soil scarification, post-harvest girdling of non-commercial trees > 40 cm of diameter breast high)	25	2	2(*)	>25	8
Secondary forest (SF)	Fallows of 8 to 12 years of regeneration after shifting cultivation	100	1	1	>75	8-12
Agricultural land (AL)	Crops in polyculture combining 2 or 3 species such as corn, peanut, pineapple, cassava, banana, and rice. The system of slash–and- burn with fallow period of 8 to 12 years	100	8 – 40	8	>75	0
Pastureland (P)	Grasslands with mostly exotic grasses 8-to 30 years old.	100	32 -240	4	>90	0

Table 2. Characteristics of the four disturbance treatments used to evaluated the effect of disturbance intensity on plant community properties. The four treatments represent a gradient in disturbance intensity, from Control (C), Normal (N) and Light silviculture (L-S), to Intensive silviculture (I-S). FCT= future crop trees (i.e., trees of commercial species with 10-50 cm (or 10-70 cm for two species) in dbh that are likely to be harvested in the next cutting cycle). All practices in italics are standard practices that the company carries out before and during logging operations. Harvested trees are trees with >50 cm in dbh (or > 70 cm for two species). (*) only for 14 commercial species, (**) for 14 commercial and 10 potential commercial species. For more details on experimental design see Peña -Claros et al. 2008b.

Management practices/disturbance intensity	**Treatments**				**References**
	C	**N**	**L-S**	**I-S**	
Practices pre-logging					
Pre-harvest inventory of commercial trees	yes	yes	yes	yes	A
Skid trail planning	no	yes	yes	yes	A
Lianas cut on harvestable tree 6 month before logging	no	yes	yes	yes	A
Pre-harvest marking on future crop trees (FCT)>10 cm DBH	no	no	yes*	yes**	A
FCTs liberated from lianas 2-5 month before logging (trees ha^{-1})	0	0	9.2	14.5	C
Practices during logging					
Directional felling	no	yes	yes	yes	A
Trees harvested (ha^{-1})	0	2.3	2.1	4	A
Volume harvested (m^3 ha^{-1}; > 50-70 cm dbh)	0	10.4	9.4	14.4	A
Retention of harvestable trees as seed trees (%)	100	20	20	20	A
Logging impact					
Trees damaged or dead (%)	0	6.8	6.3	10.3	B
Area in logging gaps (%)	0	6.3	5.3	9	A
Area in skid trails (%)	0	4.3	3.9	5.1	A
Practices post-logging					
Girdling of non-commercial trees to liberate FCTs or for stand refinement (trees ha^{-1})	0	0	3.4	4	C
Soil scarification on felling gaps (gaps ha^{-1})	no	no	no	1.1	A

A) Peña-Claros et al. 2008a, Peña-Claros et al. 2008b.
B) Mostacedo et al. 2006
C) IBIF unpublished data

communities. I analyse changes at communtiy level of 12 response traits 8 years after disturbance. I also evaluate *changes in functional diversity based on effect traits related to primary productivity and decomposition rate*.

In chapter 4 I compare three land use types (mature forest, secondary forest, and agricultural fields) to measure the decompostion rate of 23 plant species that are typical for each land use type. Using 14 leaf and litter traits I *evaluate whether individual species traits, and species' position along the leaf economics spectrum are good predictors of decomposition rate*.

In chapter 5 I use the long LUI gradient to evaluate *effects of land-use intensification on litter decomposition rate*. Specifically I asses to what extent differences in environmental site conditions and litter quality along the LUI gradient influence decomposition rate, and how their interaction drives the actual site-specific decomposition of each land use type.

In chapter 6 I discuss and relate the results of the chapters 2-5 and use a path model to *evaluate the relationship between LUI, community functional properties, and decomposition rate* based on four traits that were identified as drivers of decomposition rate at species level in chapter 4.

Study site

This study was conducted in the province of Guarayos, in tropical lowland Bolivia (15^{o} 54'S, 63^{o}11'W; Fig. 5). The Guarayos province covers an area of 27,343 km^2. It is characterized by an annual precipitation of 1,580 mm y^{-1}, with a dry season (<100 mm month) from April to October. The area is partially situated on the Precambrian Brazilian shield (Cochrane 1973) and its soils have a sandy loam texture, neutral pH, total N of 0.32% and total P of 11.23 cmol kg^{-1} (Peña-Claros et al. 2012). The mature forest can be classified as semi-deciduous tropical moist forest (Toledo et al. 2011), with a canopy height of ca 27 m, tree species richness of 59 per ha, density of 368 trees per ha, and basal area of 19.7 m^2 per ha (all for trees >10 cm diameter at breast height [dbh]). About 160 tree species are found in the area, the most common ones (> 10 cm dbh) being *Pseudolmedia laevis* (Moraceae), *Ampelocera ruizii* (Ulmaceae) and *Hirtella triandra* (Chrysobalanacea; Peña-Claros et al. 2012).

About 60% of the province is covered with mature forest, 32% with crops under slash –and- burn agriculture (with fallow period of 7 to 15 years), and 8% with natural and cultivated pasturelands (GMAG 2006). From an economic and social point of view, the most important activities are timber production (88% of Guarayos' forest is used as production forest), agriculture, and livestock production. More than 10 agricultural crop species (e.g., corn, rice, cassava, banana, and peanut) are produced, mostly for local consumption and local markets. Cattle ranching is practiced at medium to large-scale farms, using mainly exotic grasses, such as *Brachiaria brizantha*, as fodder (GMAG 2006). Consequently, for this study I focus on five dominant land use type that represent a long gradient of LUI: mature-, logged-, secondary forest, agricultural land, and pastureland (Table 1). Besides, for logged forest I evaluate a short gradient of LUI based on four treatments with different intensities of logging and of application of silvicultural treat-

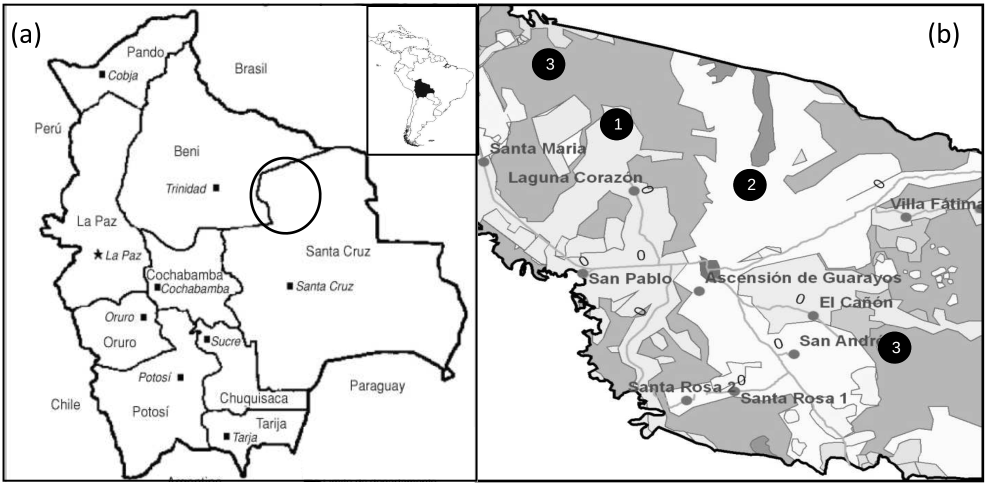


Figure 5. Location of the study sites in the eastern lowlands of Bolivia. (a) Upper right, South America and Bolivia in black; Bolivia and Guarayos province indicated by a circle; (b) land use categories in the central area of Guarayos province. The land categories are 1) small scale agriculture, 2) pastureland, and 3) forest under management. Modified from Plan-International 2007.

ments: control, normal, light silvicultural, and intensive silvicultural (Table 2) .

The framework of this PhD thesis

This PhD thesis was developed in the framework of the project entitled “Functional biodiversity effects on ecosystem processes, ecosystem services and sustainability in the Americas: an interdisciplinary approach” (the DiverSus project), led by Prof. Dr. Sandra Díaz (University of Cordoba, Argentina). The DIVERSUS project focuses on the design and implementation of a new interdisciplinary framework to analyze and compare field studies of land use change in the Americas from the tropics to the tundra . The framework links major land use change trajectories, functional diversity, ecosystem processes and services, and vulnerability-sustainability of the production systems that are based on them. In order to develop an interdisciplinary framework the following objectives are addressed (1) To construct a network of scientists addressing links between land use as a driver of global change, functional diversity shifts, and ecosystem processes and services in the Americas; (2) To develop the first comparison of the effects of land use on functional diversity and to establish how this in turn has the potential to modify ecosystem processes in systems under different degrees of climatic control; (3) To establish links between functional diversity, ecosystem functioning and major ecosystem services perceived by different local and non-local stakeholders; (4) To develop a conceptual framework and a set of empirical tools and recommendations, available to a wide community of scientists, para-scientist and land-managers, to be used as the basis for management decisions aimed to assess and optimize the ecosystem-service value of the land considering the interests of different stakeholders. For more information on the network visit http://www.nucleodiversus.org.

Agricultural field with bananas

Chapter 2

Response of community functional properties to land-use intensification in tropical ecosystems

Geovana Carreño-Rocabado, Marielos Peña-Claros, Frans Bongers, José Chuviña, and Lourens Poorter

Abstract

There is a general consensus that plant biodiversity and ecosystems processes are negatively affected by land-use intensification, but, at the same time there is empirical evidence that there is a large heterogeneity in the responses. This heterogeneity is especially poorly understood in tropical ecosystems that are characterized by a high biodiversity and a high variation in the way people use their land.

We evaluated changes in community functional properties across five common land use types in the tropics (mature forest, logged forest, secondary forest, agricultural land, and pasture land) that represent a long gradient in land use intensification (LUI). We measured for the most dominant species 12 functional response traits that are related to their life history, and acquisition, conservation, and use of resources. We used three single-trait metrics to describe community functional properties, and quantified for each of the functional traits the central tendency with the community abundance-weighted mean, trait variation with the coefficient of variation and trait distribution with the kurtosis.

The community-weighted mean of all 12 traits clearly responded to LUI. We found that an increase in LUI resulted in communities dominated by plants with acquisitive leaf traits such as high specific leaf area and low leaf dry matter content. However surprisingly, secondary forests had more conservative trait values (i.e., lower specific leaf area and higher force to punch) than mature-and logged forest, probably because they were dominated by palms that responded to frequent burning of these secondary forests. Contrary to our predictions, functional diversity (high coefficient of variation and low kurtosis) peaked at intermediate land use intensity (i.e., secondary forest and agricultural land), in line with the intermediate disturbance hypothesis. The high functional diversity of these systems is due to a combination of how response traits (and species) are filtered out by environmental filters and how management filters introduced “exotic – traits” into the local pool. Finally, the three metrics tended to be correlated and to be complementary to each other. These metrics also showed differential sensitivity to environmental and management filters.

Our results confirm the exception to the rule, not in all cases LUI results in either communities with more acquisitive traits nor in communities with less functional diversity. These are promising results because they suggest that it may be possible to ameliorate the negative impacts LUI on plant community functional properties, and hence many ecosystem services, while meeting the provisioning services demands of local people.

Keywords

Land use intensification, community trait properties, functional diversity, plant community, tropical forest, secondary forest, traits dispersion.

Introduction

The deleterious effects of land-use change and its intensification on natural systems has been widely supported by empirical evidence, and highlighted as one of the biggest ecological problems for the maintenance of ecosystem capacity to provide ecosystem services. It is also recognized that land-use intensification (LUI) is driven by human's necessity for food and fiber, which is expected to increase (MEA 2005a). Together, both statements, show the urgency of understanding the extent of LUI effects and propose alternatives to ameliorate them (du Toit et al. 2004). Beyond the general conclusion that LUI negatively affects the ecosystem, some studies have found a high heterogeneity of responses which are explained by differences in regions, spatial scales, taxonomical groups, metrics, and disturbance intensities (Mayfield et al. 2005, Mayfield et al. 2006, Garnier et al. 2007, Laliberté et al. 2010, Gibson et al. 2011). This heterogeneity is even larger for tropical ecosystems, where the biodiversity is high and the social heterogeneity, en consequently the way how land is used, is large as well (Chazdon 2003, Stork et al. 2009).

A more direct mechanism to link LUI effects with ecosystem functioning is through changes in plant community assembly (Díaz and Cabido 1997, Diaz et al. 2004). Some meta-analysis have concluded that increases in LUI reduces plant functional redundancy and response diversity in temperate and tropical ecosystems (Laliberté et al. 2010), whereas other studies did not find clear changes in plant diversity across agricultural land with different intensities of management (Flynn et al. 2009), or good level of conservation of trait states in deforested areas (Mayfield et al. 2006). Such discrepancies can be explained by the scale of evaluation, the range of intensification and the type of land use considered (Fédoroff et al. 2005, Jackson et al. 2009).

Land use intensification may be understood as a disturbance factor that alters the plant community in a different way than natural disturbance does. Disturbance caused by LUI is the result of a combination of elements such as land use type, the amount of biomass lost, the frequency and duration of management practices, the magnitude of disturbance, and the recovery time after disturbance (Garnier et al. 2007, Jackson et al. 2009). Species response to LUI will be driven by change in environmental factors (i.e. resource availability and biotic interactions), and by management practices such as introduction of non-native species (and functional traits), suppression of native species through weed control, or increase in crop production by increasing soil fertility (Altieri 2004). Besides, LUI creates at the landscape-level a mosaic of natural and cultivated systems whose synergistic effects have also an impact on community assembly (White and Jentsch 2001).

Most studies on LUI effects have focused on natural assemblages established on agricultural land in different stages of abandonment (Quétier et al. 2007a, Quétier et al. 2007b) without considering crop species (see Flynn et al. 2009). Less studies have focused on novel human-assembled plant communities in cultivated systems (but see Vandewalle et al. 2010, Pakeman 2011a). Studies that consider both natural and cultivated systems cannot only provide information on the extent of diversity loss, but also on the remaining diversity and how cultivated systems function compared to natural systems.

Trait-based approach for natural and human-modified plant communities

A trait-based approach can be used to obtain a mechanistic understanding of plant community assembly; it is based on environmental constraints (i.e., temperature, disturbances) that filter out certain functional traits, thus modifying species composition and community functional properties (Weiher et al. 1998, Shipley 2010). Such a trait-based approach has been used to assess 1) the effect of environmental gradients on species assembly of natural communities (Kraft et al. 2008), 2) the assembly of novel communities in response to human-induced disturbances (Mayfield et al. 2006, Quétier et al. 2007b, Mayfield et al. 2010), and 3) the consequences for ecosystem processes and services (Hooper et al. 2005, Diaz et al. 2011). Changes in *response traits* along environmental gradient are related with assembly processes and changes in *effect traits* are related with effects on ecosystem processes (sensu Lavorel and Garnier 2002).

Plant functional traits not only influence community assembly in natural communities, they also play a key role in the assembly of human-modified communities. At the species level some functional traits such as plant and inflorescence structure, seed casing, seed colour, or plant height have been selected during the process of plant domestication (Doebley et al. 2006). Later, modern breeding techniques selected for desirable traits those conferring drought tolerance (e.g., root length), resistance to herbivory (leaf toughness), or high productivity (leaf nitrogen concentration; Sponchiado et al. 1989). At the community level these selected traits have become dominant either in monocultural systems, or in polycultural systems that combine different crops. It is important to consider that the structure and species composition of polycultures has been designed to mimic the trait-structure of successional vegetation based on enhancing resource partition among species (Ewel 1986). Consequently, agricultural systems can conserve some functional diversity, despite the fact that they are heavily managed.

Measuring community-functional properties: functional composition and functional diversity

Community- functional properties can be described using metrics that quantify the central tendency, the dispersion and the distribution of functional traits within a species assemblage or community (Fig. 1; Weiher et al. 1998, Kraft et al. 2008, Shipley 2010). The community-weighted mean (CWM) describes the central tendency of trait values in the community. It expresses the dominant attribute of the community, or the trait value of an average individual in the community (Shipley 2010). Since CWM represents the state of a trait in the community, it is a metric of functional composition (Pla et al. 2012) and has been shown to be a good indicator of changes in leaf economic variation at the community level (Wright et al. 2004). The CWM of response traits indicates

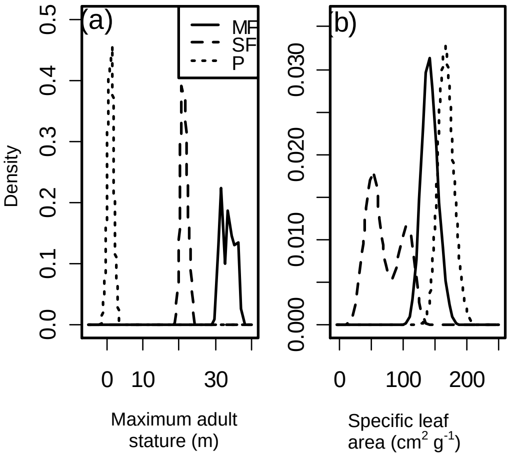


Figure 1. Examples of community functional properties comparing mature forest (MF), secondary forest (SF) and pastureland (P). The position of each curve on the x axis is related to the community weighted mean (CWM), the width of each curve is related to the coefficient of variation and the peakedness of the distribution with the kurtosis. Figure (a) shows a clear separation of CWM of maximum adult stature between the three land use types, going from small to tall individuals as land-use intensification decreases. The same pattern is observed for kurtosis, but trait variation of mature forest is higher. Figure (b) shows that the CWM, trait variance and trait distribution of specific leaf area are similar for mature forest and pasture, but secondary forest shows more conservative trait values (i.e., a low SLA) with more variation and less dominance.

what traits are filtered by the environment or land use intensification, and can inform about the underlying assembly processes (e.g., Lebrija-Trejos et al. 2010, Shipley 2010). The CWM of effect traits indicates, in line with the mass ratio hypothesis (Grime 1998), how communities affect ecosystem processes (Diaz et al. 2007).

Trait dispersion and trait distribution describe the *variation* of trait values in the community, and represent therefore the functional diversity (Cornwell and Ackerly 2009, Pla et al. 2012). Functional diversity has often been described using multivariate indices (e.g., functional richness and functional dispersion) that are based on a number of traits. These multi-trait indices are useful and elegant to summarize multivariate trait variation in a single number, but they are also complex to understand because it is not clear 1) what traits drive the variation in the multivariate index, and 2) whether the relevant traits that respond strongest to the environmental filters or that have the strongest effect on ecosystem functioning have been considered.

To better understand the underlying drivers of functional diversity, a single-trait approach can provide important complementary insights. The coefficient of variation describes the *dispersion* of traits in the community (with as additional advantage that all traits are compared at a similar standardized scale), whereas the kurtosis describes the *distribution* (i.e., peakedness) of traits in the community (Magurran and McGill 2011). Metrics of traits- dispersion and distribution have been used to test community assembly rules and functional diversity for undisturbed (Kraft et al. 2008, Cornwell and Ackerly 2009) and human-disturbed systems (Mayfield et al. 2010). Low traits dispersion indicates little trait variation and high importance of environmental filtering, while high values indicate high traits variation and high importance of competitive displacement (Magurran and McGill 2011).

We evaluated the influence of land use intensification (LUI) on community functional properties using a single-trait approach. We compared natural and human-assembled communities from five important and widespread land use types in the tropics; three dominated by natural vegetation (mature-, logged and secondary forest), and two cultivated systems (agricultural land and pastureland, see details in Table 1, chapter 1). For each land use type we measured the traits of the dominant species. We selected 12 functional response traits that are important for plant growth and survival (Poorter and Bongers 2006) and that have been under human selection (Kendal et al. 2012; Table 1, chapter 1). For each community, its functional properties were described in terms of the community-weighted mean (as an indicator of the central tendency of trait values in the community), and the coefficient of variation (CV) and kurtosis (K) (as indicators of trait variation and trait distribution, and hence, functional diversity).

Our first objective was to evaluate how the five land use types differ along a gradient of land use intensification in their functional composition (CWM) and the functional diversity (CV and K). We hypothesized a stronger separation in functional composition between natural systems and cultivated systems than within each of these groups. As a general trend we expect that the leaf economic spectrum will run from slow (i.e. high SLA) to quick returns on investment of nutrients and dry mass in leaves (i.e. low leaf dry matter content) as land use is intensified, but this trend may be less clear within cultivated systems. Low levels of disturbance in mature forest will enhance slow-growing species with conservative traits, whereas in logged- and secondary forest an increase in disturbance will enhance establishment of fast-growing species with more acquisitive traits. For cultivated systems we expect a mix of acquisitive and conservative traits due to a combination of fast-growing species with high productivity per unit leaf area and slow-growing species with resistance to drought that are selected for food provision (Abbo et al. 2012). We expect that functional diversity is reduced as land use is intensified, thus coefficient of variation and kurtosis will gradually change from high CV and low K in mature forest to low CV and high K in pastureland (Kraft et al. 2008, Flynn et al. 2009, Laliberté and Legendre 2010). Our second objective was to examine how the three metrics that describe community functional properties are related to each other, and how this relationship is influenced by land use intensification. We expect that the three metrics will provide complementary information on the plant community functional properties. These metrics thus may not be necessarily highly correlated, they even may be orthogonal. However, not all traits will respond in the same way and metrics of traits with large differences along the gradient of land use intensification may be better correlated than metrics of traits with small differences.

Materials and methods

Study site

This study was conducted in the province of Guarayos, in tropical lowland Bolivia (15^o 54'S, 63^o11'W). Annual precipitation is 1,580 mm y^{-1}, with a dry season (<100 mm month) from April to October. The area is situated on the Precambrian Brazilian shield (Cochrane

1973) and its soils have a sandy loam texture, neutral pH, total N of 0.32% and total P of 11.23 cmol kg^{-1}(Peña-Claros et al. 2012). The vegetation can be classified as semi-deciduous tropical moist forest (Toledo et al. 2011a), with a canopy height of ca 27 m, tree species richness of 59 per ha, density of 368 trees per ha, and basal area of 19.7 m^2/ha (all for trees >10 cm diameter at breast height [dbh]). About 160 tree species are found in the area, the most common ones (> 10 cm dbh) being *Pseudolmedia laevis* (Moraceae), *Ampelocera ruizii* (Ulmaceae) and *Hirtella triandra* (Chrysobalanacea; Peña -Claros et al. 2012).

The Guarayos province covers an area of 27,343 km^2. About 60% of this area is covered with mature forest, 32% with crops under slash–and- burn agriculture (with fallow period of 7 to 15 years), and 8% with natural and cultivated pasturelands (GMAG 2006). From an economic and social point of view, the most important activities are timber production (88% of Guarayos' forest is used as timber production forest), agriculture, and livestock production. More than 10 agricultural crop species (e.g., corn, rice, cassava, banana, and peanut) are produced, mostly for subsistence and local markets. Cattle ranching is practiced at medium to large scale farms, using mainly exotic grasses, such as *Brachiaria brizantha* , as fodder (GMAG 2006).

Plot design and data collection

Land use intensification gradient: We selected the five most important land use types in the region, which cover the whole gradient of land use intensification. Their management intensity was qualitatively assessed based on five parameters (Lambin et al. 2003, Jackson et al. 2009): management intensity (in terms of pre-disturbance biomass loss), frequency of management practices, duration of management practices, magnitude of disturbance (percentage of undisturbed forest in a radius of 1 km) and time since disturbance (time for natural regeneration). Based on their average scores, the land use types could be ranked from low to high land use intensification in the following order: mature forest, logged forest, secondary forest, agricultural land and pastureland (See details in table 1, chapter 1).

Plot design: To describe species composition and quantify their relative abundances, eight plots were established per land use type. For mature- and logged forest data came from the 1-ha plots of the Long-Term Silvicultural Research Program of IBIF in the La Chonta forest concession (15°47'S, 62°55'W), 30 km east of the city of Ascención de Guarayos (for details see Peña-Claros et al. 2008b). Within each plot, all trees ≥10 cm dbh were identified and their dbh measured. Data used for this study come from the control and the intensity logged plots, and corresponds to measurements made 8 years after logging. For secondary forest, agricultural land and pastureland 0.5 ha plots (50 x100 m) were established around the village Ascención de Guarayos. Secondary forest plots were the result of slash-and-burn agriculture, and ranged from 8 to 12 years in age since abandonment. All trees ≥10 cm dbh were sampled in the whole plot, and trees ≥ 3 cm dbh were sampled in four 10 x 10 m sub-plots in each corner of the main plot. Agricultural land consisted of swidden agriculture in which a patch of (mature or secondary) forest is slashed and burned. Agricultural fields are typically ≈ 0.5 ha large, and are managed using intercropping systems or polyculture systems with seasonal crop rotation during 5 to 7 years, after which the area is abandoned for agriculture and it is allowed to fallow for a period of 7-15 years. Pasturelands were at least 10 ha in size and 20 years old. They consisted of a mixture of native and non-native grasses, and were grazed 1 to 2 weeks continuously 3 to 5 times per year by cattle and/or sheep. In the agricultural and pasturelands all plants > 2 cm in height were sampled using the point intersection method. Within each plot, 100 points were sampled, by randomly establishing 100-m long diagonal transects, and measuring 10 sample points (i.e., at every 10 m) along each transect. At each sampling point, the intersected individual(s) was/were identified, and its/their height was/were measured.

<u>Traits</u>: We selected 12 response traits associated with the response of plants to LUI based on the resource acquisition of species (Aarssen and Schamp 2002). These functional traits not only show sensitivity of species to changes in resources availability, but also reflect the effect of management on the community trait structure (Table 1, chapter 1). Maximum adult stature is strongly related with species ability to compete for light (Westoby 1998), and is also closely associated with life forms (Falster et al. 2011). Wood density is important for stem construction costs, stability, and hydraulic conductivity, and is therefore a good indicator of species growth rate (Van Gelder et al. 2006, Poorter et al. 2010). Leaf traits such as specific leaf area, thickness, dry matter content, chlorophyll content, nitrogen- and phosphorus concentration reflect species ability to acquire, use, and conserve resources (Poorter and Bongers 2006, Bakker et al. 2011), whereas the force to punch and to tear leaves is closely associated with leaf defence against herbivores and biophysical hazards, and hence, with leaf longevity (Onoda et al. 2011). These traits are also related to land use intensification because crop selection for food production is often based on the species' ability to grow fast and/or to resist stress, or to have less chemical and physical defences against herbivores but higher palatability (Lin et al. 2011, Abbo et al. 2012).

For this study the leaf was defined as the sum of the blade (leaflets plus rachis for compound leaves), plus the petiole (collar region and sheath in case of grass species) plus the stipules. Functional traits for species belonging to mature forest and logged forest come from Rozendaal et al. (2006), Poorter (2008), Bakker *et al.* (2011) and Carreño-Rocabado et al. (2012). The same protocols were used for tree species belonging to secondary forest. For palm species, crops and grasses, 3-5 healthy and mature individuals per species and 3-5 young, fully expanded leaves were selected that did not have epiphylls or herbivore damage. Because palms have very large leaves, we selected a subsample of each leaf (3-5 folioles, 3 sections of rachis, and petiole), measured the leaf traits, and weighed the subsample and the whole leaf. For each leaf, the leaf thickness was measured with a micrometer, toughness was determined with a penetrometer (mass necessary to penetrate a punch-head of 7 mm^2

though the lamina) and chlorophyll content was measured with a SPAD meter (Minolta SPAD 502 Chlorophyll Meter, Spectrum Technologies Inc., Plainfield, IL, USA). Leaves were scanned with a flatbed scanner and analysed for their leaf area with ImageJ (Abramoff et al. 2004). Leaf fresh mass was measured after leaf hydration in a refrigerator for 12 hours. Leaves were oven-dried for 48 h at 70 °C and then weighed. Trait values were averaged per individual, and individual trait values were averaged per species. For further details on the trait measurements, see Rozendaal et al. (2006).

With these measurements we calculated the following morphological traits: specific leaf area (SLA; leaf area/leaf dry mass, $cm^2\ g^1$), leaf dry matter content (LDMC; leaf dry mass/leaf fresh mass, $g\ g^{-1}$), leaf toughness (LTo; force/head area, $N\ cm^{-2}$), leaf chlorophyll content per unit leaf area (Chl = 139 × SPAD-1129, $\mu mol\ m^{-2}$; Anten and Hirose 1999). The nitrogen- (N_{mass}, *% DM*) and phosphorus concentration per leaf dry mass (P_{mass}, *% DM*) were determined for a pooled leaf plus petiole sample per species. Maximum adult stature (H_{max}, *m*) for species belonging to secondary forest was calculated for each species using the stem diameter of the third-thickest individual and a forest-wide regression equation for the region that relates height to stem thickness (Poorter et al. 2006). For crop and grass species H_{max} was calculated as an average of the ten tallest individual registered in all our plots. For species belonging to secondary forest stem samples (bark, cambium and heartwood) were taken for 3-5 individuals per species (10-30 cm dbh) at 0.5-1m stem height. The volume of the stem sample was measured using the water displacement method, after which samples were oven-dried for at least 48 h at 70°C and weighed, wood density was calculated as the dry mass over the fresh volume.

<u>*Trait coverage:*</u> Traits were collected for the most dominant species in each community, as they indicate how the community in general responds to the environment, and as they have the strongest impact on ecosystem processes. For the forest communities dominant species were selected based on their relative contribution to the total community basal area, as basal area scales closely with tree biomass and cover. For agricultural land and pastures communities dominant species were selected based on a dominance index which combines species cover (number of dots with presence of x species) and the height of each individual plant. We had functional trait data for 88 to 100% of the dominance per plot, depending on the trait considered (Table S1).

<u>*Metrics describing the community functional property:*</u> Using the non-transformed trait values we calculated three metrics of community functional property: the community weighted mean (CWM), coefficient of variation (CV) and kurtosis (K) of trait distribution (Kraft et al. 2008). The CWM or community-aggregated traits expresses the dominant trait value in the community or the trait value of an average individual in the community (Shipley 2010). Its sensitivity to land use changes has been documented for different organisms (Vandewalle et al. 2010). Functional diversity has often been described using complex multivariate metrics, based on a number of traits. Three of these metrics

(functional richness, evenness and divergence) describe independent and complementary components of functional diversity (Villeger et al. 2008, Mouchet et al. 2010). Conceptually, in a single-trait approach, a metric that quantifies trait dispersion and -distribution can be used to assess these functional diversity's components. High values of dispersion and low values of distribution indicate high trait variation and high functional diversity (Magurran and McGill 2011). Moreover, because CV expresses the trait variation in percentages, it allows to use untransformed data and compare among traits without the influence of different units and scales. In order to preserve trait variation and distribution of the real trait values, we calculated CV and K by assigning the corresponding species-trait value to each individual in the community (i.e., we weighed the species trait value by species abundance). To be consistent, we also weighed the CWM by abundance. However, because trait cover was calculated for the dominant species based on their basal area/dominance index, we evaluated the correlation per land use type and functional trait between CWM basal area/dominance index weighted and abundance weighted. Fifty out of 53 correlation were statistically significant with r between 0.8 and 1, only three correlations had r ≤ 0.35 (Table S2).

Statistical analysis

Differences in CWM, CV and K among land use types, were tested for each trait using an ANOVA, or a Kruskal-Wallis test when the data were not normally distributed. Seven trait-metric combinations were square-root transformed to meet with normality and homogeneity of variances. Multiple comparisons were done between pairs of land use types with a LSD-test (in case of a normal distribution), and a Wilcoxon rank-sum test (in case of a non-normal distribution). We did not do Bonferroni corrections in the pairwise Wilcoxon test in order to reduce the Error type II when differences between land use types were tested. Relationship amongst the three aspects of community functional properties were analysed with Pearson correlations, pooling all land use types (N=40 plots). Association between aspects of functional properties and land use intensification were done with PCA using three metrics (CWM, CV, and K), 10 functional traits (wood density was excluded because no such data were available for the herbaceous species in agricultural land and pastureland; force to tear was excluded because it is closely related with force to punch), and the five land use types. A series of PCA analyses was done to zoom in into differences among less contrasting land use types by progressively excluding plots belonging to the most disturbed system. To evaluate the complementarity and sensitivity to land use intensification of the three metrics, independent PCAs were done for each metric and the five land use types. All PCAs were based on correlation matrices. Analyses of variance, Wilcoxon rank-sum tests, and correlations were done using R 2.12.1 (R Development Core Team 2011), whereas PCA analyses were done using CANOCO 5.0 (Ter Braak and Šmilauer 1998)

Results

Differences in functional composition and diversity

__Community functional composition.__ For all 12 evaluated traits, the CWM differed amongst land use types (one-way ANOVA or Kruskal-Wallis test, p< 0.001, Table 1). Post-hoc tests revealed three different groups: mature- and logged forest (which were statistically similar for nine out of 12 traits), secondary forest, and cultivated systems (agricultural land and pastureland, which were statistically similar for 6 out of 11 traits). Mature- and logged forest had, compared to other land use types, the highest adult stature, P concentration, wood density, and leaf toughness (force to punch and - tear). Within this forest group, the logged forest had higher specific leaf area, lower leaf dry matter content and thinner leaves than mature forest.

Secondary forest differed significantly from the other land use types in six traits (Table 1). Secondary forest had the largest leaf area, high leaf chlorophyll content, intermediate adult stature and the lowest specific leaf area and leaf N concentration. Agricultural land and pastureland had the highest specific leaf area, force to punch , and leaf slenderness and the lowest leaf dry matter content. Within these cultivated systems, agricultural land had higher adult stature, leaf thickness, leaf chlorophyll content and leaf N and P concentration than pastureland (Table 1, Fig. 2).

__Trait variation and distribution__. Trait variation within each community was described with the coefficient of variation (CV). For the 480 plot-trait combinations (i.e., 40 plots x 12 traits), CV averaged 38% and ranged between 14 and 690%. The CV differed significantly (ANOVA or Kruskal-Wallis test p ≤ 0.001, Table 1) amongst land use types for all functional traits but leaf chlorophyll content and leaf N concentration. In general, CV tended to be highest for secondary forest and agricultural land, intermediate for mature and logged forest, and lowest for pasture land (with the exception of CV of Hmax, which was highest in pasture land, Fig. 2, Table 1).

Trait distribution within each community was described with the kurtosis. The kurtosis of all evaluated functional traits differed significantly amongst land use types (ANOVA p ≤ 0.03 or Kruskal-Wallis test p< 0.005, Table 1). Mature forest, logged forest and pastureland had the highest kurtosis for leaf area, and force to punch and -tear; cultivated systems had the highest kurtosis for adult stature; and pastureland had the highest kurtosis for the other seven traits. Secondary forest had in general the lowest kurtosis (Table 1, Fig. 2).

Association among the three aspects of community traits properties

The three aspects of community functional properties were often significantly correlated with each other; CWM versus K for 10 traits, CWM versus CV for 6 traits, and CV versus K for 8 traits (Table 2). Most of these significant correlations were negative (19 out of 24). Four traits (adult stature, wood density, leaf area, and force to punch) were significantly correlated for all three pairwise correlations (Table 2).

Table 1. Variation in three elements of community functional properties along a long gradient of land use intensification in tropical systems (ranked in increasing order of intensification): mature forest (MF), logged forest (LF), secondary forest (SF), agricultural land (AL), and pastureland (P). The average per land use type (n=8) of the community abundance-weighted mean, coefficient of variation, and kurtosis are presented. The traits are maximum adult stature (H_{max}), wood density (WD), leaf area (La), leaf slenderness (Lsl), specific leaf area (SLA), leaf thickness (LTh), leaf dry matter content (LDMC), force to tear (Ft), force to punch (Fp), leaf chlorophyll (LCh), N and P concentration per unit leaf mass (N_{mass}, P_{mass}). P-values from ANOVA and Kruskal-Wallis tests area given. Means accompanied by a different letter are significantly different at p <0.05 given by multiple comparisons of LSD-tests without Bonferroni correction and Wilcoxon Rank-Sum test (Mann-Whitney U).

Traits	**COMMUNITY WEIGHTED MEAN**										
	p-value	***MF***		***LF***		***SF***		***AL***		***PA***	
H_{max}	*<0.001*	28.59	a	28.45	a	21	b	3.48	c	0.8	d
WD	*<0.001*	0.58	a	0.57	a	0.46	b				
LA	*<0.001*	971.93	b	1304	b	24980	a	2537	b	701.48	b
LSl	*<0.001*	2.25	b	2.16	b	2.26	b	15.36	a	13.3	a
SLA	*<0.001*	137.87	c	149.65	b	97.1	d	172.61	a	169.18	a
LTh	*<0.001*	0.2	c	0.19	d	0.29	a	0.31	a	0.22	b
LDMC	*<0.001*	0.36	a	0.34	b	0.37	a	0.29	c	0.28	c
Ft	*<0.001*	11.46	b	11.71	b	67.2	a	39.38	a	56.6	a
Fp	*<0.001*	42.54	b	41.6	b	96	a	63.33	a	71.49	a
LCh	*<0.001*	5.5	b	5.39	bc	6.45	a	4.84	c	3.28	d
N_{mass}	*<0.001*	2.08	bc	2.15	b	1.9	c	2.38	a	0.97	d
P_{mass}	*<0.001*	0.18	a	0.19	a	0.15	b	0.17	a	0.14	b
	COEFFICIENT OF VARIATION (%)										
H_{max}	*<0.001*	31.63	bc	32.99	b	28.6	c	188	a	177.7	a
WD	*0.0013*	19.04	b	20.89	b	27.9	a				
LA	*<0.001*	690.05	a	613.21	a	184	b	452	a	173	b
LSl	*<0.001*	25.54	c	24.52	c	47.8	b	88.7	a	22.5	c
SLA	*<0.001*	25.06	b	29.7	b	52.9	a	27.86	b	10.34	c
LTh	*<0.001*	21.13	b	17.48	b	29.92	a	47.26	a	6.32	c
LDMC	*<0.001*	15.33	a	17.93	a	14.26	a	19.69	a	4.15	b
Ft	*<0.001*	115.14	a	115.96	a	130.3	a	91.65	a	20.37	b
Fp	*<0.001*	47.11	b	48.23	b	97.9	a	80.6	a	17.9	c
LCh	*0.15*	19.34		19.29		27.8		25.19		19.12	
N_{mass}	*0.133*	23.08		26.05		30.03		27.1		33.1	
P_{mass}	*<0.001*	35	b	36.8	b	51.9	a	17.2	c	10.19	d
	KURTOSIS										
H_{max}	*<0.001*	2.56	c	2.28	c	3.26	b	12	a	32.23	a
WD	*0.038*	5.82	a	6	a	2.78	b				
LA	*<0.001*	86.02	a	97.45	a	4.42	c	36.85	b	39.15	ab
LSl	*<0.001*	4.82	b	5.14	b	2.81	c	2.71	c	27.74	a
SLA	*<0.001*	9.84	b	6.59	bc	4.29	c	5.78	c	38.6	a
LTh	*<0.001*	5.48	b	5.8	b	1.9	c	14.98	ab	33.25	a
LDMC	*0.002*	4.81	b	4.37	b	4.23	b	4.69	b	32.97	a
Ft	*<0.001*	68.87	a	73.52	a	4.31	c	21.98	b	35.47	ab
Fp	*0.003*	54.64	a	42.19	ab	4.54	c	26.64	b	37.49	ab
LCh	*<0.001*	5.35	b	4.65	b	2.35	c	8.77	ab	31.08	a
N_{mass}	*0.005*	4.58	b	3.48	b	3.06	b	5.05	b	34.51	a
P_{mass}	*<0.001*	4.58	b	3.87	b	5.33	b	8.42	b	40.25	a

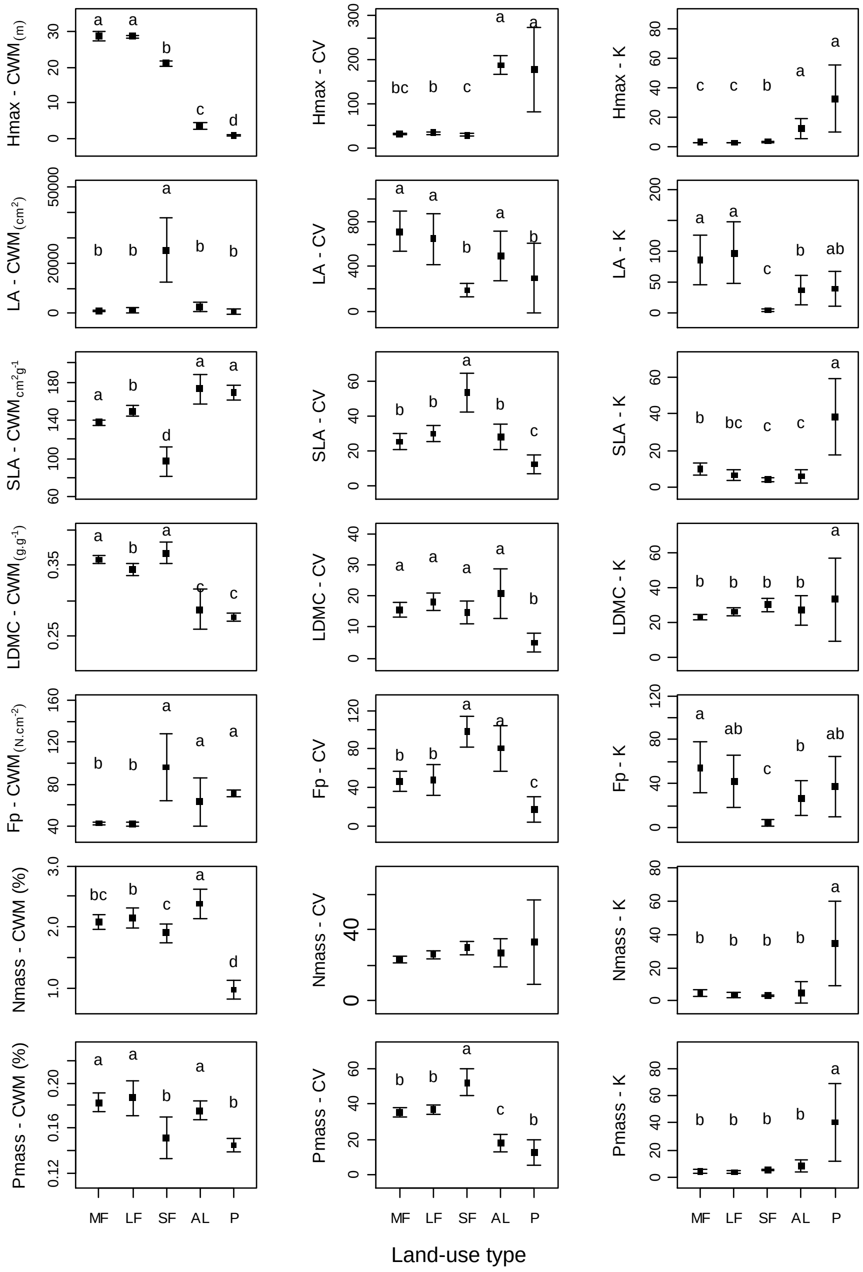


Figure 2. Differences of three elements of community functional properties along a long gradient of land use intensification: mature forest (MF), logged forest (LF), secondary forest (SF), agricultural land (AL) and pastureland (P). The community weighted mean (CWM), coefficient of variation (CV) and kurtosis (K) of 7 functional traits are shown. The traits are maximum adult stature (H_{max}), leaf area (La) , specific leaf area (SLA), leaf dry matter content (LDMC), force to punch (Fp), N and P concentration per unit leaf mass (N_{mass}, P_{mass}). Means and confidence intervals are shown (n=8). Bars accompanied by a different letter are significantly different at p<0.05 (LSD-tests without Bonferroni correction and Wilcoxon Rank-Sum test (Mann-Whitney U)).

Table 2. Correlations between community weighted mean (CWM), coefficient of variation (CV) and kurtosis of five land use types for 12 functional traits, in lowland Bolivia. The traits are maximum adult stature (H_{max}), wood density (WD), leaf area (La), leaf slenderness (Lsl), specific leaf area (SLA), leaf thickness (LTh), leaf dry matter content (LDMC), Force to tear (Ft), force to punch (Fp), leaf chlorophyll (LCh), N and P concentration per unit leaf mass (N_{mass}, P_{mass}). ** $p < 0.01$, * $p < 0.05$, n= 40 plots, but 24 plots for WD.

Pair of metrics	H_{max}	WD	N_{mass}	P_{mass}	LDMC	Fp	SLA	LCh	La	LTh	LSl	Ft
CWM-kurtosis	-0.58**	0.47*	-0.73**	-0.47**	-0.37*	-0.45**	0.25	-0.71**	-0.45**	-0.07	0.33*	-0.51**
CWM-CV	-0.79**	-0.76**	-0.07	0.12	-0.05	0.33*	-0.69**	0.17	-0.4*	0.71**	0.15	-0.3
CV-kurtosis	0.79**	-0.69**	-0.25	-0.56**	-0.54**	-0.44**	-0.60**	-0.09	0.75**	-0.02	-0.40*	0.02

Association between metrics of community functional properties and land use intensity

Associations between the three aspects of community functional properties, and the land use types were analysed with a PCA (Fig. 3). The first two PCA axes explained 60% of the variation (Fig. 3a). The first axis separates the forested systems (mature-, logged- and secondary forest) at the left, from the cultivated systems (agricultural land, pastureland) at the right, with pastureland occupying the extreme right side of the axis. The second axis separates forested systems into mature- and logged forest at the bottom and secondary forest, at the top.

The first axis was strongly positively associated with kurtosis (k.) of all traits, and negatively associated with the community weighted mean (cwm.) and coefficient of variation (cv.; Fig. 3b) of some traits. The natural systems at the left were characterized by high CWM of N_{mass}, LDMC, and H_{max}, high CV of P_{mass} and LDMC. The cultivated systems at the right were characterized by high kurtosis of eight traits, high CV in H_{max}, and high CWM of leaf slenderness and SLA. The second axis was associated with all three metrics. The high forests at the bottom were characterized by high CWM of H_{max} and P_{mass}, high CV and kurtosis of leaf area, and high kurtosis of force to punch. The secondary forests at the top were characterized by high CWM of force to punch, leaf thickness, and leaf area (Fig. 3b).

To zoom in on more subtle differences along the gradient of land use intensification we removed step-by–step the plots with the most intense land use type. We only show the PCAs that provided extra information. Only considering forest systems high kurtosis is associated with mature forest (Fig. S1). A PCA with only mature- and logged forest showed that logged forest tended to have high CV and more acquisitive species (Fig. S2). A PCA with only agricultural land and pastureland showed that CWM and K separate those systems (Fig. S3), with a high CWM for agricultural land and high K for pastureland.

To explore how each metric was influenced by land use type we did a separate PCA per metric. The PCA with the CWM explained 75% of the variation with the first two axes (Fig. S4a). This PCA clearly separat-

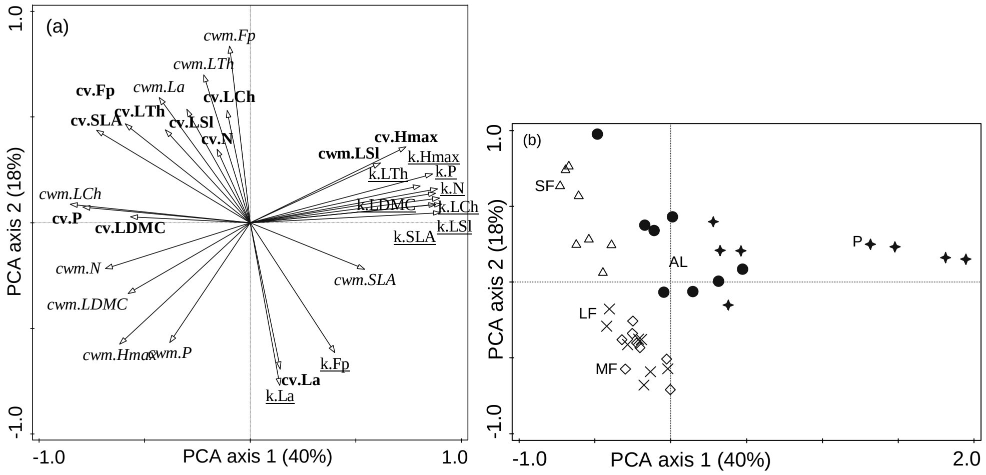


Figure 3. Principal-component analysis of metrics of community functional properties: community weighted mean (cwm), coefficient of variation (cv) and kurtosis (k) of 10 functional traits (traits abbreviation are found in Table S1, wood density and force to punch were not included because not all land use type had woody species into their composition and the trait was highly correlated with force to tear). (a) Loading metrics of community functional properties in the first (explained variation is 40 %) and the second axis (explained variation is 18 %). (b) Loading plots of land use types on the first and second axes: mature forest (diamond, MF), logged forest (x mark, LF), secondary forest (triangle, SF), agricultural land (circle, AL) and pastureland (star, P).

ed each land use type, although it made a less clear distinction between mature- and logged forest. The PCA based on CV (60% variation explained) some plots of pastureland were not distinct from mature forest and agriculture land (Fig. S4b). The PCA based on kurtosis (90% variation explained) mainly separated pastureland from the other land use types (Fig. S4c). All axes from PCAs with a single metric ordered the plots along a gradient of land use intensification, which was also obtained with the PCA that included all three metrics (Fig. S4).

Discussion

We evaluated changes in plant community functional properties along a gradient of land use intensification. Using five land use types we analysed the central tendency (CWM), the variation (coefficient of variation) and the distribution (kurtosis) of single traits within a community. Here we discuss our main results of differences amongst land use types, correlations between the three metrics, association and/or complementarity between metrics along a gradient of land use intensification, and implications for conservation and the provision of ecosystem services.

Functional composition amongst land use types

We measured differences in functional composition and leaf economic variation amongst land use types (at local spatial scale) via community abundance-weighted mean of 12 functional traits (Wright et al. 2004, Pla et al. 2012) . These functional traits clearly responded to LUI (Table 1). Our results partially confirm our hypotheses and results of earlier studies that leaf traits involved in the acquisition-conservation trade-off (Grime 2001), such as specific leaf area, leaf dry matter content, and leaf nitrogen and phosphorus concentration, are sensitive enough to detect functional responses to LUI (Garnier et al. 2007, Laliberté et al. 2010). At the community level an increase in LUI results in dominance of plants with acquisitive leaf traits such as high SLA and low LDMC, however other acquisitive leaf traits such as N_{mass} and P_{mass} do not show a clear directional pattern. We also hypothesized that CWM clearly separates our natural systems from cultivated systems, going from conservative to acquisitive CWM. This hypothesis was supported for some traits when forest systems (mature- and logged- but not secondary forest) were compared against cultivated systems: mature- and logged forest indeed had more conservative traits (higher LDMC, lower SLA) than cultivated systems (Table 1). However, similarities in leaf area, leaf chlorophyll content, and leaf P concentration between these two contrasting systems did not confirm our predictions. These similarities may result from the use of multiple cropping systems or intercropping (growing of two or more crops simultaneously on the same field) in the sampled agricultural land plots. Intercropping to some extent resembles natural systems where resource use is complementary rather than competitive (Coolman and Hoyt 1993, Denevan et al. 1995). For example, solar radiation can be more fully used by differentiation in maximum photosynthesis rate, different pathways of carbon fixation or by manipulating leaf area and leaf density through combining maximum adult stature, shade tolerance of leaf angle (Ewel 1986). Polyculture systems may combine annual species with more less acquisitive traits (pineapple or cassava) and seasonal and fast-growing species with more acquisitive traits (rice, maize and peanuts; cf. Ewel 1999).

In contrast to our expectations within forest systems, only CWM of three leaf traits (specific leaf area, leaf dry matter content and leaf thickness; Table 1) changed towards fast-growing species with more acquisitive traits in response to intensification (logging and silvicultural treatments). The lack of response in the other nine traits either can be attributable to a short recovery time after the disturbance (8 years) or to the fact that heterogeneity amongst plots is large, and that we did not consider the relative change with respect to the initial state of the plots (but see Carreño-Rocabado et al. 2012 for this approach). Such lacking of effects of logging were reported earlier: functional diversity of leaf area and maximum adult stature did not respond to logging disturbance in temperate forest 50 years after logging (Mayfield et al. 2010). Surprisingly, secondary forests had more conservative trait values (i.e., lower SLA and higher force to punch and tear) than mature-and logged forest (Table 1, Fig. 2). This contrasts with the results of an earlier study that showed that early secondary forests tend to be dominated by fast-growing pioneer species with acquisitive traits (Chazdon et al. 2007), and may be explained by the high abundance of palm species *(Astrocaryum murumuru, Attalea speciosa* and *Attalea phalerata)* in our secondary forests, which might have become abundant due to repeated burning in the region. Their large, strong and heavy leaves have led to conservative CWM values (Fig. 2). These abundant tough-leaved palms in secondary forest and the thick-leaved pineapple in cultivated systems also may explain the high CWM for force to punch and force to tear of these land use types (Table 1).

Within cultivated systems, we expected consistent differences between agricultural land and pastureland because the obvious differences in species composition with peanut (*Arachis hypogea*), banana (*Musa sp.*), cassava (*Manihot esculenta*), and rice (*Oriza sativa*) being abundant for agricultural land and an exotic grass “braquiarion” (*Brachiaria brizantha*) being dominant in pastureland. They indeed differed in maximum adult stature, leaf- thickness, chlorophyll content and N and P concentration, but in six traits we did not find significant differences (Table 1).

Whether or not the leaf economic spectrum is related to LUI largely depends on the geographic proximity among the land use types and on the gradient length. At a large spatial scale (across Europe) Garnier and coworkers (2007) showed that high LUI leads to a shift in community dominance toward plants with more acquisitive leaf traits. In our local scale study, however, we found that the systems with intermediate levels of intensification (i.e., secondary forest) may have less acquisitive traits than systems with low levels of intensification. At small scale, additional factors as proximity to mature forest or plot size may overrule the general LUI effects on diversity maintenance (Ewel 1999). Also land use type itself has an effect here (Jackson et al. 2009). For instance, large -scale oil palm plantations and soybeans fields are both intensively managed land use types, but whereas the oil palm has very conservative traits the soybeans has very acquisitive traits.

Functional diversity amongst land use types: Trait variation and trait distribution

We described functional diversity in terms of trait variance, measured here as the coefficient of trait variation (CV) and the trait distribution measured as the kurtosis (K; Shipley 2010, Magurran and McGill 2011). We hypothesized that K increased and CV decreased when land use is intensified, because intensified systems are dominated by low diversity of domesticated plants specialized in the provision of food, fodder, and fiber (MEA 2005a). Contrary to our predictions our results showed that systems with intermediate position along LUI (secondary forest and agricultural land) had higher trait variation (high CV) and more even trait distribution (low kurtosis) than systems at the extremes of the gradient (Table 1, Fig. 2). In our study, we only found a reduction of functional diversity in the most extreme of the gradient of LUI (i.e, pastureland). Although as a general conclusion early studies did find that functional diversity decreases with increase in LUI (see Laliberté et al. 2010, Pakeman 2011a), they also showed that at local scales and dependent on the effect group functional diversity can increases along LUI (Laliberté et al. 2010). However, differences among different studies in functional diversity metrics, the large heterogeneity of land use types, range of land use intensification, and the range of variations in the environmental factors makes a general conclusion about the effects of land use intensification difficult (Wright et al. 2005). High trait variance in secondary forest can be both the result of environmental heterogeneity (which leads to differences in plant strategies; Lebrija-Trejos et al. 2010) and the consequence of traditional management practices that enrich or enhance secondary forest species with subsistence and commercial value (Adjers et al. 1995, Peña-Claros et al. 2002). These results are also in agreement with the intermediate disturbance hypothesis (Bongers et al. 2009), which states that at an intermediate level of disturbance species richness and hence, functional diversity, is higher, because of the coexistence of early successional acquisitive species with late-successional conservative ones. The large trait variation in agricultural land can be attributed to the intercropping systems, in which more than one species of crop are cultivated with different strategies of resource acquisition (Coolman and Hoyt 1993). Slash-and-burn techniques thus maintain species and functional diversity (Altieri 2004, Chazdon et al. 2009). High kurtosis in pastureland suggests that dominant non-native grass species suppress plant diversity and that a high level of disturbance due to management (like continuous grazing by domesticated livestock) does not permit the establishment of other species (Quétier et al. 2007b).

The use of single-trait metrics to evaluate LUI effects on community functional properties can facilitate to communicate the effects of LUI to stakeholders (Diaz et al. 2011) because they are intuitively more straightforward to understand than multiple-trait indices (Casanoves et al. 2008).

Association between the three aspects of community functional properties

Community functional properties have been described with parameters that measure the average values, variance and trait distribution within a community (Kraft et al. 2008). Although it is assumed that each parameter shows a different aspect of community functional properties, how they behave and how much they are associated among different plant communities has still not been assessed. Our comparison among the three metrics calculated for 12 functional traits showed that they tend to be partly correlated (24 out of 36 correlations were significant; Table 2) and partly independent. We hypothesized and found that large differences in CWM among land use types also result in large differences in CV and kurtosis. This result is consistent with other studies that evaluated a LUI gradient, and showed that some traits are more sensitive in detecting changes than others (Mayfield et al. 2006, Garnier et al. 2007). A clear example was adult stature, for which all three metrics were correlated (Table 2). A reduction in adult stature and increase in K with LUI indicates that management filters are at play, as humans prefer small species because of their easy manipulation (Abbo et al. 2012) and because only small species are able to grow and complete their life cycle within the time intervals between disturbance events (Cornelissen et al. 2003).

Half of our traits showed negatively correlations between CV and K, and the rest of traits showed positive or no correlation. We believe that high correlation between metrics (e.g, CWM-CV or CWM-kurtosis) does not mean redundancy in the capacity to detect LUI effects on functional traits properties, but it does mean complementarity (Ricotta and Moretti 2011). Thus, whereas one metric is sensitive to species response to environmental filters, another metric is sensitive to management filters. This is also supported by the fact that using only one metric is not enough to distinguish among the five land use types (Fig. S4), whereas a global PCA using all three metrics (Fig. 3) separated the three forest systems based on CWM and CV, and the cultivated systems based on kurtosis.

Environmental filters and management filters drive community assembly along LUI

Responses of community assembly to environmental filters (abiotic and biotic factor) have been largely documented for natural communities (Cornwell et al. 2006, Ackerly and Cornwell 2007), and recently also for human-modified communities (Mayfield et al. 2010). The growing literature of LUI effects on plant communities starts to show the importance of management filters (sometimes called “extinction filters”) to explain change in functional trait diversity (i.e. from forested land to pastoral land; Mayfield et al. 2010). However, few studies have evaluated the relative importance of these two filters for changes in community assembly with LUI. Besides, little has been discussed regarding the direct effects of management filters on community functional properties by introduction of non-native species (and their traits) into the local species pool.

Changes in community functional properties due to LUI are driven by both environmental and management filters (Jackson et al. 2009, Diaz et al. 2011). Our results suggest that, although both filters act at the same time along the LUI gradient, environmental filters are more important at low levels of LUI, whereas management filters are more important at high levels of intensification. Within our forest systems, an increase in LUI resulted in an increase in CV and a decrease in kurtosis (Fig. S1, S2), indicating larger trait variation. This larger trait variation may be the result of the larger environmental heterogeneity, created by logging gaps in the logged forest plots (Peña-Claros et al. 2008a), which allows a diverse range of species to coexist. The high CWM SLA and low leaf dry matter content in logged forest compared with mature forest also suggests that increased light availability drives response in the tree community (Castro et al. 2010, Carreño-Rocabado et al. 2012).

Responses to both environmental- and management filters are found in secondary forest. It is well-documented that environmental filter play a strong role in community assembly during secondary succession (Breugel et al. 2006, Chazdon et al. 2007, Lohbeck et al. 2012) whereas the strong negative association between CV and kurtosis in secondary forest is probably the result of enrichment of secondary forest with commercial and/or fruiting tree species (Ivan Avi, pers. comm.). Besides, the occurrence of more conservative traits in secondary forest (i.e. low CWM of specific leaf area; Fig. S1) was explained by the high abundance of palm species. This high abundance is probably due to the use of fire for land clearing and wildfires and the fact that palms are able to survive fire events.

Our results suggest a differential sensitivity of different metrics for different filters. However, this suggestion is based on our assumption that the initial state of all our plots was mature forest, in which case differences in metrics among land-use type would reflect effects of LUI. All three metrics were able to distinguish differential cultivated systems (Fig. S3). High CV in our agricultural systems and high kurtosis for pastureland indicate a strong influence of management filters as a) an increase in trait variation is likely to be due to the introduction of exotic species and possible different functional traits into a regional species pool, and b) a peakedness in trait distribution is related with increasing yields from cultivation through practices, such as weed control or soil fertilization. In both processes response traits are determining the more suitable species for domestication and also the “native” species (weed in agricultural systems) that survive and persist and form part of the agricultural fields (i.e. weeds). Consequently, our results suggest that the three metrics have a large potential to detect the effect size of different types of filters (i.e., environmental and management filters), but further research is needed to test their consistency across other land use types.

Conclusions

There is a general consensus that plant biodiversity and ecosystems processes are negatively affected by land-use intensification, but at the same time there is empirical evidence that there is a large heterogeneity in the responses. As it is expected, we found that, along a long gradient of land-use intensification in the tropics, community assembly is driven by environmental- as well as management filters. However, against our expectations, systems with high land use intensification and consequently highly influenced by management filter had as well a high functional diversity (i.e. agriculture land). As LUI increases the plant community tends to shift towards smaller plants with shorter lifespan and more acquisitive leaf traits. Secondary forests tended to be more conservative than expected, probably because of the large abundance of palms in these frequently burned systems. Functional diversity did not decline with LUI, but peaked at intermediate land use intensity (i.e., secondary forest and agriculture land), in line with the intermediate disturbance hypothesis and with the introduction of non-native species (traits) into the local species pool. We used three simple and straightforward metrics (CWM, CV, and K) to describe community functional properties and have shown that they are very well able to functionally distinguishing the different land use types. Overall, our results confirm the exception to the rule, not in all cases LUI results in communities with more acquisitive traits, and it neither results in less functional diversity.

Acknowledgements

This research is part of the Long-term Silvicultural Research Program of IBIF, and we would like to thank all IBIF's personal for the data, field work, and for monitoring the permanent plots. We thank the personnel of La Chonta Agroindustria Forestal for permission to work in the concession and for assistance with plot establishment and monitoring. We thank as well the farmers and owners of pasturelands to allowing us to work in their areas and for helping us during the field work (Asencia Uranoi, Choco Mercado, Cornelio Candawiri, Diberato Irapiri, Francisco Bae, Francisco Borins, Herlan Pesoa, Hernan Ativena, Ignacio Egnar, Ivan Avi, Jesus Paz Añez, Jesus Uracoi, Juan Pesoa, Mario Sockock, Matha Severiche, Pascual Iraipi, and Victor Peredo). This study was partly funded by the DiverSus project through Inter-American Institute for Global Change Research (IAI) CRN 2015 and SGP-CRA2015, which were supported by the US National Science Foundation grants GEO-0452325 and GEO-1138881. GCR was funded by DiverSus and by a fellowship from NUFFIC. We appreciate the incredible assistance of field workers, especially Angel Mendez, Ricardo Mendez , and Jorge Irapiri.

Appendices

Table S1. Traits descriptions, ecological and management significance as response traits, and trait coverage per land use type. Trait coverage of dominant species was calculated with basal area and with a dominance index which combines species cover and the height of each individual plant.

Traits (Abbreviations; unit)	Ecological significance	Significance for management	References	Trait coverage				
				MF	LF	SF	AL	P
Maximum adult stature (H_{max}; m)	Competitive ability for light capture, lifespan, survival, resistance to disturbance	Indicator of frequency of disturbance	Mayfield et al. 2010 Poorter et al. 2006 Westoby 1998	100	100	100	100	100
Wood Density (WD; g cm^{-3})	Carbon investment, growth rate, photosynthesis, mortality rate, water potential, attack by pathogens and fungi, accumulation of standing biomass, decomposition rate	Selected for construction	Poorter 2008	88	87	38*	-	-
Leaf area (LA; cm^2)	Competitive ability for light capture	Selected for construction	Bazzaz and Pickett 1980	95	97	93	89	88
Leaf slenderness index (LSI)	Heterogeneity of microhabitats for decomposition	Indicator of frequency of disturbance	Scherer-Lorenzen 2008	95	97	93	89	88
Specific Leaf Area (SLA; cm^2 gr^{-1})	Leaf life span, light capture, leaf construction, net photosynthetic capacity, potential relative growth rate Net primary productivity, herbivory, decomposition rate	Crop production, palatability to herbivores, sensitivity to plagues	Falster et al. 2011 Lavorel and Garnier 2002 Evans and Poorter 2001 Westoby 1998 Elger and Willby 2003	95	97	92	89	88
Leaf Thickness (LTh; mm)	Light absorption per unit leaf mass, photosynthetic capacity per unit area, light acclimation, herbivory, decomposition rate	Crop production, palatability to herbivores, sensitivity to plagues	Rozendaal et al. 2006 Agusti et al. 1994 Klich 2000	95	97	92	89	88
Leaf Dry Matter Content (LDMC; g g^{-1})	Growth rate, leaf life span, leaf construction cost, herbivory, decomposition rate	Crop production, palatability to herbivores, sensitivity to plagues	Lavorel and Garnier 2002 Westoby 1998 Bakker et al. 2011	95	97	92	89	88
Leaf chlorophyll (LCh; μmol cm^2)	Light capture, light plasticity , net primary productivity, herbivore, decomposition rate	Crop production, palatability to herbivores, sensitivity to plagues	Poorter 2000 Rozendaal et al. 2006 Bakker et al. 2011 Sims and Pearcy 1989	95	97	92	89	88
N concentration content per unit leaf mass (N_{mass}; % DM)	Photosynthetic carbon gain, net primary productivity, herbivory, decomposition rate	Crop production, palatability to herbivores, sensitivity to plagues	Bakker et al. 2011 Poorter and Evans 1998	94	96	89	85	87
P concentration content per unit leaf mass (P_{mass}; % DM)	Photosynthetic carbon gain, net primary productivity, herbivory, decomposition rate	Crop production, palatability to herbivores, sensitivity to plagues	Poorter and Evans 1998	94	96	89	85	87

Table S2. Pearson correlation between the abundance-weighted CWM- and the basal area/ importance index weighted CWM- for all community functional traits for each of the five land use types. All correlation were statistically significant $p < 0.05$, but not leaf thickness in mature forest (ns). Traits abbreviation are found in Table S1.

Land use type	**H_{max}**	**WD**	**N_{mass}**	**P_{mass}**	**LDMC**	**SLA**	**LCh**	**La**	**LTh**	**LSI**	**Fp**
Mature forest	0.98	0.78	0.91	0.68	0.81	0.77	0.86	0.75	0.12 ^{ns}	0.83	0.89
Logged forest	-0.05	0.80	0.95	0.96	0.96	0.83	0.96	0.98	0.34	0.94	0.71
Secondary forest	0.62	0.75	0.96	0.92	0.91	0.92	0.65	0.84	0.95	0.80	0.84
Agricultural land	0.95	-	0.92	0.95	0.96	0.98	0.95	0.98	1.00	0.96	0.99
Pastureland	0.89	-	1.00	0.99	0.96	0.98	0.88	0.98	0.94	0.92	0.96

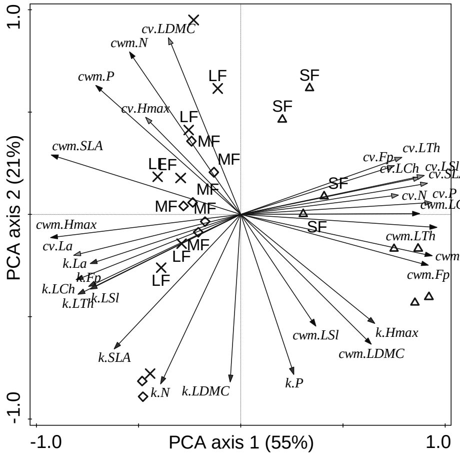


Figure S1. Principal-component analysis of metrics of community functional properties and land use types. Functional properties are community weighted mean (cwm), coefficient of variation (cv) and kurtosis (k) of 10 functional traits (traits abbreviation are found in Table S1, wood density and force to punch were not included because not all land use type had woody species into their composition and the trait was highly correlated with force to tear). Land use types are mature forest (diamond, MF), logged forest (x mark, LF), and secondary forest (triangle, SF).

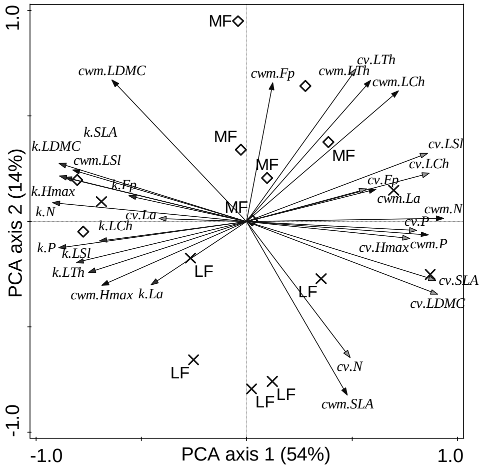


Figure S2. Principal-component analysis of metrics of community functional properties and mature forest and logged forest. Functional properties are community weighted mean (cwm), coefficient of variation (cv) and kurtosis (k) of 10 functional traits (traits abbreviation are found in Table S1, wood density and force to punch were not included because not all land use type had woody species into their composition and the trait was highly correlated with force to tear). Land use types are mature forest (diamond, MF) and logged forest (x mark, LF).

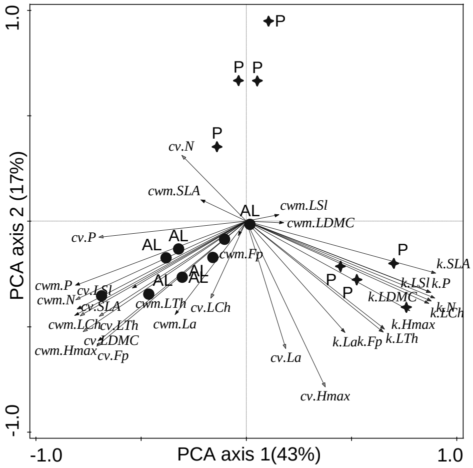


Figure S3. Principal-component analysis of metrics of community functional properties and cultivated systems as land use types. Functional properties are community weighted mean (cwm), coefficient of variation (cv) and kurtosis (k) of 10 functional traits (traits abbreviation are found in Table S1, wood density and force to punch were not included because not all land use type had woody species into their composition and the trait was highly correlated with force to tear). Land use types are agricultural land (circle, AL) and pastureland (star, P).

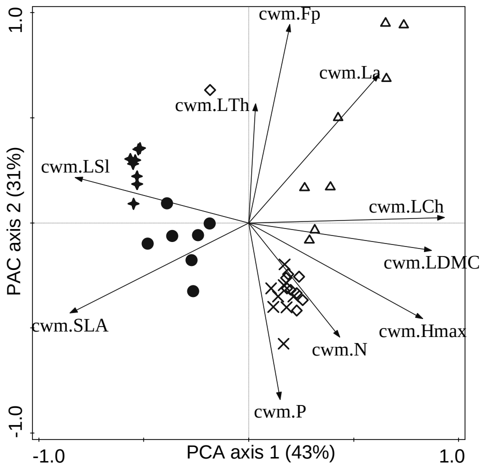


Figure S4. Principal-component analysis of five land use types and community weighted mean (cwm) of 10 functional traits (traits abbreviation are found in Table S1, wood density and force to punch were not included because not all land use type had woody species into their composition and the trait was highly correlated with force to tear). Land use type are mature forest (diamond), logged forest (x mark), secondary forest (triangle), agricultural land (circle) and pastureland (star).

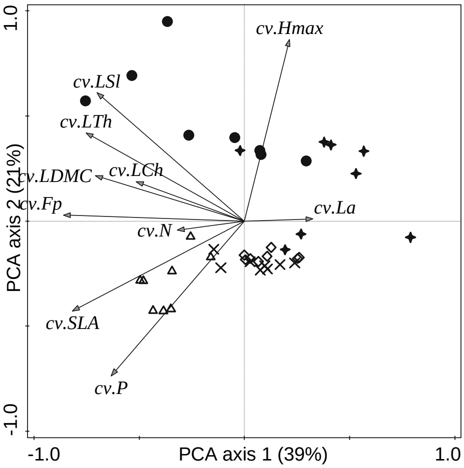


Figure S5. Principal-component analysis of five land use types and coefficient of variation (cv) of 10 functional traits (traits abbreviation are found in Table S1, wood density and force to punch were not included because not all land use type had woody species into their composition and the trait was highly correlated with force to tear). Land use type are mature forest (diamond), logged forest (x mark), secondary forest (triangle), agricultural land (circle) and pastureland (star).

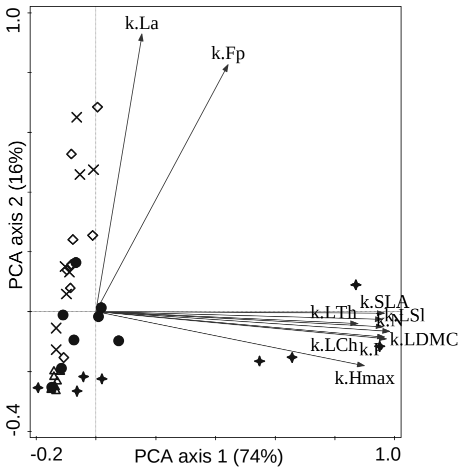


Figure S6. Principal-component analysis of five land use types and kurtosis (k) of 10 functional traits (traits abbreviation are found in Table S1, wood density and force to punch were not included because not all land use type had woody species into their composition and the trait was highly correlated with force to tear). Land use type are mature forest (diamond), logged forest (x mark), secondary forest (triangle), agricultural land (circle) and pastureland (star).

Cavanillesia hylogeiton growing in IBIF permanent plots

Chapter 3

Effects of disturbance intensity on species- and functional diversity in a tropical forest

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Published in Journal of Ecology 100(6): 1453-1463,2012

Abstract

Disturbances are widespread and may affect community assembly, species composition, (functional) diversity, and hence, ecosystem processes. It remains still unclear to what extent disturbance-mediated species changes scale up to changes in community functional properties, especially for species-rich tropical forests.

A large-scale field experiment was performed in which the dynamics of 15000 stems > 10 cm in diameter was monitored for 8 years in 44 one-ha forest plots. Twelve functional -effect and -response traits were measured for the most dominant tree species. The effects of different intensities of disturbance caused by logging and silvicultural treatments on the species- and functional diversity of a Bolivian tropical forest community were evaluated, along with how these changes were driven by underlying demographic processes.

Disturbance treatments did not affect species diversity or functional diversity indices based on multiple traits related to primary productivity and decomposition rate. This result suggests that species richness is conserved and trait *variation* is maintained, which can buffer the community against environmental change.

In contrast, disturbance intensity affected the *average* plant trait values in the community (the community-weighted mean) for seven out of 12 traits evaluated. At high disturbance intensity, the community had a lower wood density of stem and branches, lower leaf toughness and dry matter content, but higher specific leaf area and leaf N- and P concentration, with the value of these traits changing on average 6% over the 8-year period. The functional spectrum of the community changed, therefore, from “slow”, conservative, shade-tolerant species towards “fast”, acquisitive, light-demanding species. These functional changes in *mean* trait values may enhance primary productivity and decomposition rate in the short term.

Temporal changes in community functional properties were mainly driven by recruitment, and little by mortality or survival.

Synthesis. Moderate levels of (logging) disturbance neither affected species diversity nor functional diversity per-se in the 8-year period after logging. Disturbance did, however, change the functional community composition towards “fast” species with more acquisitive traits, thus potentially fuelling primary productivity and nutrient- and carbon cycling. In conclusion, tropical forest management may contribute to conserving functional biodiversity of trees while providing forest resources.

Keywords

Bolivia, demography, determinants of plant community diversity and structure, disturbance, functional diversity, functional traits, logging, tropical forest

Introduction

Land-use change is currently one of the most important drivers of biodiversity loss and changes in ecosystem processes and services (MEA 2005b) and its effects depend strongly on the type, severity, frequency and timing of disturbance (White and Jentsch 2001, Foley et al. 2005). Nowhere is land use change occurring more rapidly than in the tropics (MEA 2005c), where it often comes at the expense of the area of tropical forests. Sustainable forest management has been proposed as an alternative to other types of land use, because it provides forest resources while potentially maintaining biodiversity (Putz et al. 2001). However, an increase in logging intensity and silvicultural practices is often needed to balance economic, social and ecological needs (Putz *et al.* 2001), and such an increased disturbance may adversely affect biodiversity, community assembly, and ecosystem processes (Gibson and Sodhi 2011, but see Putz et al. 2012).

The effects of disturbance can be described using taxonomic and functional diversity (Connell 1978, MEA 2005b, Isbell et al. 2011). Functional diversity has been defined as the value, range, and relative abundance of functional traits of organisms in a given community (Chapin et al. 2000, Díaz et al. 2007). Recent studies have shown that functional diversity, rather than taxonomic diversity, determines ecosystem processes (Hooper et al. 2002, Diaz et al. 2004, Vandewalle et al. 2010). Thus, a trait-based approach, which scales up traits from the species level to the community level, can improve our understanding of how plant communities respond to environmental change, and how these communities, in turn, affect ecosystem processes (Suding et al. 2008, Mayfield et al. 2010). We focus here on two ecosystem processes that are important for sustainability of site productivity: decomposition rate (which determines nutrient and carbon cycling) and net primary productivity.

Functional diversity can be described by the community-weighted mean (CWM), which indicates for a single trait the *average* trait value of plants in the community. The CWM is a good indicator of how species respond to the environment, and shows a high sensitivity to disturbance (Díaz and Cabido 1997, Vandewalle et al. 2010). Functional diversity can also be described by multiple-trait indices, such as functional richness, evenness and divergence, that describe trait *variation* (Villeger et al. 2008, Pla et al. 2012).

An important consideration for such a trait-based approach is to identify which functional traits and which species are relevant (Suding et al. 2008). *Response* traits are important because they indicate how species respond to environmental change, whereas *effect* traits are important because they indicate how species affect ecosystem processes (Lavorel and Garnier 2002). For instance, leaf nitrogen concentration can be both a response trait and an effect trait, as it enhances carbon assimilation and plant growth at high irradiance . Disturbances, such as logging, that lead to higher irradiance will also lead to an increased abundance of species with high leaf nitrogen concentrations (*response*), thus affecting community assembly and primary productivity (*effect*; Chapin 2003). Not all species are of equal importance for ecosystem processes; as dominant species make up the bulk of the community biomass, they will also be responsible for most of the ecosystem fluxes in energy and resources (Grime 1998, Garnier et al. 2004).

Disturbances lead to biomass removal and changes in resource availability. Species responses to disturbance are, therefore, governed by their ability to maximize the acquisition of resources or to maximize the conservation of resources (Grime 1974, Wright et al. 2005). Thus, species have been classified along a fast–slow continuum from acquisitive species with fast returns on resource investments to conservative species with slow returns on resource investments (Diaz et al. 2004) . In forests the continuum ranges from fast-growing shade-intolerant pioneer tree species with high specific leaf area, high leaf nitrogen concentrations, high photosynthetic- and respiration rates, soft wood and leaves, and short leaf lifespan, to slow-growing shade-intolerant species characterized by the opposite suite of traits (Poorter and Bongers 2006). Within a forest community functional traits vary gradually and continuously with species light requirements, and these traits allow light-demanding species to grow faster and shade-tolerant species to survive better (Poorter and Bongers 2006).

The response of tree species to disturbance can follow different trajectories (Flynn et al. 2009) depending on disturbance intensity (biomass loss; Pickett and White 1985) and recovery time. For instance, disturbance can cause changes in functional diversity but not in taxonomic diversity, or vice versa (Mayfield et al. 2010). Most studies that have evaluated the effects of logging disturbance have focused on taxonomic diversity (e.g. Gibson and Sodhi 2011, Putz et al. 2012), whereas changes in functional diversity have rarely been evaluated. It is known that functional groups such as pioneer tree species increase their recruitment, growth and abundance in response to disturbance (Peña-Claros et al. 2008a). Consequently, pre -defined functional groups, such as pioneers and shade-tolerant species (Finegan et al. 1999, Gondard and Deconchat 2003), or softwood and hardwood species (Verburg and van Eijk-Bos 2003) have been used to evaluate forest responses to disturbance. Yet, it is still unclear till what extent those floristic changes scale up to changes in community functional properties, because within each functional group (pioneers, shade tolerants) there is still a large variation in functional trait values (Poorter et al. 2006)

Demographic processes such as mortality, recruitment and growth of surviving individuals shape species responses to disturbance, and determine their relative contribution to the community. Survivors respond slow to disturbance and tend to make a large contribution to community biomass because they are large (Chazdon et al. 2007), whereas (small) recruits respond fast to disturbance and contribute more to abundance (Van Breugel et al. 2007). The consequences of these demographic processes for community functional properties can be evaluated by using either basal area (as an indicator of biomass) or abundance as a weighting factor in the analysis.

Here we use an 8-year, replicated field experiment to evaluate how a disturbance gradient, caused by timber harvesting and silvicultural treatments, affects the taxonomic diversity and functional diversity of a Bolivian tropical forest community and how this is driven by underlying demographic processes. We monitored the dynamics of 15 000 stems in 44 one-ha forest plots and measured 12 functional response traits of the 77 dominant species. Six of these traits are also effect traits that are known to be important for two ecosystem processes: decomposition rate and net primary productivity. We ask four questions: 1) how do taxonomic- and functional diversity of response-traits change along a disturbance gradient?, 2) do the results differ with the type of weighting factor (i.e. abundance- or basal area of the species?, 3) how are those changes driven by underlying demographic processes, such as mortality, survival and recruitment?, and 4) how does functional diversity of effect-traits (that are important for net primary productivity and decomposition rate) change along the disturbance gradient?

We hypothesized that: (1) species richness will not be affected because only large individuals were harvested, or will slightly increase because of the establishment of pioneers. The Shannon index will decrease at high levels of disturbance. Because disturbance will lead to the establishment of fast-growing pioneer species with acquisitive traits, we expect the community-weighted mean trait values to shift towards high specific leaf area and leaf nutrient concentrations, soft leaves, and a low wood density; (2) changes in community-weighted mean trait values are mainly driven by recruitment and mortality rather than by increased growth of surviving individuals in response to disturbance; we predict therefore that abundance-weighted traits show stronger responses to disturbance than basal-area weighted traits; (3) at higher disturbance intensities those trees that recruit will have on average more acquisitive trait values compared to dead or surviving trees; (4) the functional diversity of effect traits will increase with disturbance intensity, because a greater trait variation will be found due to an increase in recruitment rates of species with more acquisitive traits.

Materials and methods

Study site

The study was conducted in the La Chonta forest concession (15°47’S, 62°55’W), 30 km east of Ascención de Guarayos, Bolivia. The region receives an annual precipitation of 1580mm with one month where potential evapotranspiration exceeds precipitation (Peña-Claros et al. 2012).The forest is located on the Precambrian Brazilian shield (Cochrane 1973), and its soils have a sandy loam texture, neutral pH, an average total N of 0.32% and total P of 11.23 cmol kg^{-1} (Peña-Claros et al. 2012). The forest is a semi-deciduous tropical moist forest, has a mean canopy height of 27 m, and for trees > 10 cm diameter at breast height (d.b.h.) the stem density is 368 ha^{-1}, basal area is 19.7 m^{2}ha^{-1} and tree species richness is 59 ha^{-1}. About 160 tree species are found in the area, the most common ones being *Pseudolmedia laevis* (Moraceae), *Ampelocera ruizii* (Ulmaceae) and *Hirtella triandra* (Chrysobalanaceae) (Peña-Claros et al. 2012).

Experimental design and plots

Data were collected within the plots of the Long-Term Silvicultural Research Program (LTSRP) established in 2000-2001 by the Instituto Boliviano de Investigación Forestal (IBIF) in La Chonta forest concession. The LTSRP aims to evaluate the long-term effects of different intensities of logging and of application of silvicultural treatments on forest dynamics, biodiversity, and ecosystem functioning (Peña-Claros et al. 2008a, Villegas et al. 2009). In three 800-ha harvesting compartments four 27-ha plots were established using a nested design. The plots were randomly assigned to four disturbance treatments (Table 2, chapter 1): unharvested forest as a control (C), normal logging using reduced-impact logging techniques (N), normal logging plus light silviculture (L-S) and double logging intensity plus intensive silviculture (I-S). The treatments represent a gradient in disturbance in terms of biomass loss (due to a gradual increase in the number of trees harvested, dead trees due to logging, number of girdled trees, and liana cutting), biomass damage (due to damaged trees during logging operations), opening up of the forest canopy (due to tree harvesting and tree girdling), and soil disturbance (due to skid trails and soil scarification). For details on the experimental design see Table 2 in chapter 1.

Within each 27-ha plot there were four 1-ha plots that we used for this analysis, as in these plots all trees > 10 cm in d.b.h. had been mapped, tagged, identified and measured for their diameter (Peña-Claros *et al.* 2008a). Hence, for every treatment there were twelve 1-ha plots. Each 1-ha plot was inventoried just before the logging disturbance (hereafter T_0), and re-measured 8 years after disturbance (hereafter T_8). Four 1-ha plots were excluded from the analyses (3 for C and 1 for L-S) because of a fire event in 2004. Recruitment, survival and mortality were calculated for the dominant species only (see below) by comparing T_0 with T_8. Over this 8-year period there were for our subset of 77 species on average 57 deaths, 41 recruits and 170 survivors per 1-ha plot. There were five plots that had few recruits (between 4-7); four of these plots belonged to the control treatment and one to the normal treatment.

Data collection

Functional traits: For 77 of the most dominant tree species 12 functional traits were selected; of these, all 12 are response traits are important for plant growth, -survival and -responses to environmental change. Six of the functional are also important effect traits for the two ecosystem processes addressed in this study: net primary productivity and decomposition rate . Maximum adult stature is strongly related to species ability to compete for light (Poorter et al. 2006); wood density and branch density are indicators of construction costs, stability, hydraulic conductivity and volumetric growth rate (Chave et al. 2009); leaf traits such as thickness, dry matter content, toughness, chlorophyll content, nitrogen- and phosphorus concentration are related to light capture ability, light plasticity, leaf defence, leaf lifespan and decomposability (Table S1; Poorter et al. 2006, Bakker et al. 2011, Onoda et al. 2011).

Leaf traits of 45 species come from Rozendaal *et al*. (2006) and Bakker *et al.* (2011)and 19 additional species were measured for this study following the protocols of Cornelissen *et al.* (2003). Traits were measured for 4-5 individuals per species (with a d.b.h. of 10 - 30 cm) that grew in high light conditions with overhead light on the whole crown. Leaf traits were averaged per species. For *Ficus sp.*, *Inga edulis, Inga sp*. and *Cordia sp*. average genus-level trait values were used, whereas for *Bougainvillea modesta*, *Ceiba samauma* and *Chorisia speciosa* trait values from trees growing in a dry forest were used (Markesteijn et al. 2007). Leaf trait variation across species is large compared to variation within species (Rozendaal et al. 2006) and our average-trait value per species should therefore be a relatively good estimator for community-level properties (Baraloto et al. 2010).

For each individual, five young fully expanded leaves without epiphylls or herbivore damage were selected from five branches from the outer leaf layer halfway along the crown length. For each leaf the leaf thickness was measured with a micrometer, toughness was determined with a penetrometer (mass necessary to penetrate a punch-head of 7 mm^2 though the lamina), and chlorophyll content was measured with a SPAD meter (Minolta SPAD 502 Chlorophyll Meter, Spectrum Technologies Inc., Plainfield, IL, USA). Leaves were scanned with a flatbed scanner and analyzed for their leaf area with ImageJ. Leaf fresh mass was measured after leaf hydration in a refrigerator for 12 hours. Internode length was measured with a caliper as the distance between the first node and the starting point of the petiole; internode diameter was measured in two perpendicular directions, and internode volume was calculated as a cylinder. Leaves, petioles and internodes were oven-dried for 48 h at 70 °C and then weighed.

From these measurements we calculated the following morphological traits: specific leaf area (SLA; leaf area/leaf dry mass, $cm^2 g^{-1}$), leaf dry matter content (LDMC; leaf dry mass/leaf fresh mass, $g\ g^{-1}$), leaf toughness (LTo; force/head area, $N\ cm^{-2}$), leaf chlorophyll content per unit leaf area (Chl = 13·9 × SPAD-112·9, µmol m-2; Anten and Hirose 1999) and branch density (BD; internode dry mass/internode volume, $g\ cm^{-3}$). The nitrogen- (N_{mass}, % DM) and phosphorus concentration per leaf dry mass (P_{mass}, % DM) were determined for a pooled leaf plus petiole sample per species, and the N and P content per unit leaf area were calculated (N_{area} and P_{area} respectively, $mg\ cm^{-2}$). For species with compound leaves, leaf area and mass were based on leaflets plus rachis plus the petiole. For palm species only three leaves of three individuals were measured, and traits were determined using only their leaflets.

For 55 species the maximum adult stature (H_{max}, *m*) was calculated as its asymptotic height using species-specific height–diameter relationships, whereas for 22 species maximum adult stature was calculated using a forest-wide regression equation (Poorter et al. 2006). For most species wood density (WD, $g\ cm^{-3}$) data come from Poorter (2008). For few additional species, wood samples (bark, cambium and wood) were taken for 4-5 individuals per species (10-30 cm d.b.h.) at 0.5-1m stem height. Sample volume was measured using the water displacement method, after which samples were oven-dried for at least 48 h at 70 ^{o}C and weighed.

Data analysis

All diversity metrics were calculated independently for each 1-ha plot and for each date (T_0 and T_8). The relative contribution of species was taken into account by weighting the metrics by the basal area or by the abundance of the species. By weighting for basal area we emphasized the contribution of growing surviving individuals (old individuals with large basal area) to biodiversity change, and by weighting for abundance we evaluated mainly the contribution of recruited individuals (young and small but abundant) to biodiversity change.

Taxonomic diversity was evaluated using all 17 751 individuals belonging to 177 species (of which 17 are morphospecies), 120 genera and 53 families in the plots. Three metrics were calculated using EstimateS 8.2 (Colwell 2009) with 50 runs: observed species richness (S), estimated species richness (S’) with the Jackknife-2 estimator (Brose et al. 2003) and Shannon index (H’) as $H'=-\sum(\ln p_i)$, where p_i is the proportion of individuals or basal area found for species i.

Functional diversity was assessed using the 77 most dominant species (making up 80 ±2 % of the cumulative community basal area). These species belonged to 61 genera and 33 families, and they are the most important species as they are the strongest determinants of ecosystem functioning and ecosystem response to environmental change (Grime 1998, Pakeman and Quested 2007). Dominant species were selected independently for each 1-ha plot and for T_0 and T_8. The functional composition was calculated with single traits as the Community Weighted Mean (CWM; Díaz et al. 2007, Violle et al. 2007) weighted by its relative basal area or abundance. Additionally, the effect traits were assigned to two groups related to decomposition rate (SLA, LDMC, LCh, and Nmass; Cornelissen et al. 1999, Bakker et al. 2011), and net primary productivity (Hmax, WD, SLA, and Nmass; Table S1; Westoby 1998, Falster et al. 2011). Although many traits may co-determine decomposition or net primary productivity, we selected only the four most important effect traits for each ecosystem process. The reason for this is that the functional trait indices calculated below require that the number of species per plot must be higher than the number of functional traits (Villeger et al. 2008).

For each group (decomposition rate or net primary productivity) three multivariate functional indices were calculated: functional richness (FRich) quantifies the volume of the multidimensional-functional space occupied by the community, and the algorithm to calculate the convex hull hyper-volume (Cornwell et al. 2006) identifies the extreme species and then estimates the volume in the trait space; functional evenness (FEve) indicates the regularity of the distribution of abundance in this volume; and functional divergence (FDiv) quantifies the divergence in the distribution of abundance in this volume. FEve and FDiv scale from 0 to 1; a high value indicates more regularity and more deviation, respectively, in the distribution of abundance of individuals in this volume (Villeger et al. 2008, Mouchet et al. 2010). Standardized trait values were used for calculating functional indices, with a mean of zero and a standard deviation of one. The calculations were done using FDiversity (Casanoves et al. 2011), the equations are given in Appendix S1.

For three metrics (H', CWM of H_{max} and CWM of WD), we checked whether the diversity of the 80% most dominant species was indeed representative of the diversity of the whole community. The H' for the dominant species was indeed highly correlated with those of all species across plots when basal area was used as a weighting factor (Pearsons r= 0.98, p<0.001, N=48 plots) and the same applies to H_{max} (r=0.98) and WD (r=0.91). Slightly weaker correlations were found when abundance was used as a weighting factor (r=0.48, 0.69 and 0.78, P<0.001 in all cases).

Observed and estimated species richness were compared among the four treatments and the two dates using species accumulation curves (±95 % confidence intervals). To evaluate treatment disturbance on H', CWMs and functional indices, we calculated their relative changes (Δ, in %) between T_0 and T_8: $\Delta = [T_8\text{-}T_0]/T_0{*}100$. In this way we control for temporal dynamics and for pre-treatment differences amongst plots. To evaluate what population process underlies the effect of disturbance on response traits, we compared the CWM among trees that died, survived, or recruited during the 8-year period.

Statistical tests were carried out with linear mixed models, using the maximum-likelihood ratio method and, respectively, CWM and Δs as dependent variables. The model tests the magnitude and significance of treatment as a fixed factor, and the variance component caused by the grouping structure of the data (i.e. harvesting compartments) as a random factor. Moreover, maximum likelihood works unambiguously for unbalanced data (Pinheiro and Bates 2000, Faraway 2006). The assumptions of equal variances, normal distribution and uncorrelated residuals of the model were evaluated graphically (Faraway 2006), and logarithmic transformations were applied when necessary. A multiple comparison among treatments was done with Tukey's HSD tests. Multiple comparisons among dead, surviving and recruiting individuals were done independently for each treatment to avoid the interaction between treatment and demographic groups (i.e. survivors, dead and recruits). All statistical analyses were run with R 2.12.1 (R Development Core Team 2010), using the lme4 and multcomp functions from the correlated data library.

Results

Neither the observed species richness (S) nor the estimated species richness (S') per 1-ha plot differed significantly among the four treatments at T_0 or T_8. Total species richness per treatment varied between 122 and 130. This number corresponds to 85% (±0.01 SD; n= 9-12) of the total expected (Jackknife-2 estimation) species richness for this forest. Similarly, the Δ-H' weighted by basal area and abundance did not differ significantly among treatments. After 8 years, H' had changed between 0.5±1.73 and -3.1±1.17 % (Table 1).

Eight years after disturbance, the treatments had a significant effect on CWM changes for 7 out of 12 response traits evaluated (Table 2). Seven traits differed significantly when abundance was used as a

Table 1. Effects of four disturbance treatments (ranked in increasing order of disturbance) on taxonomic- and functional diversity over an 8-year period. Total observed species richness (S) ha^{-1} and Jackknife-2 estimated species richness ha^{-1} (S') were calculated before (T_0) and after (T_8) disturbance. Means ±95 % confidence intervals are shown. The percentage difference between T_0 and T_8 of Shannon index (Δ-H'), functional richness (Δ-FRich), functional evenness (Δ-FEv) and functional divergence (Δ-Fdiv) was tested using mixed models (LM method). All diversity indices but one are calculated by weighting species for abundance (A) or for basal area (B). Effect traits used for primary productivity were potential adult stature, wood density, specific leaf area and leaf nitrogen concentration, and for decomposition rate were leaf dry matter content leaf chlorophyll, specific leaf area and leaf nitrogen concentration. P-values and means ±standard errors are shown.

Metric	Date		Control (n=9)	Normal (n=12)	Light silviculture (n=11)	Intensive silviculture (n=12)
S	T_0		123 ± 1.85	132 ± 1.78	130± 1.75	128 ± 1.78
	T_8		122± 1.84	125± 1.95	131± 1.90	130± 1.86
S'	T_0		153± 2.33	166± 1.45	157± 1.44	156± 1.43
	T_8		146± 1.24	162± 2.33	172± 1.43	165± 0.95
	Weighted by	*P*				
Δ-H'	A	0.1 2	-3.06 ± 1.17	-0.27 ± 0.80	-0.71 ±1.01	-1.26 ± 0.89
	B	0.5 7	-1.51 ± 0.45	0.49 ± 1.37	-0.69 ± 0.19	0.48 ± 1.19
Net primary productivity						
Δ-Frich		0.62	51.5 ± 65.4	41.1 ± 35.8	7.2 ± 18.9	58.6 ± 31.7
Δ-Feve	A	0.85	12.2 ± 10.3	12.1 ± 8.7	3.9 ± 2.1	12.5 ± 8.2
	B	0.11	8.2 ± 7.4	6.5 ± 4.1	-4.6 ± 3.8	8.7 ± 6.4
Δ-Fdiv	A	0.36	5.6 ± 6.2	2.6 ± 4.2	9.7 ± 7.1	10.7 ± 3.4
	B	0.25	5.5 ± 4.2	-0.6 ± 2.6	5.3 ± 4.9	6.8 ± 2.5
Decomposition rate						
Δ-Frich		0.78	22.6 ± 15.9	28.2 ± 23.9	21.6 ± 21.1	52.3 ± 35.1
Δ-Feve	A	0.34	6.2 ± 4	10.4 ± 10	12 ± 5.2	18.1 ± 6.4
	B	0.71	2.6 ± 1.9	4.7 ± 3.1	0.4 ± 3.7	7.5 ± 7.2
Δ-Fdiv	A	0.56	5.3 ± 6.8	6.7 ± 4.4	14.8 ± 6.9	9.3 ± 2.6
	B	0.96	3.7 ± 3	4 ± 4	6.5 ± 5.5	4.6 ± 3

weighting factor, and four traits differed significantly when basal area was used. Branch density, leaf dry matter content, leaf toughness and P concentration showed consistently significant changes, when weighting either by abundance or by basal area. Wood density, specific leaf area and N concentration were only affected when weighting by abundance (Table 2). With an increase in disturbance intensity the CWM changed towards species with low branch density, wood density, leaf toughness and leaf dry matter content, but high specific leaf area, N and P concentration. At the highest disturbance intensity (intensive silviculture treatment) the absolute change in CWM of the above-mentioned traits over the 8-year period (Δ-CWM) was on average 6%, ranging from 3.7

Table 2. Disturbance effects on response traits 8 years after disturbance in a Bolivian tropical moist forest. Relative changes in community-weighted mean (Δ-CWM) are shown for the four treatments. The CWM is calculated by weighting species for abundance (A) or for basal area (B). Means ± standard error are given. The traits are maximum adult stature (Hmax), wood density (WD), branch density (BD), leaf thickness (LTh), Leaf Dry Matter Content (LDMC), Leaf toughness (LTo), Leaf chlorophyll (LCh), N and P concentration per unit leaf mass (Nmass, Pmass), and N and P content per leaf area (Narea, Parea). P-values from mixed models (LM method) are given (in bold when P<0.05).

Trait	**Weighting factor**	***P***	**Δ-CWM (%)**			
			Control (n=9)	**Normal (n=12)**	**Light silviculture (n=11)**	**Intensive silviculture (n=12)**
H_{max}	A	0.603	2.85 ± 0.85	-0.26 ± 3.02	2.55 ± 1.92	-0.91 ± 2.38
	B	0.273	1.51 ± 0.50	-1.31 ± 1.91	-1.70 ± 1.39	-3.03 ± 1.53
WD	A	**0.003**	1.34 ± 1.07	0.28 ± 1.62	-4.73 ± 2.04	-4.73 ± 0.93
	B	0.174	1.01 ± 0.72	2.49 ± 1.32	-0.74 ± 1.54	-0.83 ± 1.26
BD	A	**0.003**	2.58 ± 1.37	1.17 ± 1.92	-3.70 ± 2.24	-5.49 ± 1.49
	B	**0.044**	1.86 ± 1.62	3.54 ± 1.05	-0.76 ± 1.80	-1.58 ± 1.44
SLA	A	**0.002**	-2.56 ± 1.17	0.79 ± 1.14	8.27 ± 3.73	6.85 ± 1.59
	B	0.119	-2.19 ± 1.19	-0.30 ± 1.65	2.20 ± 2.49	3.22 ± 0.77
LTh	A	0.115	-1.45 ± 0.56	-1.46 ± 0.64	-1.60 ± 1.25	0.82 ± 0.76
	B	0.725	-0.12 ± 0.63	-0.60 ± 0.57	0.68 ± 1.30	0.17 ± 0.78
LDMC	A	**0.001**	1.72 ± 0.65	-0.15 ± 0.74	-3.17 ± 1.62	-3.72 ± 0.78
	B	**0.023**	1.14 ± 0.86	0.79 ± 0.55	-1.34 ± 1.19	-1.81 ± 0.61
LTo	A	**0.043**	0.93 ± 0.79	-1.54 ± 1.49	-3.58 ± 1.99	-5.33 ± 1.45
	B	**0.020**	-0.13 ± 0.63	0.43 ± 0.59	-0.81 ± 1.42	-3.52 ± 1.02
LCh	A	0.197	0.88 ± 0.63	-1.06 ± 0.69	-0.80 ± 0.63	-0.12 ± 0.77
	B	0.474	0.47 ± 0.76	-1.19 ± 0.55	-0.38 ± 0.42	-0.29 ± 1.05
N_{mass}	A	**0.001**	-1.14 ± 1.04	2.30 ± 1.59	5.70 ± 1.72	7.57 ± 1.58
	B	**≈0.057**	-1.26 ± 0.74	0.38 ± 0.72	2.56 ± 1.56	2.65 ± 1.24
P_{mass}	A	**0.043**	-0.69 ± 1.44	3.45 ± 1.49	5.85 ± 3.28	7.70 ± 2.17
	B	**0.047**	-1.53 ± 1.55	0.91 ± 0.95	4.85 ± 2.55	5.77 ± 2.51
N_{area}	A	0.355	1.49 ± 0.97	1.80 ± 1.44	-1.25 ± 1.64	0.86 ± 1.16
	B	0.860	1.43 ± 0.96	0.66 ± 1.72	-0.11 ± 1.32	-0.30 ± 1.43
P_{area}	A	0.355	1.43 ± 1.46	3.09 ± 2.07	-1.90 ± 1.38	1.91 ± 1.77
	B	0.697	0.77 ± 1.30	1.32 ± 1.40	1.27 ± 1.47	2.84 ± 2.56

for LDMC to 7.7% for P_{mass} (Table 2). Five out of seven traits that responded to disturbance intensity showed a gradual change. Only two traits (specific leaf area and wood density) showed an abrupt change with an increase in disturbance intensity; i.e. the control and normal treatments formed one group, and the light and intensive silvicultural treatments formed another group (Fig. 1).

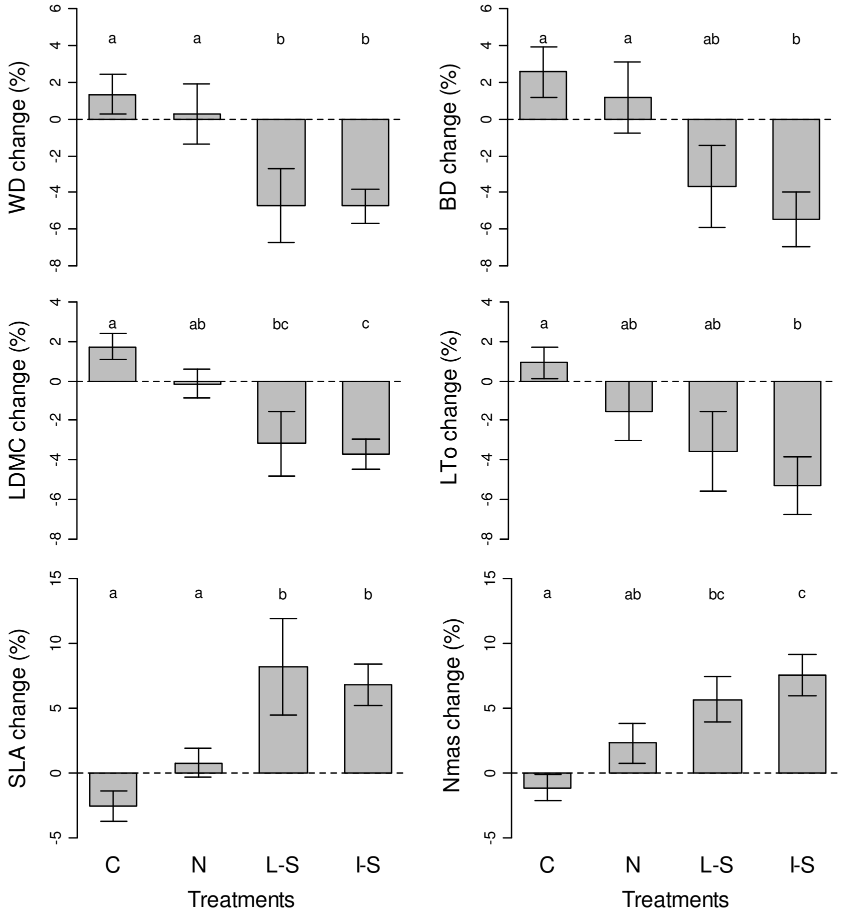

Figure 1. Disturbance effects on response traits 8 years after the disturbance in a Bolivian tropical moist forest. The relative change in the abundance-weighted community mean of six response traits was compared among Control (C), Normal (N), Light Silviculture (L-S) and Intensive Silviculture (I-S) disturbance treatments. The functional traits are branch density (BD), wood density (WD), leaf toughness (LTo), leaf dry matter content (LDMC), leaf nitrogen concentration (N_{mass}) and specific leaf area (SLA). Means and standard errors are shown (n=9, 12, 11, and 12 respectively). Bars accompanied by a different letter are significantly different at p<0.05 (Tukey's HSD test).

Individuals that died, survived and recruited during the 8-years period differed significantly in their abundance-weighted CWM for nine functional traits. With an increase of disturbance intensity, recruiting individuals had a lower CWM for WD, branch density, leaf toughness and LDMC, but a higher CWM for SLA and leaf N and P concentrations, compared with dead or surviving individuals (Fig. 2). Seven of these nine traits were also significantly affected by disturbance treatments (Table 2), suggesting that changes in CWM over time are mainly due to the recruits. The three demographic groups differed also significantly in H_{max} and leaf thickness (Table S2), despite the fact that

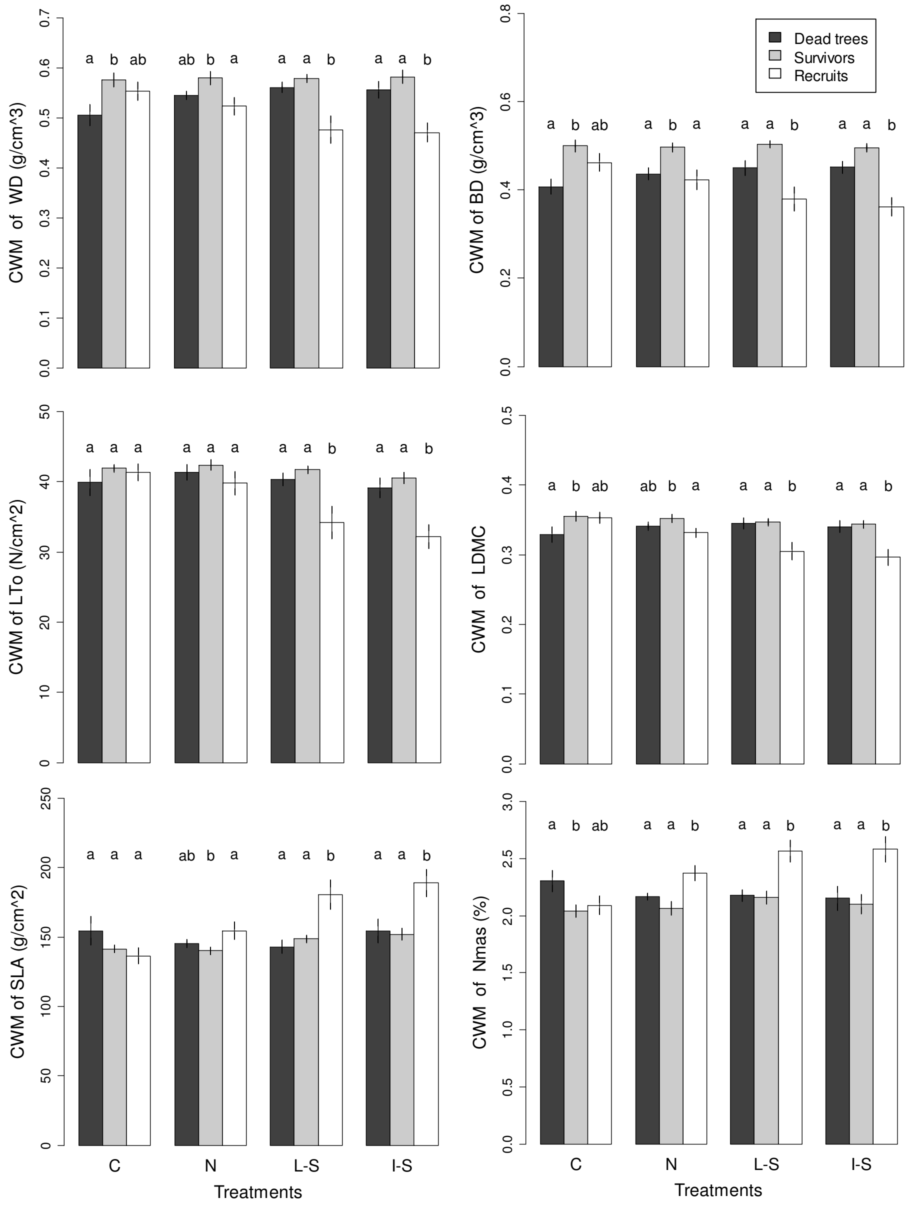

Figure 2. Differences in the abundance-weighted community mean of six response traits among groups of individuals that died, survived and recruited 8 years after the disturbance in a Bolivian tropical moist forest. The treatments are Control (C), Normal (N), Light Silviculture (L-S), and Intensive Silviculture (I-S), and functional traits are branch density (BD), wood density (WD), leaf toughness (LTo), leaf dry matter content (LDMC), specific leaf area (SLA), and leaf nitrogen concentration (N_{mass}). Means and standard errors are shown (based on n=9, 12, 11, and 12 plots, respectively). Significant differences among groups were tested separately per treatment. Bars within treatments accompanied by a different letter are significantly different at $p<0.05$ (Tukey's HSD test).

these parameters did not differ in Δ-CWM among treatments (Table 2).

In general, functional diversity indices of effect traits (i.e. traits related to net primary productivity or to decomposition rate) increased over time, but, in contrast to our prediction, these changes did not vary significantly among treatments (Table 1).

Discussion

We evaluated the effect of a disturbance gradient on the taxonomic diversity and functional diversity of a tropical tree community using a large-scale field experiment. Eight years after disturbance, no significant effects of logging intensity on taxonomic diversity were observed, whereas the tree community had changed towards species with more acquisitive traits. These changes were mainly driven by recruitment and little by mortality or survival rate. Surprisingly, we found no clear effects of disturbance on functional multi-trait indices related to net primary productivity and litter decomposition rate. Here we discuss the ecological significance of our results and their implications for sustainable forest management.

Disturbance does not affect taxonomic diversity

Neither species richness nor S' were significantly affected by the disturbance intensity (Table 1). This lack of effect was probably due to the low logging intensities and the high felling limit: only up to 4 trees per ha were logged (Table 2, chapter 1), and these species will still be present as smaller individuals below the diameter cut-off limit for harvest (for most species > 50 cm d.b.h.). Our hypothesis that Shannon index (H') decreases at high disturbance intensity because of prolific recruitment of a few pioneer species was not supported (Table 1). Similarly, no effect of logging on taxonomic diversity (S, Fishers' α) was reported 16 years after a low to moderate logging intensity (2-9 m^2 ha^{-1}) of trees > 15 cm d.b.h. in a Bornean rainforest (Verburg and van Eijk-Bos 2003), and 50 years after logging disturbance in a semi-arid forest (Mayfield et al. 2010). In contrast, S and Simpson's index diminished 15 years after high-intensity logging in a moist evergreen forest in Uganda (Muhanguzi et al. 2007). Differences amongst studies can be explained by differences in management practices (Toledo et al. 2012). For example, the above-mentioned studies varied in logging intensity, and hence, differed in damage to the remnant stand and changes in environmental conditions (Muhanguzi et al. 2007, Van Kuijk et al. 2009). Additionally, other factors may explain the differences amongst studies, such as the diameter threshold considered, the evaluated time period since disturbance, and the initial disturbance state of the stands.

Trait changes in response to disturbance

In contrast to taxonomic diversity, functional composition of the community did clearly respond to disturbance (Table 2, Fig. 1). With an increase in disturbance intensity the CWM changed from conservative traits towards more acquisitive traits. Higher disturbance intensities promoted species with low leaf construction costs (i.e. low leaf dry matter content), poorly defended leaves (i.e.

low leaf toughness), and short leaf lifespan (Fig. 1, cf. Kitajima and Poorter 2010, Onoda et al. 2011). Such species also had high SLA and leaf nitrogen concentration. In combination, the large light-capturing surface per unit biomass and high photosynthetic rates result in high carbon gain in high-light environments (Sterck et al. 2006). As a consequence, these species have high growth rates but die fast as well . In contrast, low disturbance intensities (i.e. control- and normal logging treatments) promoted species with the opposite suite of traits (Loehle and Namkoong 1987). These results suggest that increased light availability (due to logging gaps and gradual death of damaged individuals) is the main factor driving functional responses in the tree community (Finegan and Camacho 1999, Castro-Luna et al. 2011).

We also expected that a higher disturbance would lead to an increase in the CWM of other acquisitive traits (e.g. high leaf thickness, leaf chlorophyll-, N- and P content per leaf area and potential adult stature; Westoby 1998, Falster and Westoby 2005, Poorter et al. 2006) but none changed significantly (Table 2). Our results also showed that the CWM of H_{max} was lower for acquisitive recruits than for survivors in our high-disturbance-intensity treatment (Table S2). This reflects the fact that light-demanding early successional species tend to be small whereas light-demanding late-successional species tend to be tall (Falster and Westoby 2005).

Recruitment as a driver of change

We hypothesized that changes in response traits were driven by recruitment (of individuals that reached our minimum size limit of 10 cm d.b.h. at T_8) rather than growth of surviving individuals (as larger growth would lead to a larger basal area of these individuals at T_8), and by using abundance as a weighting factor we would stress this influence (Van Breugel et al. 2007, Van Kuijk et al. 2009). We indeed found that at high disturbance intensity abundance-weighted traits showed stronger changes than basal-area weighted traits (Table 1). The strong influence of recruits in changing the CWM was also supported by the fact that, at high disturbance intensity, recruits differed in traits from survivors, whereas at low disturbance intensity (control treatment) recruited individuals had similar traits compared to surviving and dead individuals (Fig. 2, Table S2). However, the apparently similar trait values for recruits in the control treatment should be interpreted with care, as recruitment rates are low in the undisturbed control forest (four out of nine plots had only 4-6 recruits per plot) which makes it more difficult to precisely estimate their CWM trait values. Logging-related changes in abundance can be picked up quickly; after 5-10 years small individuals that were already established in the stand, or newly established individuals of fast-growing pioneer species may recruit to 10 cm d.b.h., the lower size limit that we used in our plots. Increased recruitment of light-demanding species in the first years after disturbance has also been reported for rainforest saplings in Bolivia (Peña-Claros et al. 2008b), and for rainforest trees in Costa

Rica (Finegan et al. 2001) and Borneo (Verburg and van Eijk-Bos 2003). In contrast, changes in basal area can be picked up relatively slowly (after 20-30 years, Ghazoul and Hellier 2000).

Effect of disturbance on functional diversity indices

The three functional diversity indices (that describe trait *variation* and consider multiple effect traits) increased across the disturbance gradient, in line with the hypothesis, although not significantly. An increase in FRich would indicate a fuller occupation of the potential niche, an increase in functional evenness (FEve) would indicate a fuller utilization of resources, and an increase in FDiv would indicate a higher competition for specific resources (Mason et al. 2003).

In contrast to previous studies (Lavorel et al. 2008, Vandewalle et al. 2010), changes in CWM in response to disturbance (i.e. changes toward more acquisitive traits at high disturbance intensity; Table 2), were not paralleled by changes in multivariate functional diversity indices or by changes in species diversity.

Implications for the maintenance of ecosystem processes

Disturbance intensity affects net primary productivity and decomposition rate, and hence, the carbon balance of the forest (MEA 2005b). Disturbance has direct effects by increasing resource availability, or indirect effects through changes in community functional properties (Suding et al. 2008). Effect traits such as H_{max}, WD, SLA and N_{mass} have been shown to be good predictors of changes in primary productivity (Westoby 2007, Falster et al. 2011) and acquisitive leaf traits have been shown to be good predictors of decomposition rate (Santiago 2010, Bakker et al. 2011).

At high disturbance intensity the CWM of SLA and N_{mass} increased and WD decreased (Table 2, Figs 1,2), which suggests an increase in primary productivity and carbon- and nutrient cycling in the short-term. Indeed, Kaul, Mohren & Dadhwal (2010) found that an increase in fast-growing species in early stages of forest regeneration was accompanied by increases in primary productivity. In contrast, over longer time scales primary productivity is predicted to be determined by species with low SLA and high wood density, because those species increase their abundances at the expense of fast-growing species. As we found that high disturbance intensities reduced recruitment of species with low SLA and high WD, we expect in the medium term a decrease in primary productivity.

Single CWM trait values have shifted clearly with disturbance intensity, whereas multi-trait-based functional diversity indices (that describe trait *variation*) stayed the same. This indicates that average trait values shift, but that trait variation around this average is maintained, which is important because this trait variation may buffer ecosystem processes against environmental variation and change (Suding et al. 2008, Isbell et al. 2011).

Conclusions and implications

The 8-year field experiment showed that disturbance neither affected species diversity nor functional diversity (i.e. trait variation) per-se, but that it did affect the functional composition of the community. At high disturbance intensity the community changed towards fast-growing species with more acquisitive traits such high SLA and low WD. These changes are driven by recruitment rather than by selective mortality of species with certain trait values or by disturbance-induced increases in growth rates of survivors that have specific trait values.

These results may, of course, change if a longer time frame is considered and as succession proceeds. Tropical forests regrow rapidly after disturbance after which the canopy closes again (Broadbent et al. 2006). The strongest changes in dynamics or composition are in general detected in the first few years after logging (Toledo et al. 2011b, 2012 and references therein), that is, within the time frame that we used for this study. We expect that after this disturbance pulse the forest will slowly return to its initial stage; however, when exactly this will happen requires further study.

The disturbance gradient represents a combination of logging intensity and silvicultural treatments (Table 2, chapter 1). Most traits responded gradually to this disturbance gradient, but the abrupt disturbance effects on CWM for two functional traits (WD and SLA; Table 2) were unexpected, and indicate that for these traits the application of additional silvicultural practices had a stronger disturbance impact than tree harvest itself (Putz et al. 2001). We conclude that the modest harvesting levels used here did not have strong effects on the forest tree community, and that forest management indeed provides a viable land use option that provides forest resources while maintaining (functional) biodiversity of trees.

Acknowledgements

This research is part of the Long-term Silvicultural Research Program of IBIF, and we would like to thank all IBIF’s personal for the data, field work, and for monitoring the permanent plots. We thank the personnel of La Chonta Agroindustria Forestal for permission to work in the concession and for assistance with plot establishment and monitoring. This study was partly funded by the DiverSus project through Inter-American Institute for Global Change Research (IAI) CRN 2015 and SGP-CRA2015, which were supported by the US National Science Foundation grants GEO-0452325 and GEO-1138881. G.C.R. was funded by DiverSus and by a fellowship from NUFFIC and L.P. and M.P. were partly funded by the European Community's Seventh Framework Programme ([FP7/2007-2013]) under grant agreement n° 283093; Role Of Biodiversity In climate change mitigatioN (ROBIN). We appreciate the incredible assistance of field workers, especially Angel Mendez, Ricardo Mendez, José Iraipi, Peter Van Buuren and Benoit Chevallier. We thank Laura Pla for help with the data analysis and Bryan Finegan, Sandra Diaz, Fabrice de Clerck and an anonymous reviewer for helpful comments on the manuscript.

Table S1. List of 12 functional traits, the abbreviators used and their relevance in plant functions, as 'response-traits', and their relevance for two ecosystem processes (net primary productivity and decomposition rate as 'effect-traits').

Traits (Abbreviation; unit)	**Plant functions (response-traits)**	**Ecosystem processes (effect-traits)**		**References**
		NPP	**DR**	
Maximum adult stature *(H_{max}; m)*	competitive ability for light capture, lifespan, survival,	X		Poorter *et al.* 2005 Westoby 1998
Wood Density (WD; g cm^{-3})	carbon investment, growth rate, photosynthesis, mortality rate, resistance to drought-induced embolism, water potential, attack by pathogens and fungi, mechanical breakage	X		Kraft & Ackerly 2010
Branch density (BD; g cm^{-3})	See wood density. Also crown width, crow stability,			Sterck *et al.* 2006
Specific Leaf Area (SLA; cm^2 gr^{-1})	leaf life span, light capture, leaf construction, net photosynthetic capacity, potential relative growth rate	X	X	Falster *et al.* 2011 Lavorel & Garnier 2002 Evans & Poorter 2001 Westoby 1998
Leaf Thickness (LTh; mm)	light absorption per unit leaf mass, photosynthetic capacity per unit area, light acclimation			Rozendaal *et al.* 2006 Vile *et al.* 2005
Leaf Dry Matter Content (LDMC; g g^{-1})	growth rate, leaf life span, leaf construction cost		X	Lavorel & Garnier 2002 Westoby 1998 Bakker *et al.* 2011
Leaf toughness (Lto; N cm^{-2})	leaf life span, protection, carbon fixation			Onoda *et al.* 2011
Leaf chlorophyll (LCh; μmol cm^2)	light capture, light plasticity		X	Rozendaal *et al.* 2006 Bakker *et al.* 2011
N concentration content per unit leaf mass (N_{mass}; % DM)	photosynthetic carbon gain	X	X	Bakker *et al.* 2011 Poorter & Evans 1998
P concentration content per unit leaf mass (P_{mass}; % DM)	photosynthetic carbon gain			Poorter & Evans 1998
N content per unit leaf area (N_{area}; mg cm^{-2})	light plasticity, photosynthetic capacity			Evans & Poorter 2001 Poorter & Evans 1998
P content per unit leaf area (P_{area} ;mg cm^{-2})	light plasticity, photosynthetic capacity			Evans & Poorter 2001 Poorter & Evans 1998

Table S2. Differences in the abundance-weighted community mean of six response traits among groups of individuals that died, survived and recruited 8 years after the disturbance in a Bolivian tropical moist forest. The treatments are Control (C), Normal (N), Light Silviculture (L-S) and Intensive Silviculture (I-S), and functional traits are potential adult stature (H_{max}), leaf thickness (LTh), leaf chlorophyll content (LCh), P concentration (P_{mass}) and P- and N content per unit area (P_{area} and N_{area}). Means of 1-ha plots are shown (n=9, 12, 11 and 12 respectively). Differences in community-weighted mean (CWM) among demographic groups (deaths, survivors, recruits) were tested separately per treatment using a Tukey's HSD test, and significantly different groups (p<0.05) are shown with different letters.

Treat-ments	**Means of CWM**							
	Traits	**Dead**	**Survivals**	**Recruits**	**Traits**	**Dead**	**Survivals**	**Recruits**
C	H_{max}	28.1 a	32.9 b	31.5 b	P_{mass}	0.20 a	0.18 b	0.18 ab
N		28.5 a	31.3 a	27.9 a		0.18 a	0.18 a	0.21 b
L-S		26.2 a	32.4 b	26.6 a		0.19 a	0.19 a	0.23 b
I-S		28.3 a	31.9 b	26.2 a		0.18 a	0.19 a	0.22 b
C	LTh	0.21 a	0.19 b	0.21 ab	N_{area}	0.16 a	0.15 a	0.16 a
N		0.22 a	0.20 b	0.21 ab		0.16 a	0.15 a	0.16 a
L-S		0.21 a	0.19 a	0.20 a		0.16 a	0.15 a	0.15 a
I-S		0.19 a	0.19 a	0.20 b		0.15 a	0.14 a	0.15 a
C	LCh	0.20 a	0.18 a	0.18 a	P_{area}	0.01 a	0.01 a	0.01 a
N		0.18 a	0.18 a	0.21 a		0.01 a	0.01 a	0.01 a
L-S		0.19 a	0.19 a	0.23 a		0.01 a	0.01 a	0.01 a
I-S		0.18 a	0.19 a	0.22 a		0.01 a	0.01 a	0.01 a

Appendix S1 . Equations used in Fdiversity software to calculated Functional evenness (FEve) and functional divergence (FDiv; Casanoves, et al. 2011; Pla, Casanoves & Di-Rienzo 2012)

Equation (1)

$$\boldsymbol{FEve} = \frac{\sum_{b=1}^{S-1} \min\left(PWE_b, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$$

Where S is the number of species, b is the branch length

- $\boldsymbol{PWE_b}$ is a partial weighted evenness

$$\boldsymbol{PWE_b} = \frac{EW_b}{\sum_{b=1}^{S-1} EW_b}$$

- **EW**$_b$ is the weighted evenness

$$\boldsymbol{EW_b} = \frac{d_{ij}}{w_i + w_j}$$

Where d_{ij} is the Euclidean distance between species i and j, and w_i and w_j are the relative abundance of these species.

Equation (2)

$$\boldsymbol{FDiv} = \frac{\Delta d + dG}{\Delta|d| + dG}$$

- $\Delta \boldsymbol{d}$ is abundance-weighted deviance

$$\Delta d = \sum_{i=1}^{s} w_i \times (dG_i - \overline{dG})$$

- $\Delta|\boldsymbol{d}|$ is absolute abundance-weighted deviance

$$\Delta|d| = \sum_{i=1}^{s} w_i \times |dG_i - \overline{dG}|$$

being w_i the relative abundance of species 'i'

- $\boldsymbol{dG_i}$ is the Euclidean distance of each species from this point

$$\boldsymbol{dG_i} = \sqrt{\sum_{t=1}^{T} (x_{ti} - g_t)^2}$$

- $\boldsymbol{g_t}$ is the coordinate of the gravity center for trait 't'

$$\boldsymbol{g_t} = \frac{1}{V} \sum_{i \in SV}^{V} x_{ti}$$

where SV is the subset of all the V species forming the vertices of the convex hull, $\boldsymbol{x_{ti}}$ is the coordinate (trait value) of species 'i' on the 't' trait, and T is the total number of traits

- $\overline{\boldsymbol{dG}}$ is the mean distance of the S species to the gravity center

$$\overline{dG} = \frac{1}{S} \sum_{i=1}^{s} dG_i$$

The ideal place to rest after a day of hard fieldwork, under the shadow of a mango tree .

Measuring plant composition in pastureland. In the picture Maartje, José Chuviña, and Geovana

Chapter 4

Leaf economics traits predict litter decomposition of tropical plants and differ among land use types

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Published in Functional Ecology 25(3): 473-483, 2011

Abstract

Decomposition is a key ecosystem process that determines nutrient and carbon cycling. Individual leaf and litter characteristics are good predictors of decomposition rates within biomes worldwide, but knowledge on which traits are the best predictors for tropical species remains scarce. Also, the effect of a species' position on the leaf economics spectrum and regeneration light requirements on decomposition rate are, until now, unknown. In addition, land use change is the most immediate and widespread global change driver, with potentially large consequences for decomposition.

Here we evaluate 14 leaf and litter traits, and litter decomposition rates of 23 plant species from three different land use types (mature forest, secondary forest, and agricultural field) in the moist tropics of lowland Bolivia.

Leaf and litter traits were closely associated and showed, in line with the leaf economics spectrum, a slow-fast continuum ranging from species with tough, well-protected leaves (high leaf density, leaf dry matter content, force to punch and litter C:N ratio) to species with cheap, productive leaves (high specific leaf area and nutrient concentrations in leaves and litter).

Fresh green leaf traits were better predictors of decomposition rate than litter traits, and leaf nitrogen concentration was a better predictor of decomposition than leaf phosphorus concentration, despite the widely held belief that tropical forests are P-limited.

Multiple regression analysis showed that leaf nitrogen concentration, specific leaf area and chlorophyll content per unit leaf area had positive effects on decomposition, explaining together 65-69% of the variation. Species position on the leaf economics spectrum and regeneration light requirements were also positively related to decomposition.

Plant communities from agricultural fields had significantly higher leaf nitrogen concentrations and SLA than communities from mature forest and secondary forest. Species from agricultural fields had a higher average decomposition rates than from other ecosystems, and tended to be at the fast end of the LES.

Both individual traits of living leaves and species' position on the leaf economics spectrum persist in litter, so that leaves lead influential after lifes, affecting decomposition, nutrient and carbon cycling.

Key-words

Chlorophyll; Decomposition; Functional traits; Global change; Land use; Leaf economics spectrum; Nitrogen; Phosphorus; Plant strategy; Specific leaf area; Tropical forest

Introduction

Decomposition is a key ecosystem process that connects all trophic levels. Through the activity of decomposers and trophic transfer, nutrients like nitrogen and phosphorus are made available to primary producers and higher trophic levels (Campbell & Reece 2002; Wardle *et al.* 2004). Litter decomposition is controlled by three main factors: environmental conditions, the decomposer community, and substrate quality (Perez-Harguindeguy *et al.* 2000; Castanho & de Oliveira 2008). Environmental conditions such as climate and soil have occasionally been found to be the best predictors of litter decomposition (Aerts 1997). However, Cornwell *et al*. (2008) showed in a global meta-analysis that the traits of plant species exert a dominant control over litter decomposition rates.

Both litter and fresh leaf traits have successfully been used to predict litter decomposition rate, and both sets of traits have advantages. Where litter traits shed light on the initial quality of decomposing leaves, fresh leaf traits are more closely linked to the plant's growth strategy and are more widely available. Decomposition rate has been found to correlate positively with litter nitrogen (Kurokawa & Nakashizuka 2008; Parsons & Congdon 2008), phosphorus (Alvarez-Sanchez & Enriquez 1996; Cornwell *et al.* 2008; Parsons & Congdon 2008), and cation concentrations, (Mg, K and Ca; Alvarez-Sanchez & Enriquez 1996) while it correlates negatively with molecules consisting of large carbon chains, such as lignin and cellulose (Vaieretti *et al.* 2005; Kurokawa & Nakashizuka 2008; Parsons & Congdon 2008).

Taking a step further away from the decomposition process, fresh leaf N, Mg, K and Ca concentration, and total base content (Cornelissen 1996; Santiago 2007; Parsons & Congdon 2008) turned out to be good predictors of decomposition rate. Leaf nitrogen concentration (LNC) was better at predicting decomposition rate than litter nitrogen concentration (Cornwell *et al.* 2008). Physical leaf properties are also related to decomposition rate. Specific leaf area (SLA; leaf area divided by leaf dry mass) has a positive effect on litter decomposition rate (e.g. Cornelissen *et al.* 1999; Vaieretti *et al.* 2005; Santiago 2007; Kurokawa & Nakashizuka 2008), while leaf dry matter content (DMC; ratio leaf dry:fresh mass; Kazakou *et al.* 2006; Cortez *et al.* 2007; Cornwell *et al.* 2008; Kurokawa & Nakashizuka 2008) and leaf toughness (Cornelissen & Thompson 1997; Cornelissen *et al.* 1999) have a negative effect.

There is no unambiguous answer to the question whether chemical or physical traits determine decomposition rate – and in fact, both groups are closely associated, because they are both the result of the plant's strategy. Plants follow different physiological strategies that lead to roughly the same fitness levels for coexisting species. They produce either low-quality leaves at low energy costs, or high-quality leaves at high structural costs, thus showing a trade-off between either fast growth and high photosynthesis or slow growth and persistent, long-lived leaves (Wright *et al.* 2004; Poorter & Bongers 2006; Santiago 2007). This continuum is referred to as the leaf economics spectrum (LES). In tropical forests, for example, the LES ranges from slow-growing shade-tolerant tree species to fast-growing pioneer species with high light requirements for regeneration (Poorter & Bongers 2006).

The 'economic' value of a leaf influences its afterlife, because many of the physiological and protective features of green leaves persist through senescence and after shedding. For example, traits that make leaves resistant to physical damage and herbivores (such as high leaf toughness, LDMC and low SLA and nutrient concentrations) are at the same time effective barriers against soil decomposers. Leaf palatability and litter decomposition rates are therefore positively correlated (Grime *et al.* 1996).

So far, leaf economic value has never been related directly to litter decomposition rate, although several previous studies have shown the relevance of individual leaf traits associated with the LES to decomposability (Kazakou *et al.* 2006; Cortez *et al.* 2007; Fortunel *et al.* 2009). Also, for tropical rain forest trees, there is a striking lack of published studies on the relation between individual leaf traits and litter decomposition rate. Although some work has been done on the influence of environmental conditions like soil, climate, water availability, and decomposer organisms on decomposition rate (e.g. Sherman 2003; Rueda-Delgado, Wantzen & Tolosa 2006; Powers *et al.* 2009), knowledge on the relation between leaf traits and decomposition rate is scarce in this part of the world (but see Santiago 2007; Kurokawa & Nakashizuka 2008; Santiago 2010). Furthermore, no study has explicitly evaluated the consequences of land use change on leaf decomposition rates in the tropics. Human-induced changes on land use lead to major changes in plant community composition (Boyle & Boyle 1994; Huntley *et al.* 1997) and ecosystem processes (Chapin *et al.* 2000; Díaz & Cabido 2001) such as litter decomposition and nutrient cycling (Vitousek 1997; Vitousek *et al.* 1997). The relation between land use, green leaf traits of the plant community and decomposability has been shown for herbaceous communities across Europe (Fortunel *et al.* 2009), Chinese grasslands (Zheng *et al.* 2010), and Australian grasslands and forests (Dorrough & Scroggie 2008), but never for slash-and-burn agriculture and secondary forest succession in tropical ecosystems. Yet, it is important to observe changes in plant communities and ecosystem processes in the tropics, because especially in poor, largely rural tropical countries people rely directly on ecosystem services that plant communities provide, like food, shelter, and water regulation (Díaz *et al.* 2006).

Here we present the results of a decomposition study with 23 plant species with different growth strategies from a range of common land use types in the moist tropics of lowland Bolivia. The following questions were addressed: (1) How are green leaf- and litter traits associated? (2) Which leaf and litter traits are good predictors of decomposition rate? (3) How do leaf traits and decomposition rates differ between species that are typical for different land use types? We had the following corresponding hypotheses: (1) not only leaf traits but also litter traits show a slow-fast continuum, in line with the leaf economics spectrum; (2) litter traits are better predictors of decomposition than green leaf traits because they directly affect decomposers; P is a better predictor than N because tropical soils are P limited, and not only individual leaf and litter traits predict decomposition rate, but also the position of a leaf on the leaf economics spectrum; (3) leaf nutrient concentrations and decomposition rates are lowest for mature forest species, intermediate for secondary forest species, and highest for agricultural species.

Materials and methods

Study site and species

Fieldwork was carried out in northeastern Bolivia (department Santa Cruz, province Guarayos). Mean annual temperature in the region is 25.3 °C. Annual precipitation is 1,580 mm (range 1,269 – 1,871 mm, data collected at La Chonta sawmill from 1994 to 2006), with a dry season (<100 mm/month) from May until September and one month (July) during which potential evapotranspiration exceeds rainfall. The area is situated on the southwestern border of the Brazilian Shield, characterized by rolling hills with thin soil mostly derived from gneiss, granitic, and metamorphic rocks (Crochane 1973; Navarro & Maldonado 2004). Soils have been described as inceptisols with 10-15 percent of the area being covered by anthropogenic soils (Paz-Rivera & Putz 2009). Inceptisols are soils of relatively new origin and are usually arable and fertile.

Land use types selected for this study were the moist tropical forest of the timber concession of La Chonta (15° 47'S, 62° 55'W) and agricultural systems close to Ascensión de Guarayos (15° 54'S, 63° 11'W). The agricultural systems consist of slash-and-burn agriculture in which local subsistence farmers fell and burn a patch of (secondary) forest. Crop cultivation takes place for 2-6 years. Then the sites are abandoned for a fallow period of 5-20 years and a secondary forest develops. Research took place in agricultural fields and in secondary forests aged between 5 and 15 years. Common crop species in the shifting cultivation systems are corn, rice, cassava, banana, and peanut.

For each land use type (mature forest, secondary forest, and agricultural field) three 0.5 ha plots were established (50x100m). A vegetation survey was made in each plot. The methodology differed between land use types, because of the differences in vegetation structure. For mature forest, all trees with a diameter at breast height (DBH) > 10 cm were identified and measured. Because stems tend to be smaller in secondary forests, in these forests also four subplots of 10x10m were established in which trees between 5 and 10 cm DBH were measured. In the agricultural field five 100 m transects were laid out, and every 10 m species touching or being within 10 cm of the transect were identified. Thus 50 measurements were made in each plot. The relative abundance of a species was calculated based on its basal area (for the secondary and mature forest species), or based on its relative frequency (for the agricultural fields).

A total of 24 plant species, which belonged to the most abundant species (in terms of basal area or cover) was selected (Table 1): eighteen trees, three palms, one shrub and two herbs. Species differed in their light requirements for regeneration (i.e., the inverse of shade tolerance), expressed as the average juvenile crown expo

Table 1. Twenty-four tropical species included in the study, their land use type (MF=mature forest, SF=secondary forest, AF=agricultural field), guild (TST=total shade tolerant, PST=partial shade tolerant, LL=long-lived pioneer, SLP=short-lived pioneer, PALM=palm, H=herb, S=shrub) and decomposition rate (% biomass loss after 8 weeks).

Species	**Land use type**	**Guild**	**Decomposition**
Ampelocera ruizii	MF	TST	33.2
Attalea phalerata	MF	PALM	19.7
Ficus boliviana	MF	LLP	43.3
Ficus eximia	MF	LLP	24.0
Hura crepitans	MF	PST	75.3
Licaria triandra	MF	TST	20.8
Ocotea sp.	MF	PST	18.1
Ocotea sp.	MF	PST	20.8
Pourouma cecropiifolia	MF	PST	12.6
Pouteria macrophylla	MF	PST	35.1
Pseudolmedia laevis	MF	TST	24.6
Schizolobium parahyba	MF	LLP	47.0
Stylogyne ambigua	MF	TST	21.0
Syagrus sancona	MF	PALM	67.9
Terminalia oblonga	MF	PST	51.2
Zanthoxylum sprucei	MF	LLP	60.2
Attalea speciosa	SF	PALM	20.7
Cecropia concolor	SF	SLP	38.3
Cecropia polystachya	SF	SLP	18.6
Heliocarpus americanus	SF	SLP	67.0
Trema micrantha	SF	SLP	46.8
Arachis hypogea	AF	H	87.6
Manihot esculenta	AF	S	81.9
Oryza sativa	AF	H	60.8

sure of a 2 m tall sapling of the species, occurring in the forest. The juvenile crown exposure (CEjuv) varied from 1 for a species whose saplings were only found in the shaded understory, to 3 for a species whose saplings were only found with full overhead light in gaps (Poorter & Kitajima 2007). CEjuv was only available for 17 tree species (Poorter & Kitajima 2007).

Collection of leaf and litter material

To measure fresh leaf traits, outer-canopy leaves were collected from sun-exposed plants of 23 species (for all species but *Oryza*). Seedlings were avoided. Leaves of truly shade-tolerant species, never found in full sunlight, were collected from the least shady places found. Relatively young but fully expanded and hardened leaves from adult plants were chosen, if possible without pathogen and herbivore damage and without substantial epiphyll cover. Leaves were generally collected from five individuals per species, 4-5 leaves per individual (cf. Cornelissen *et al.* 2003). A minimum of five individuals and two leaves per individual was used. For palms, which have few extremely large leaves, a minimum of three individuals and two leaves per individual was measured. Whole twig sections with the leaves still attached were collected. The partial hydration method (Vaieretti *et al.* 2007) was used: samples were put in sealed plastic bags in which air was exhaled, so that leaves closed their stomata because of the high CO_2-concentration and thus remained water-saturated. Measurements took place as soon as possible after collecting, certainly within a few days. Leaves were not removed from the twigs until just before measurement.

To collect litter material thirty rectangular litter traps (70x100 cm) were installed in the mature forest and leaf litter was collected from September 2007 until April 2008 at a monthly basis. Litter was stored in an air-conditioned building until the litter decomposition experiment was started in May 2008. Litter was then sorted per species and species that contributed enough material were used in the experiment. Palm leaves were collected afterwards, because palm fronds remain on the plant for several months after senescence. The most recent senesced frond was taken that had no remaining green pigment. In addition, just prior to the experiment freshly shed, senesced, and undecomposed leaf litter was collected for species from the agricultural systems, by collecting leaves from the soil surface or by gently shaking plants.

Leaf and litter trait measurement

For most species from mature forest leaf traits had already been measured by Rozendaal *et al.* (2006). We used the same method as in those measurements. In general, measurements were done on the leaf lamina only. For a few species the petiole was included in the measurements, but its effect on calculated trait values is believed to be negligible (Cornelissen *et al.* 2003). For species with compound leaves, leaf area and mass were based on the total of leaflets plus rachis, with the exception of palms, for which only leaflets were used.

Leaf area (LA, cm^2) was determined by scanning the leaves with a flatbed scanner and analyzing the pictures with pixel-counting software (ImageJ, National Institutes of Health). Leaf thickness (LTh, mm) was measured with a micrometer, as close as possible to the middle of the leaf, avoiding the veins. For determining fresh mass (g), leaves were rehydrated during the night in plastic bags filled with moist tissue. Following the rehydration procedure, the leaves were cut from the branch and gently blotted dry with tissue paper to remove any surface water before measuring water-saturated fresh mass. Each leaf sample was then dried in the oven at 60°C for at least 72 h and its dry mass (g) was determined.

Force to punch (F_p, N cm^{-2}) is an indicator for the resistance of plants to herbivory (Coley 1983). F_p was measured with a penetrometer, which measures the mass that is needed to penetrate the leaf, between the veins, with the head of a nail. The weight on the nail was gradually increased until the nail penetrated the leaf. F_p was calculated as $mass*9.81/(\pi*r^2)$, in which mass was expressed in kg and r represents the radius of the head of the nail in cm (0.181 in our study). Specific force to punch (SF_p) was calculated as F_p divided by leaf thickness, and is an indicator of the leaf material toughness (cf. Onoda *et al.*, unp. ms.). Chlorophyll content per unit area (Chl, in SPAD-units) was determined with a chlorophyll meter (SPAD-502, Konica Minolta, Osaka, Japan). The correspondence between SPAD values and independent measurements of chlorophyll contents is very good (Anten & Hirose 1999). For a pooled sample of leaves per species, the leaf nitrogen concentration (LNC, nitrogen mass per unit leaf mass, %) and leaf phosphorus concentration (LPC, phosphorus mass per unit leaf mass, %) . LNC is a proxy for the photosynthetic capacity of the leaf. For leaf litter, nitrogen (LitterNC, %), phosphorus (LitterPC, %), and carbon concentrations (LitterCC, %) were measured.

From these data the following parameters were derived: specific leaf area (SLA, one-sided area of a fresh leaf divided by its oven-dry mass, expressed in cm^2 g^{-1}), as a measure of the amount of leaf area for light capture per unit biomass invested; leaf dry matter content (LDMC, oven-dry mass of a leaf divided by its fresh mass, expressed in g g^{-1}); leaf density (LD, in g cm^{-3}); and litter carbon:nitrogen ratio (Litter C:N).

Litter decomposition experiment

Litter decomposition rate was determined using the litter bag technique. Per species, 16 bags (size 10 * 15 cm) with one gram of air-dried litter were prepared. Litter bags had a mesh size of 2.5 mm. This mesh size prevents the loss of small litter fragments but allows access of mesofauna (Swift, Heal & Anderson 1979). Mesh size may affect absolute decomposition rate, but it does not significantly change the species ranking based on litter mass loss (Cornelissen & Thompson 1997). Leaf litter used in the decomposition experiment was buried in the state in which it was found. This means that some compound leaves, for example peanut leaves, had their rachis attached, while others, such as *Schizolobium parahyba* were decomposed without rachis. Although palm leaves fall down as a whole, their woody rachae were not included in the experiment. This could have led to an overestimation of their decomposition rate.

The litter bags were placed in an experimental litter bed in the tropical moist forest of La Chonta. Such a purpose-built outdoor leaf-mould bed normally hosts a naturally developed decomposer community. The bed had been established by clearing a flat area in the forest understory and consisted of 16 randomized blocks in which each block (0,5*0,75 m^2) contained one sample of each species. On 24 and 25 May 2008, the bags were buried at approximately 4-5 cm depth. Since the experiment started at the beginning of the dry season, and since humid conditions are favourable for decomposers, the leaf decomposition bed was watered daily with approximately 5 l water per m^2. This amount of water corresponds to the precipitation per day in La Chonta averaged throughout the year.

After one and two months, eight bags per species were collected from the decomposition bed. The content of the litterbags was gently brushed clean, after which the litter was oven-dried at 65 °C for 48 h and weighted. Decomposition rate (Dec, in %) was calculated as the percentage of initial dry mass lost after one or two months. A 5 g subsample per species had been set aside before the start of the experiment, in order to establish the relationship between the air-dry litter placed in the field and oven-dry litter mass, and for litter chemical analyses.

Community-weighted mean trait values per land use type

For each plot, the community-weighted mean (CWM) of LNC and SLA were calculated, based on the relative abundance of those species that made up 80% of the basal area (for the mature and secondary forest), or cover (for the agricultural field). Tree basal area scales closely with crown area, and is therefore a good indicator of tree cover. The rationale of the 80% cut-off limit is that the most abundant species contribute most to vegetation characteristics and ecosystem processes (Garnier *et al.* 2004). CWM was calculated for each plot as the sum of (the relative abundance of the species, multiplied by their species-specific trait value).

Statistical analyses

To evaluate how leaf traits of species were associated, a Principal Component Analysis (PCA) was done with 10 leaf traits and 4 litter traits, using species (n=23) as data points. A correlation analysis was carried out, to test how leaf and litter traits were correlated with decomposition rate. To evaluate which traits were the best predictors of decomposition rate, a forward and a backward multiple regression analysis were done, using the leaf - and litter traits as independent variables. A one-way ANOVA with Tukey HSD post-hoc tests was used to evaluate whether leaf traits and decomposition rates varied between species belonging to different land use types. A one-way ANOVA with Tukey HSD post-hoc tests was used to evaluate whether the CWM differed between land use types. Data were tested for homoscedasticity and leaf area was $\log_{10}$-transformed prior to analysis. All statistical analyses were carried out using SPSS 15.0 (SPSS Inc., Chicago).

Results

Association amongst leaf traits

Associations amongst the 14 leaf- and litter traits were analyzed with a PCA (Fig. 1a). The first axis explained 46% of the variation, and was positively related with SLA and nutrient

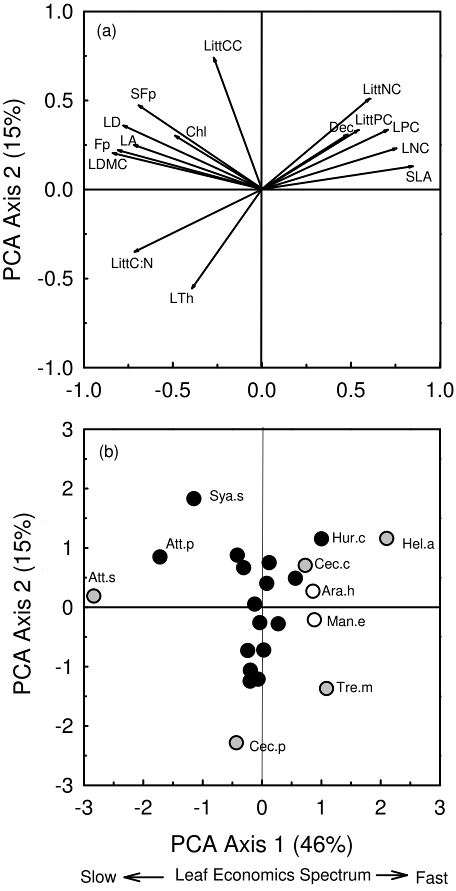

Fig. 1 Principal Component Analysis of 14 leaf and litter traits of 23 herbaceous and tropical tree species. a) Loading plots of traits, b) Species regression scores of mature forest species (black circles), secondary forest species (grey circles), and agricultural field species (open circles). Decomposition after two months (Dec) was not included in the analysis but has been plotted in the figure afterwards. Traits included are: LA = leaf area; LTh = leaf thickness; SLA = specific leaf area; LDMC = leaf dry matter content; LD = leaf density; Fp = force to punch, SFp=specific force to punch; Chl = chlorophyll content; LNC = leaf nitrogen concentration; LPC = leaf phosphorus concentration; LittNC = litter nitrogen concentration; LittPC = litter phosphorus concentration; LittCC = litter carbon concentration; LittC:N = litter C:N ratio.

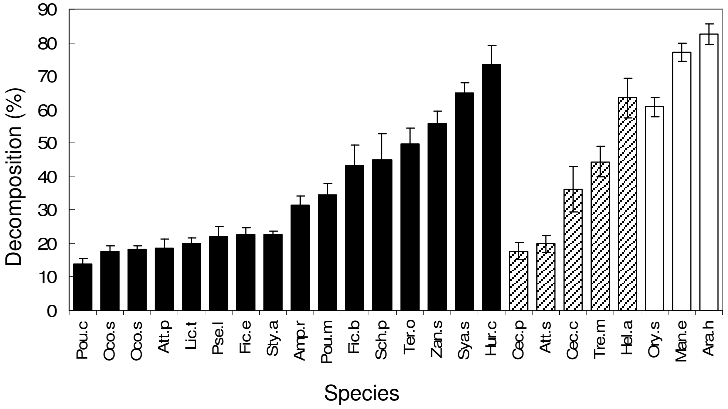

Figure 2. Decomposition rate of 24 herbaceous and tropical tree species belonging to different land use types in which they are most common: mature forest (black bars), secondary forests (hatched bars), and agricultural field (open bars). Litter weight loss (%) is calculated after two months (N=8). Means and SE are shown. Species names are indicated by the first three letters of their genus name and the first letter of their species name (see Table 1).

concentrations in leaves and litter and negatively related with leaf density, leaf dry matter content, force to punch, and leaf area. The second axis explained 15% of the variation and was positively related with litter carbon concentration and negatively related with leaf thickness.

Species are grouped in this multivariate trait space according to their functional types. Pioneer species such as *Heliocarpus* and *Trema*, and agricultural species such as *Arachis* and *Manihot* are found at the right side of the first PCA axis, palm species from the *Attalea* genus are found at the left side, and most mature forest species were found in the middle (Fig. 1b). Pioneer tree species, agricultural species, shade-tolerant tree species and palm species are each grouped together, indicating that these functional groups occupy different positions in the leaf economics spectrum.

Interspecific variation in decomposition rate

Species differed significantly in decomposition rate (ANOVA, F=30.0, P<0.001; Fig. 2). After one month, average litter mass loss across species was 24 %, ranging from 8 % for *Pourouma cecropiifolia* to 76 % for *Manihot esculenta*. After two months, litter mass loss was on average 41 %, with *Pourouma cecropiifolia* still being the least decomposed (13 %) and the peanut, *Arachis hypogea*, the most decomposed species (88 %, Table 1). Across species, litter mass loss after the first month was strongly correlated with litter mass loss after the second month (Pearson's r=0.89, n=23, P<0.001). Mass loss differed between the two harvests (paired t-test: t=-9.52, df=22, P<0.001), and was always larger after two months than after one month. For further analysis we will use the decomposition rate after two months because interspe-

Table 2. Pearson correlations between 14 leaf and litter traits, the position of a leaf on the leaf economics spectrum, juvenile crown exposure and leaf decomposition after 2 months for 23 plant species from three land use types. Significant correlations are indicated in bold (P<0,05), bold and italics (P<0,01), or bold, italics and underlined. Leaf area was log-transformed prior to analysis.

	Trait															
Trait	Lth	lgLA	LD	SLA	LDMC	Fp	SFp	Chl	LNC	LPC	Litter NC	Litter PC	Litter CC	Litter C:N ratio	LES	CEjuv
lgLA	0,29															
LD	-0,09	***0,56***														
SLA	**-0,49**	**-0,50**	***-0,70***													
LDMC	0,06	***0,59***	***0,83***	***-0,74***												
Fp	0,34	***0,70***	**0,52**	**-0,49**	***0,60***											
SFp	-0,08	***0,63***	***0,55***	-0,36	***0,64***	***0,86***										
Chl	0,29	0,40	**0,44**	**-0,47**	0,31	**0,44**	0,30									
LNC	-0,38	-0,36	***-0,61***	***0,80***	***-0,66***	**-0,49**	-0,37	-0,10								
LPC	-0,38	-0,35	**-0,49**	***0,67***	**-0,46**	**-0,43**	-0,28	**-0,45**	***0,57***							
LitterNC	-0,30	-0,29	-0,29	0,40	**-0,45**	**-0,41**	-0,33	0,04	**0,47**	**0,44**						
LitterPC	-0,31	-0,24	-0,26	**0,49**	-0,34	-0,32	-0,15	-0,28	0,34	***0,70***	0,37					
LitterCC	-0,18	0,27	0,40	-0,17	0,28	0,33	**0,44**	0,37	-0,04	0,09	0,21	-0,04				
Litter C:N ratio	0,38	**0,44**	0,38	**-0,48**	**0,50**	***0,55***	**0,44**	0,07	***-0,54***	**-0,42**	***-0,94***	-0,34	0,05			
LES	0,39	***0,72***	***0,78***	***-0,85***	***0,84***	***0,81***	***0,69***	**0,49**	***-0,76***	***-0,71***	***-0,61***	***-0,55***	0,27	***0,71***		
CEjuv	0,12	**0,53**	-0,25	0,31	-0,44	***-0,62***	**-0,60**	-0,08	0,35	0,05	0,05	0,32	-0,45	-0,06	-0,35	
Dec	-0,23	-0,12	**-0,44**	***0,57***	**-0,47**	-,024	-0,16	0,24	***0,77***	**0,44**	0,39	0,29	0,05	-0,39	**-0,49**	**0,50**

cific differences were larger at second harvest, thus providing a better resolution.

Leaf traits predicting decomposition rate

Interspecific variation in decomposition rate was significantly associated with the quality of fresh leaves (Table 2). Leaf nitrogen concentration turned out to be the strongest correlate (r=0.77; n=23; P<0.001; Fig. 3a), followed by specific leaf area (r=0.57; n=23; P<0.01; Fig. 3b), species position on the leaf economics spectrum (r=0.49; n=23; P<0.05; Fig. 3c), and leaf dry matter content (r=-0.47; n=23; P<0.05). Decomposition rate was not only related to leaf traits, but also to the regeneration strategy of the species, as indicated by the positive relationship between decomposition rate and juvenile crown exposure (r=0.50, n=17, P<0.05; Fig. 3d).

There were no significant correlations between decomposition and concentrations of nutrients or carbon in litter, although litter nitrogen concentration (r=0.39; P=0.067), and litter C:N ratio (r=-0.39; P=0.07) almost showed significant correlations. Litter and fresh leaf nutrient concentrations were, however, correlated (r between LNC and litterNC=0.47; n=23; P<0.05; r between LPC and litterPC=0.70; n=23, P<0.01). This means that the ranking of the species based on nutrient concentration is largely the same before and after leaf senescence.

Multiple regressions were carried out to analyze which leaf traits are the best independent predictors of decomposition rate. Forward multiple regression indicates that leaf nitrogen concentration and chlorophyll content explain variation in decomposition rate best (r^2=0.69; n=23, Decomposition rate

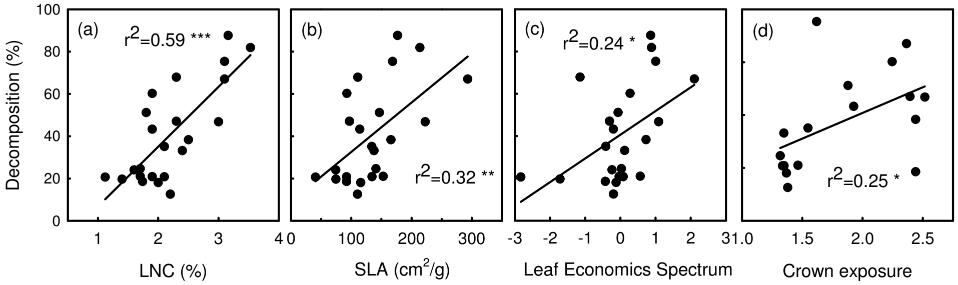

Figure 3. Litter decomposition rate (leaf litter mass loss after two months of incubation) of 23 tropical species as a function of a) leaf nitrogen concentration (LNC), b) specific leaf area (SLA), and c) species position on the leaf economics spectrum (LES). Regression lines, coefficients of determination (r^2) and significance levels are shown. Species that are dominant in different land use types are indicated with a different symbol (circle = mature forest, square = secondary forest, triangle = cultivated land).

= -55.3 + 29.4LNC+0.58Chl), while a backward regression selects both SLA and chlorophyll as the variables that best explain decomposition rate (r^2=0.65; Decomposition rate = -71.7+0.36SLA + 1.2Chl. As individual traits, LNC and SLA were significantly related with decomposition rate, but chlorophyll content turns out to be a poor predictor of decomposition (r=0.24; P=0.27).

Land use, leaf traits, and decomposition rates

Species belonging to different land use types differed significantly in their LNC (ANOVA, F=5.94; P=0.009, Fig. 4a), with species from agricultural fields having higher LNC than species from mature forest and secondary forest (Tukey HSD, P<0.05). Species from different land use types did not differ significantly in SLA (ANOVA, F=2.93, P=0.077, Fig. 4b) or their position on the leaf economics spectrum (ANOVA, F=0.99, P=0.393; Fig. 4c), but they did differ in decomposition rate (ANOVA, F=5.98, P=0.009); species from agricultural fields decomposed faster than species from secondary and mature forest (Fig. 4d).

Community-weighted mean leaf traits and decomposition rates were also calculated for each land use type, based on the relative dominance of the species making up 80 percent of the basal area or cover. Both the community-weighted mean LNC (ANOVA, F=6.63, P=0.03) and community-weighted mean SLA (ANOVA, F=8.49, P=0.018) differed significantly among land use types and were lowest in secondary forest, intermediate in mature forest, and highest in agricultural fields (Fig. 5).

Discussion

Little is known about decomposition rates of tropical plant species, and the potential effects of land use change on decomposition. We first discuss how leaf and litter traits are associated, then evaluate what drives leaf decomposition rate, and conclude how traits and decomposition rates differ for species and communities from different land use types.

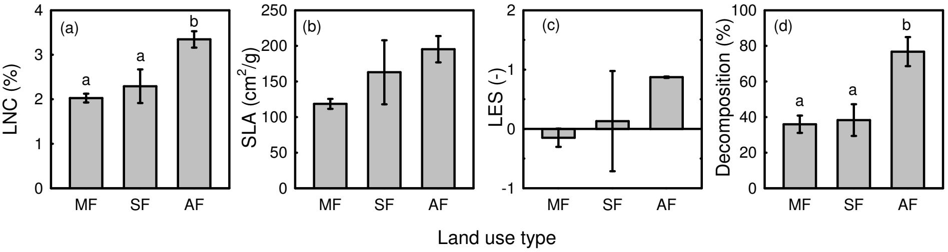

Figure 4. Traits of species belonging to three different land use types (agricultural fields (N=2-3 species), secondary forests (N=5), and mature forest (N=16). a) leaf nitrogen concentration (LNC), b) specific leaf area (SLA), c) species position on the leaf economics spectrum (LES) and d) decomposition rate. Bars indicate mean ± SE. Bars accompanied by a different letter are significantly different (Tukey HSD, P<0.05).

Association amongst leaf traits

Nearly half of leaf and litter traits (43 out of 91 possible pair-wise combinations) were significantly correlated (Table 2) and almost half of the variation in leaf and litter traits was explained by the first PCA axis (Fig. 1a). This axis was negatively related with leaf area, density, dry matter content, and toughness, and positively related with SLA and nutrient concentrations in leaves and litter. The first axis therefore represents the leaf economics spectrum, with slow, conservative traits to the left, and fast, acquisitive traits to the right. In their analysis of the worldwide economics spectrum, Wright *et al.* (2004) focused on SLA, LNC, LPC and photosynthetic traits. Our current analysis shows that apart from SLA, other leaf defence traits (leaf density, dry matter content, and toughness) form an integral part of this LES (df. Diaz *et al.* 2004; Kitajima & Poorter 2010) and that this fast-slow continuum is mirrored in litter traits (e.g., litter nitrogen concentration, litter C:N ratio, Fig. 1a).

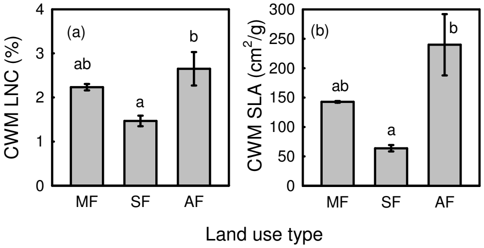

Figure 5. Community-weighted mean (a) leaf nitrogen concentration (LNC), and (b) specific leaf area (SLA) for plots (N=3) in three different land use types: mature forests (MF), secondary forests (SF) and agricultural fields (AF) Bars indicate mean ± SE. Bars accompanied by a different letter are significantly different (Tukey HSD, P<0.05).

Leaf traits predicting decomposition

The multiple regression analysis indicated that of all individual leaf and litter traits, a combination of LNC or SLA with chlorophyll content were the best predictors of decomposition rate. The relation between LNC and SLA and decomposition rate is consistent with previous studies (LCN: Santiago 2007; Cornwell *et al.* 2008; Fortunel *et al.* 2009) (SLA: Koerselman & Meuleman 1996; Diaz *et al.* 2004; Kazakou *et al.* 2006). Decomposers prefer nitrogen-rich leaves as nitrogen is an essential and limiting element for their metabolism. They might also prefer high SLA leaves, as decomposers can consume such litter more rapidly and easily, processing less leaf material per unit area or volume. In contrast, accessing C-rich and nutrient-poor material is more difficult, because decomposers need a variety of enzymes (Wieder, Cleveland & Townsend 2009).

LNC was, surprisingly, better at predicting litter decomposition rate than litter nitrogen concentration, probably because a suite of correlated leaf traits affects decomposition rate, and LNC was a better indicator of this suite of correlated traits (as summarized in the LES) than litter nitrogen concentration (Fig. 1). LNC was, also surprisingly, a better predictor than LPC, despite the fact that tropical rainforest soils are thought to be limited in P, and despite the fact that most decomposition studies in lowland tropical forests find LPC to be more important for decomposition than LNC (Vitousek 1984; Aerts 1997; Hobbie & Vitousek 2000; Santiago 2007; Wieder, Cleveland & Townsend 2009). Limitation by nitrogen is not only indicated by the results of our decomposition experiment, but also by the relatively low N:P ratios of fresh leaves (13.7) and litter leaves (12.8). A N:P ratio smaller than 14 is generally a sign of N-limitation whereas a N:P ratio higher than 16 is indicative of P-limitation (Koerselman & Meuleman 1996). Moreover, the fact that the N:P ratio declines during senescence, points out that N is preferentially resorbed over P. Two factors might explain why nitrogen played a more significant role than phosphorus in our decomposition experiments. Although phosphorus is often the most limiting nutrient in decomposition processes in tropical forests (Cleveland, Townsend & Schmidt 2002), nitrogen seems to be limiting in the forest where we carried out our experiments. The study of Cleveland *et al.* is based on a forest on extremely old, highly weathered soils in Costa Rica, whereas La Chonta forest is located on inceptisol: a soil of relatively new origin and usually fertile. In addition, black anthropogenic forest soils are relatively frequent in La Chonta forest (Paz-Rivera & Putz 2009) and these so-called terra-preta soils are especially rich in phosphorus (Peña-Claros *et al.*, unp. data). Thus, limitation by nitrogen, as has been frequently found for temperate and high latitude forests, can also be found in tropical forests. A second explanation for the importance of N during decomposition is that nitrogen is most important during early stages of decomposition, whereas P is important later on (Santiago 2007). Decomposers feed preferentially first on nitrogen, but as [N] decreases, they switch to [P] on a certain point. Our experiment might simply not have lasted long enough to detect [P] influences on decomposition.

SLA, and to a lesser extent LDMC, were also significantly correlated with decomposition rate. SLA and LDMC are highly correlated ($r=-0.74$, $n=23$, $P<0.001$), probably because they are both closely related to leaf density. A high percentage of dry matter resulted in a lower decomposition rate (cf. Kazakou *et al.* 2006; Cortez *et al.* 2007; Cornwell *et al.* 2008; Kurokawa & Nakashizuka 2008; Fortunel *et al.* 2009).

While chlorophyll content by itself is not correlated with decomposition, it explains in the multiple regression analysis a small additional part of variation in decomposition rate that is not explained by LNC or SLA. The positive effect of chlorophyll on decomposition, which to our knowledge has not been tested before, is surprising. Perhaps a high chlorophyll content is an indirect indicator of the nitrogen or magnesium concentrations in the leaf (as N and Mg are components of chlorophyll, which both directly affect decomposition rate), or an indirect indicator of SLA (as thick leaves with low LA will have a high chlorophyll content per unit leaf area). The effect of chlorophyll content suggests that it would be interesting to include it in decomposition studies, especially because it can readily and quickly be measured the SPAD meter.

We found a negative, albeit non-significant relationship between force to punch and decomposition rate (r=-0.24; n=23; P=0.266). The weak relationship between leaf toughness and decomposability could be explained by a difference in what is measured and how decomposers perceive the plant material. Possibly, microbes are responding to the strength of chemical bonds between atoms, while puncture tests work on a larger scale and respond to the size and orientation of these molecules. For example, in Cornwell *et al*. (2008) mosses are very soft by any method of toughness measurement, but have a very low decomposition rate.

Other studies, which do find a significant negative relationship between leaf toughness and leaf decomposability (Cornelissen *et al.* 1999; Perez-Harguindeguy *et al.* 2000; Kurokawa & Nakashizuka 2008) attribute this to both a dense leaf and the presence of chemically resistant elements like lignin and cellulose (Cornelissen 1996; Vaieretti *et al.* 2005; Kurokawa & Nakashizuka 2008; Parsons & Congdon 2008). We tried to capture the presence of lignin and cellulose by measuring litter carbon concentration. However, carbon was not significantly related to decomposition rate. A reason could be that only the amount, and not the nature of carbon was measured. Thus, the carbon measured could have consisted of small compounds, which do not form a barrier for decomposition, instead of large molecules like lignin and cellulose. Studies in which carbon was found to play a role in decomposition always worked with ratios between carbon and a nutrient (Perez-Harguindeguy *et al.* 2000; Kurokawa & Nakashizuka 2008), but in our study, ratios were not significantly correlated with decomposition rate either.

Not only individual leaf traits, but also species' position on the leaf economics spectrum was positively correlated with decomposition rate (r=0.49; n=23; P<0.05; Fig. 3c), with species with more "fast" acquisitive leaf traits showing higher decomposition rates than species with "slow" conservative traits. This suggests that selection for a suite of coordinated structural and chemical leaf traits that determine photosynthetic rate, productivity and leaf longevity has strong nutrient-cycling consequences. Similar results have been obtained for 35 tropical rainforest species (Santiago 2007) and 108 temperate herbaceous and woody species from a *Ponderosa* pine forest (Laughlin *et al.* 2010). However, in contrast to our hypothesis, the LES as a multivariate descriptor of leaf traits was a weaker predictor of decomposition rate than individual components of the LES, such as LNC and SLA, and the LES was not selected by the multiple regression analysis. This suggests that individual components of the LES (LNC, SLA) are the real drivers of decomposition rate, rather than the LES itself.

Leaf decomposition rate was also related to the regeneration strategy of the species, albeit indirectly, with regeneration strategy determining leaf traits, which in turn define decomposition rate. Light-demanding pioneer species decomposed faster than long-lived pioneer and shade-tolerant species (Fig 3d). This means that a plant's strategy determines its entire life cycle: pioneer species, for instance, combine high nutrient uptake rates with fast growth, leaf turnover, and litter decomposition rates. Such a positive plant-soil feedback loop might, in the case of pioneer species, enhance soil fertility (Wardle *et al.* 2004), and in this way adults of these acquisitive species may pave the road for a new generation. In other words, systems dominated by pioneer species push themselves to an overall more fertile and productive state (cf. Cornelissen *et al.* 1999; Wardle *et al.* 2004).

Land use, leaf traits, and decomposition rates

Functional parameters of the plant species in each community that are important for decomposition changed with the intensity of land use. The communities of mature and secondary forests consisted of long-lived tree species with low LNC, while in agricultural fields this community had been replaced by assemblages composed of fast-growing herbaceous species with higher LNC (Fig. 4). This reflects disturbance intensity and frequency in the different land use types with land use being least intensive in mature forest and most intensive on agricultural fields. These results are in line with other studies, which found that higher disturbance selects for acquisitive plants with leaf characteristics at the faster end of the growth spectrum (Díaz *et al.* 1999; Garnier *et al.* 2007; Dorrough & Scroggie 2008; Fortunel *et al.* 2009). SLA and position on the leaf economics spectrum did not differ significantly between land use types, although they increase gradually from mature forest to agricultural field (Fig. 4b, c), like we expected. One reason can be the relatively low number of species per land use type, another that within mature forest species and secondary forest species there is a large interspecific variation in leaf traits, due to the presence of the palm species *Attalea speciosa, Attalea phalerata,* and *Syagrus sancona.* If palms are excluded from the analysis, then SLA and LES do differ significantly between land use types (data not shown). Palm species are characterized by tough, long-lived leaves with very low LNC, SLA, and extremely low scores on the LES axis (Fig 1). A palm species like *Attalea speciosa* becomes very dominant in secondary forest fallows, when these are frequently burned through slash and burn activities, because it resists fire, as its apex is well-protected by surrounding leaves, and because it lacks a vascular cambium – an advantage, although there are, in other parts of the world, other, non-monocot species which are able to succeed in frequently burned environments despite the presence of a vascular cambium (Bond 2008). Herbaceous or woody ferns are known to become dominant in other early successional tropical and sub-tropical forests (Amatangelo & Vitousek 2008; Amatangelo & Vitousek 2009). Species from agricultural fields had a higher average litter decomposition rate than secondary and mature forest species (Fig. 4d). Secondary forests were hypothesized to show a higher decomposition rate than mature forest, but the abundance of palms lead to a lower decomposition rate than expected. This means that the value of secondary forests for increasing fertility can be questioned.

The community-weighted mean reflects the characteristics of an "average" plant in the community. Secondary forests were hypothesized to occupy an intermediate position between mature forests and agricultural fields (in line with Fig. 4), because its communities are thought to consist of rapid growing and photosynthesizing pioneer tree species with high LNC and SLA. However, secondary forests turned out to have the lowest LNC and SLA (Fig. 5), which is again explained by the high abundance of palm species; they make up 55 percent of total basal area in secondary forests. The palm species *Attalea speciosa* alone represented 46 percent of the assembly. It would be interesting to compare this high palm abundance with other secondary forests, to see whether this feature is widespread or typical for the Guarayos region.

This study showed that land use change indirectly affects decomposition rate. The indirect pathway, along which global change influences the functional composition of a community, which in turn changes ecosystem functioning, is known to be more important than the direct pathway, in which changes in abiotic conditions inluence processes in the ecosystem (Cornwell *et al.* 2008). The nature of this process has been shown for Mediterranean fields (Kazakou *et al.* 2006; Cortez *et al.* 2007; Fortunel *et al.* 2009), but this is to our knowledge the first time that it has been analyzed for tropical land use types, which are very important in global carbon and local nutrient cycles.

Conclusions

Tropical tree species show a slow-fast continuum in both the production and breakdown of their leaves. This is due to differences in leaf and litter traits, which range from tough, well-defended leaves to cheap, nutrient-rich and productive leaves. Leaf nitrogen concentration or specific leaf area combined with chlorophyll content per unit leaf area determine leaf decomposition rate of a range of tropical plant species from different land uses. Furthermore, species' position on the leaf economics spectrum and regeneration light requirements predict decomposition rate.

Communities from the land use types from which the species were derived differed not only in their average leaf traits, but also in decomposition rates. Species from agricultural fields had higher average LNC and decomposition rate than species from secondary and mature forests. Given that land use change is happening on a large scale, and results into radical changes in species composition, this study shows that large consequences for nutrient and carbon cycling are to be expected, both within an ecosystem and globally.

Acknowledgements

We would like to thank staff and personal of the Instituto Boliviano de Investigación Forestal for logistic support, La Chonta Ltda and the local farmers for access to their sites, Ricardo Mendez for help with the decomposition experiment and two anonymous reviewers for their helpful comments. This study was partly funded by the DiverSus project through Inter-American Institute for Global Change Research (IAI) CRN 2015, which is supported by the US National Science Foundation (Grant GEO-0452325). MB was financially supported by Dr. Hendrik Muller's Vaderlandsch Fonds, Stichting Nijmeegs Universiteitsfonds, Stichting Het Kronendak and Stichting Fonds Dr. Christine Buisman, and LP was supported by a grant from the Wageningen graduate school Production Ecology and Resource Conservation.

Leaf economics spectrum: palm, peanuts, and *Cecropia* leaves.

Establishing a decomposition bed in secondary forest.

Chapter 5

Influence of land use intensification on litter decomposition rate

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Abstract

Land use intensification (LUI) affects the ability of ecosystems to maintain and regulate essential ecosystem processes and services, such as decomposition and soil fertility. We evaluated the effect of LUI on decomposition by studying the effects of environmental site characteristics and litter quality across five contrasting tropical land use types: three natural systems (mature-, logged-, and secondary forest) and two cultivated systems (agricultural land and pastureland). Decomposition rate was measured as mass loss along five incubation periods, using the litterbag method.

With LUI environmental site characteristics became less favourable for decomposition potential; mature- and logged forest had better environmental site conditions for litter decomposition, followed by secondary forest, agricultural land and pastureland. Leaf litter from the five land use types varied in several litter traits. Litter from natural systems was characterized by high concentrations of lignin, tannin and nitrogen, whereas litter from cultivated systems had high concentration of cellulose. As a consequence, litter decomposability increase with land use intensification; litter from mature- and logged forest had low decomposability, followed by secondary forest, agricultural land and pastureland. These results suggest that, at community level and across a large gradient of LUI, is necessary to combine chemical and physical litter characteristics to determine litter quality and predict decomposition rate.

Against our expectations, difference in litter quality along LUI had a stronger effect on decomposability (explaining 40% of the variation) than differences in environmental site characteristics (explaining 20%). However, the actual decomposition rate was site-dependent showing different patterns of decomposition along LUI. Actual decomposition in pastureland and mature forest was generally higher than actual decomposition in secondary forest. Consequently, our results indicate that the effects of land use intensification on litter decomposition may negatively affect soil fertility mainly because of the changes in the quality of litter rather than changes in decomposition rates.

Keywords

Land-use intensification, litter decomposition, tropical forest, secondary forest, cultivated systems.

Introduction

Land use intensification (LUI) is driven by humanity's necessity to increase provisioning services, such as food and fiber. However, LUI may also an diminishes the ecosystem's capability to maintain and regulate processes and services essential to maintain life (such as primary production, climatic regulation, or nutrient cycling; MEA 2005a). Decomposition is such an essential process. It releases carbon and nutrients from organic material and is, therefore, directly linked to soil fertility (Wood et al. 2009), nutrient uptake by plants (Scherer-Lorenzen 2008), and primary production (Bengtsson 1998, Mack and D'Antonio 2003). Because of these links, decomposition has often been used as an excellent example to understand and predict the consequences of LUI on ecosystem services (Sommerville et al. 2004, Quétier et al. 2007b, Bakker et al. 2011). Although LUI effects on decomposition have been frequently studied, little is known for tropical ecosystems (Waring 2012). This is surprising because 1) many tropical areas are characterized by leached and poor soils, where most of the nutrients are locked up in the vegetation, and where litter decomposition is the main driver of nutrient availability; 2) many subsistence farmers in the tropics rely for their production on natural nutrient cycling, and do not have access to artificial fertilizers; and 3) in the recent years LUI and its impacts on ecosystem functioning have increased rapidly in the highly bio-diverse areas of the tropics.

Litter quality, climate, nutrient availability, communities of soil organisms, and site-specific factors determine the rates and patterns of decomposition (Lavelle et al. 1993, Björn and McClaugherty 2008). Litter quality, or decomposability, generally increases with litter nitrogen-, and phosphorus concentration, and decreases with, tannins-, and lignin concentration, and C:N and lignin:N ratios (Tian et al. 1995, Parsons and Congdon 2008, Bakker et al. 2011, Makkonen et al. 2012). Such traits sort plant species along a leaf economics spectrum (Wright et al. 2004), which ranges from slow-growing conservative species to fast-growing acquisitive ones (Diaz et al. 2004). This spectrum is expected to translate in slow to fast decomposability (Cornelissen 1996, Santiago 2007, Cornwell et al. 2008, Bakker et al. 2011).

Litter quality is particularly important drivers of decomposition rate at regional or local scales (Couteaux et al. 1995, Cornwell et al. 2008) . Other environmental factors such as soil properties or land management practices may also drive variation in decomposition at local scales (Quétier et al. 2007b).

Land use intensification results in vegetation types that differ greatly in environmental conditions and species composition, and therefore, in the quality of the litter (Foley et al. 2005, Garnier et al. 2007, Jackson et al. 2009). For instance, modest changes in the relative abundance of species (e.g., conversion of mature- to logged forest) slightly affect litter quality, whereas strong changes through complete species turnover (e.g., conversion of mature forest to agricultural fields) may strongly alter litter quality. In general, with intensification of land use species composition shifts from species with more resource conservative traits to species with more resource acquisitive traits (Garnier et al. 2007, Bakker et al. 2011). If litter quality is the main driver of decomposition rate (Pandey et al. 2007, Quested et al. 2007, Tateno et al. 2007), then an increase in decomposition rate with LUI can be expected (Bakker et al. 2011). Effects of LUI on soil properties and microclimate are very heterogeneous and, therefore, also their effects on the decomposition process. For instance, organic fertilization increased soil nitrogen in grassland systems but it did not affect litter decomposition (Quétier et al. 2007b); a higher pH in agricultural land compared to forest led to a decrease in decomposition rate; temperature increase after forest clearing for slash-and-burn agriculture was positively associated with decomposition (Neher et al. 2003). Soil biodiversity is also affected by LUI, which can decrease as a result of cultivation, removal or addition of plant residues (Beare et al. 1997).

In this study we evaluated comprehensively how land use intensification influences litter decomposition rate through changes in litter quality and site environment characteristics of five different land use types. Site environment encompasses soil properties, microclimate, decomposer diversity and management practices. We selected five important and widespread land use types (LUT) in the tropics that represent a gradient of land use intensification: three forest systems (mature-, logged and secondary forest), and two cultivated systems (agricultural land and pastureland, see details in Table 1, chapter 1). The following questions were addressed: 1) how do differences in site-specific characteristics among LUT affect decomposition rate (decomposition potential), and how much of these differences are explained by soil properties; 2) how does litter quality differ across LUT; 3) how much of the variation in litter decomposition rate is explained by litter quality versus land use type, and their interaction; and 4) how does the actual decomposition rate (in-situ decomposition, litter decomposed in its own land use type) vary across land use types?

Specially, we hypothesized that (1) decomposition rate of a given litter type will strongly decrease with land use intensification (without added fertilizer) because of decreased soil fertility, increased harshness of the environment (because of the high irradiance and vapor pressure deficit that come along with an open canopy), and loss of decomposer diversity; (2) litter quality will increase as land use is intensified because the plant community shifts from conservative to acquisitive species (Garnier et al. 2007, Bakker et al. 2011). As a result, there will be a shift from more recalcitrant litter with high tannin and lignin content and high C:N ratio (Tian et al. 1995), to more labile litter with high concentration of N and P (Cornelissen and Thompson 1997); (3) differences in environmental site characteristics of the land use types will influence litter decomposition rate more strongly than differences in litter quality because management intensification strongly alters decomposition-related environmental drivers, such as decomposer diversity and abiotic factors. Also (4) we expect that increased litter decomposability of cultivated systems will (partly) offset the poorer environmental conditions for decompositions, leading to site-dependent responses.

We tested these hypotheses experimentally in a Bolivian tropical lowland forest system. Changes in decomposition potential among the five LUT were measured using standard litter, and four representative soil types. Eleven litter traits were measured as indicators of litter quality. The relative contributions of litter quality versus land use type on actual (in situ) decomposition rate were evaluated using a fully crossed factorial design with reciprocal exchanges of litter types among LUT. This is the first (tropical) study that has comprehensively disentangled the interactive effects of vegetation species composition, through leaf afterlife effects on litter quality, and multiple environmental drivers, on variation in decomposition rates among land use types.

Materials and methods

Study site

This study was conducted in the province of Guarayos, in tropical lowland Bolivia (15o 54'S, 63o11'W). In the year of the experiment (2009) the precipitation was 1582 mm, with the highest monthly precipitation in March (265 mm) and December (319 mm) and the lowest in August (23mm) and September (6.5 mm; SENAMHI 2009). Mean annual minimum\maximum temperatures were 20\30 oC, the coldest and hottest months of the year were June (16 oC) and October (32 oC), respectively (SENAMHI 2009). The area is situated on the Precambrian Brazilian shield (Cochrane 1973) and its soils have a sandy loam texture, neutral pH, total N of 0.32% and total P of 11.23 cmol kg-1(Peña-Claros et al. 2012). The vegetation can be classified as semi-deciduous tropical moist forest (Toledo et al. 2011a), with a canopy height of c. 27 m, tree species richness of 59 per ha, density of 368 trees per ha, and basal area of 19.7 m2/ha (all for trees >10 cm diameter at breast height [dbh]). About 160 tree species are found in the area, the most common ones (> 10 cm dbh) being Pseudolmedia laevis (Moraceae), Ampelocera ruizii (Ulmaceae) and Hirtella triandra (Chrysobalanacea; Peña-Claros et al. 2012).

The Guarayos province covers an area of 27,343 km2. About 60% of this area is covered with mature forest, 32% with crops under slash–and- burn agriculture (with fallow period of 7 to 15 years), and 8% with natural and cultivated pasturelands (GMAG 2006). From an economic and social point of view, the most important activities are timber production (88% of Guarayos' forest is used as timber production forest), agriculture, and livestock production. More than 10 agricultural crop species (e.g., corn, rice, cassava, banana, and peanut) are produced, mostly for subsistence and local markets. Cattle ranching is practiced at medium to large scale farms, using mainly exotic grasses, such as Brachiaria brizantha , as fodder (GMAG 2006).

Land use intensification gradient: We selected the five most important land use types in the region, which cover the whole gradient of land use intensification. Their management intensity was qualitatively assessed based on five parameters (Lambin et al. 2003, Jackson et al. 2009): management intensity (in terms of pre-disturbance biomass loss), frequency of management practices, duration of management practices, magnitude of disturbance (percentage of undisturbed forest in a radius of 1 km) and time since disturbance (time for natural regeneration). Based on their average scores, the land use types could be ranked from low to high land use intensification in the following order: mature forest, logged forest, secondary forest, agricultural land and pastureland (See details in Table 1, chapter 1).

Experimental design and measurements

We compared five land use types (mature-, logged- and secondary forest, agricultural land and pastureland, Table 1 in chapter 1) using five plots per land use type distributed randomly distributed around the village of Guarayos, and for mature forest and logged forest we used the Long-Term Silvicultural Research Program (LTSRP) established by the Instituto Boliviano de Investigación Forestal (IBIF; details of plot design for the LTSRP in; Carreño-Rocabado et al. 2012), totaling 25 plots. Decomposition rate was measured using the litterbag method, which is based on the mass loss rates of dry litter content of bags that are put in the field (Wider and Lang 1982). To evaluate how land use intensification affects decomposition rate we conducted two complementary experiments. First, we used two standard materials (Homann and Grigal 1996) to test the effect of differences in environmental site characteristics of the land use types, which includes soil properties and other specific-site factors that we did not measure (e.g. climatic variables, decomposer diversity, management practices). Second, we used litter of each of the five land use types in a fully reciprocal litter transplant study (Makkonen et al. 2012) to disentangle a) the relative importance of environmental site characteristics and litter quality of the five land use types on decomposition rate, and b) site-dependent response across LUT on actual decomposition (Björn and McClaugherty 2008). Here we explain the common details of both experiments. In each of the 25 plots a litter bed of 1.5x2 m was established containing ten lines of litter bags, each line with seven litter bags belonging to one of the seven litter types (2 standard materials and 5 litter types coming from each of the 5 different LUTs). We cleaned 2-3 cm of the top soil layer from litter and roots, placed the litter bags horizontally on the ground and covered them with a layer of soil and litter. This cover layer was pressed against the litter bags to assure full contact between the bags and the soil. The cover layer was subsequently covered with a layer of wire mesh to protect against digging animals. Litter beds in pastures were also fenced to protect them against cattle. Decomposition was monitored for 10 months (March through December 2009), at five times (27,59,112,224 and 285 days after burial). At each harvest two lines of litter bags were retrieved. In total 1750 litter bags (5 land use types x 5 plots x 7 litter types x 5 harvests x 2 bags) were buried. At each harvest, the content of the litterbags was gently brushed to remove soil, and the litter was oven-dried at 70 ºC for 48 h and weighed. For some harvests we have unbalanced data due to loss of litterbags.

Decomposition potential: We evaluated the effect of environmental site characteristics of the five LUTs on decomposition potential using standardized litter types of two exotic species; Acalypha communis is a fast decomposer (labile material) and Stipa eriostachya is a slow decomposer (recalcitrant material; Vaieretti et al. 2005). The use of standard material to measure the potential of decomposition provides a standard means of comparison across systems (Neher et al. 2003). Litter bags consisted of a 0.3 mm mesh bag (10 x 7 cm) with 1 g of air-dried material. For each litterbag the initial litter (oven-dried) dry mass was calculated based on the air-dried fresh mass and the dry matter content of a subsample that was weighed at the same time as the samples, oven-dried at 50°C until constant mass and reweighed. Decomposition was calculated as percentage of loss of dry mass over the monitoring period.

*Soil properties***:** Soil samples were collected in each of the 25 plots during the study period. From each plot six soil samples were taken, one in each corner, one in the center and one where the litter bed was established. Soil samples were collected by taking a thin slice from a V-shaped hole of 15 cm depth. Soil samples from each plot were pooled and homogenized and air-dried in the field. Physical and chemical characteristics were determined at the Soil Laboratory of the Centro de Investigación Agricola Tropical (CIAT), Santa Cruz, Bolivia. Four soil properties were chosen based on their potential to influence composition and activity of microbial decomposers (Neher et al. 2003): organic matter (measured as the total carbon by the dry combustion method), N concentration (micro-Kjeldahl method), P concentration (Olsen method), and acidity (on 10-g soil samples, using 50 mL of distilled water and equilibrating for 90 min). As soil nitrogen concentration ([N]) was highly correlated with organic matter ($r=0.95$, $p<0.001$) we did not use organic matter for our analysis.

Environmental site characteristics and litter type effects on decomposition and site -dependence of actual decomposition: Litter (twigs were not considered) was collected over six months in five plots of each land use type. For mature- and logged forest we used litter traps and for the other land use types we collected un-decomposed litter from the soil. The collected litter was pooled per land use type and thoroughly mixed, air-dried, and stored. At the start of the experiment, 5 to 7 g of air-dried litter was put in 15x15 cm bags, with a mesh size of 3 mm. For each litterbag the initial (oven-dried) dry mass was calculated as described above. We calculated actual decomposition rate based on the decomposition of each litter type in its own land use type, for each of the five incubation periods (N=1 litter type in own LUT x 5 plots x 5 harvests = 25 bags, multiplied per 5 LUT, total ca 123 bags). Decomposition rate was calculated as percentage of loss of dry weight per day [g g-1 day-1] between each harvest and time 0. To evaluate the relative contribution of LUT and the 5 litter types on litter decomposition we used the total data of our factorial design for each of the 5 incubation periods (N=5 LUTs x 5 litter types x 5 plots x 5 harvests = ca 737 bags).

Litter quality: Litter chemical traits were analyzed for each of the five litter types produced by the vegetation in the five LUTs. Five samples for each litter type were separated at the same time that the litterbags were prepared. Nine litter traits were determined that potentially affect decomposition rate: litter nitrogen- (N), phosphorus- (P), carbon- (C), cellulose-, lignin-, and tannins-concentration, and the ratios of C:N, C:P, N:P, lignin:N, and lignin:P. Details of litter traits measurements are given in Appendix S1.

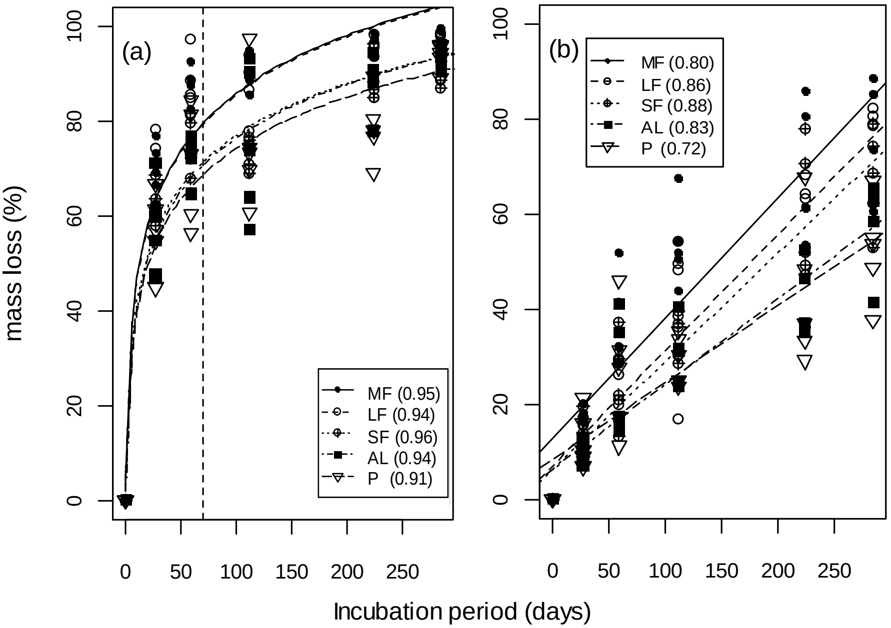
Statistical analyses

The effect of LUT and soil properties on decomposition potential was evaluated independently for recalcitrant and labile standard litter and for each of the 5 incubation periods, using two approaches. First, we carried out a one–way ANCOVA with the percentage of mass loss as dependent variable, LUT as factor and soil [N], soil [P], and soil pH as covariates. Mass loss was arcsine- or square-root transformed to meet assumptions of normality. When covariates were not significant, we did a post-hoc multiple comparison tests among LUTs. Since the analysis showed a significant effect of soil [N] after 3 months of incubation period, we ran a separate ANCOVA with only LUT and soil [N] to test the significance of intercepts and slopes. Differences among LUT in soil properties were analyzed using one-way ANOVA for each soil property, and post-hoc multiple comparison tests. To meet assumptions of normality, proportion of organic matter, total N and mass loss were ln-transformed. As a second approach we analyzed regression models (Wider and Lang 1982) using time as independent factor and mass loss at time t per land use type, which informs about the biology of the decomposition process through time.

Multivariate differences in litter quality across LUTs were described with a PCA, using five samples per litter type (N=25 samples) and eleven litter traits. Litter traits were standardized to zero mean and unit variance to avoid the influence of differences in scale amongst variables. To evaluate the relative importance of environmental site characteristics and litter quality on decomposition rate, separate two-way ANCOVAs were carried out for each of the 5 harvest periods. LUT and litter type were used as explanatory factors and ln-transformed mass loss as dependent variable, and soil properties as covariates. We followed the same steps as we did for decomposition potential tests.

The effect of LUT and time on actual decomposition was evaluated using two –way ANOVA with ln-transformed decomposition rate [g g-1 day-1] as dependent variable, and LUT and harvest as factors, after which we did post-hoc multiple comparison tests. To understand which incubation period influenced the general pattern of decomposition rate among LUT we did multiple comparisons among LUT for each harvest.

For all tests the assumptions of equal variances, normal distribution and uncorrelated residuals were evaluated with a graphical method and Shapiro and Levene tests (Lim and Loh 1996, Crawley 2007). The influence of unbalanced data in two-way ANOVA were controlled, and consequently all sum



Figures 1. Percentage of mass loss of standard labile litter (a) and recalcitrant litter (b) through time in five land use types: mature forest (MF), logged forest (LF), secondary forest (SF), agricultural land (AL) and pastureland (P). The R^2 of exponential regression models for labile and linear regression models for recalcitrant litter per land use types are reported (n=24-25 per model). Vertical line indicates the end of the first phase following Vaieretii et al. (2005).

of squares were computed following the error type I. For all post-hoc multiple comparisons we used Tukey's HSD test, either adjusting the p-values using Holm's method for data with unequal sample sizes (Crawley 2007) or using the confidence intervals of a Dunnett modified Tukey-Kramer (Dunnett 1980).

Results

Effects of environmental site characteristics on decomposition potential

Decomposition potential using labile and recalcitrant litter varied significantly with land use type (Table 1). Across the five incubation periods there was an overall trend that decomposition potential decreased as land use is intensified, however differences were not significant in all incubation periods (Fig. 1, Table 1). The temporal dynamic of decomposition potential differed between labile and recalcitrant litter: the percentage of mass loss increased logarithmically over time for labile litter and linearly over time for recalcitrant litter (Fig. 1).

Soil [N], and soil pH tended to decrease with increasing land use intensification (Fig. S1), but this was only statistically significant for pH (F4=8.63, P <0.001). Soil [P] did not differ among land use types. Soil properties (as covariates) did not affect decomposition potential across land use types (Table 1), with the exception of a significant interaction

Table 1. Summary of one-way ANCOVAS testing the influence of land use type on potential litter decomposition for labile and recalcitrant litter. Land use type was used as factor and proportion of mass loss (ln transformed) as dependent variable. Covariates are soil nitrogen (N) and phosphorus (P) concentrations and pH. Separate tests were done for each of the five incubation periods (the incubation periods cover respectively 27, 59, 112, 224, and 285 days, the table shows the equivalence in moths). Sum of squares (SS), degrees of freedom (df) and variance ratio (F) are indicated, as well as the mean percentage of biomass loss per land use type (MF=mature forest, LF=logged forest, SF=secondary forest, AL=agricultural land, P=pastureland). Means of percentage biomass loss followed by different letters are significantly different (at P=0.05), as indicated by a Tukey test and Dunnett modified Tukey-Kramer test for unequal sample sizes. **=P< 0.01; *=P<0.05, five replicates are used for all land use types but LF (n=4).

Standard litter	Incubation period (months)	d.f.	SS	F	Land use type					F value for covariates		
					MF	LF	SF	AL	P	Soil-N	Soil-P	Soil -pH
Labile	1	4,20	0.08	3.32*	69^{a}	68^{ab}	63^{ab}	56^{b}	57^{ab}	0.02 ns	0.22 ns	1.24 ns
	2	4,20	0.19	5.19*	86^{ab}	88^{a}	75^{ab}	72^{b}	71^{b}	1.02 ns	0.51 ns	1.18 ns
	3(+)	4,20	0.11	1.13 ns	87	85	74	77	77	6.5 *	0.27 ns	0.01 ns
	7	4,20	0.26	10.8 **	95^{a}	96^{a}	89^{ab}	89^{ab}	79^{b}	0.09 ns	1.51 ns	0.81 ns
	9	4,18	0.12	12.18**	99^{a}	98^{a}	92^{b}	93^{b}	94^{b}	1.25 ns	0.05 ns	0.01 ns
Recalcitrant	1	4,20	0.03	2.47	17	15	12	10	12	0.02 ns	0.38 ns	1.16 ns
	2	4,20	0.08	1.38	37	24	24	24	25	0.11 ns	0.14 ns	0.96 ns
	3	4,20	0.21	5.9*	58^{a}	41^{ab}	34^{b}	30^{b}	29^{b}	0.32 ns	0.55 ns	0.03 ns
	7	4,20	0.29	3.8*	69^{a}	57^{ab}	59^{ab}	41^{b}	43^{b}	0.51 ns	0.34 ns	4.43 ns
	9	4,18	0.25	4.8*	78^{a}	76^{ab}	68^{ab}	59^{ab}	53^{b}	0.24 ns	0.23 ns	0.24 ns

(+) When only land use type and soil nitrogen concentration are used in the ANCOVA both factors and their interaction were significant at p<0.05.

Table 2. Leaf litter (L) chemical composition (mean± SE) of the community litter from five land use types (MF=mature forest, LF=logged forest, SF=secondary forest, AL=agricultural land, P=pastureland)

Chemical traits	Litter from land use type:				
	MF	LF	SF	AL	P
Nitrogen	1.2 ± 0.02	1.7 ± 0.45	1.62 ± 0.03	0.85 ± 0.09	0.84 ± 0.09
Phosphorus	0.08 ± 0	0.13 ± 0.02	0.09 ± 0	0.09 ± 0	0.09 ± 0
Carbon	40.82 ± 1.09	45.4 ± 7.32	39.33 ± 1.11	41.23 ± 0.61	39.7 ± 1.08
Cellulose	14.73 ± 1.65	13.82 ± 1.74	13.92 ± 0.67	25.96 ± 1.03	23.12 ± 2.41
Lignin	18.72 ± 1.38	20.728 ± 0.7	23.79 ± 0.34	14.28 ± 1.21	14.51 ± 0.84
Tannins	2.2 ± 0.3	0.97 ± 0.31	0.48 ± 0.08	0.19 ± 0.04	0.19 ± 0.03
N.P	13.86 ± 0.58	13.36 ± 4.84	17.62 ± 0.74	8.84 ± 0.96	8.98 ± 1.05
C.N	34.06 ± 0.82	27.12 ± 2.71	24.2 ± 0.8	48.66 ± 5.24	47.52 ± 6.66
C.P	476.4 ± 35.95	348.96 ± 93.66	437.04 ± 12.35	423.16 ± 36.9	415.02 ± 33.3
Lignin.N	15.6 ± 1.11	12.79 ± 3.14	14.65 ± 0.4	16.79 ± 0.94	17.24 ± 1.68
Lignin.P	218.12 ± 15.54	157.3 ± 20.83	264.4 ± 4.04	146.38 ± 14.77	151.63 ± 13.6

between soil [N] and LUT (F4 = 4.774, $p < 0.05$) on the decomposition of labile litter after 3 months; mass loss was positively correlated with soil [N] in all LUTs, but not correlated with soil [N] in mature forest (data not shown)

Differences in litter quality among land use types

Leaf litter from the five land use types varied in several litter chemistry traits (Table 2). The leaf litter concentrations of N, cellulose, lignin, tannins and the N:P ratio varied the most among litter type. N concentration ranged between 1.7% for litter of logged forest and 0.84% for litter of pastureland; cellulose concentration ranged between 26 % for litter of agricultural land and 14% for litter from natural systems; tannins concentration ranged between 2.2% to 0.19% for litter of cultivated systems (Table 2). The PCA shows clear differences in litter quality between forest systems and cultivated sys-

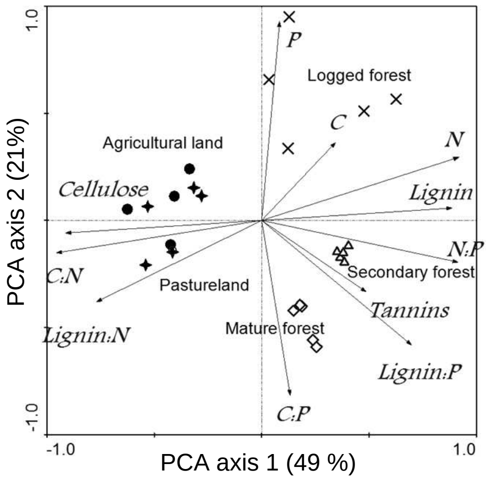


Figure 2. Principal-component analysis of litter type from the five land use types (mature forest [diamond], logged forest [x mark], secondary forest [triangle], agricultural land [circle] and pastureland [star]) and litter traits, nitrogen (N), phosphorus (P), carbon (C), lignin, cellulose and tannins concentrations, and ratios of N:P, C:N, C:P, lignin:P, and lignin:N. The first axis explains 49 % of the variation and the second axis 21 % of the variation.

Table 3. Two-way ANCOVA to test the effects of difference in environmental site characteristics (LUT) and litter types (litter) of the five land use types on litter decomposition rate. LUT and litter were used as factors and proportion of mass loss (log transformed for 1^{th},2^{th}, and 3^{th} harvest) as dependent variable. Covariates are soil nitrogen (N) and phosphorus (P) concentrations and pH. Separate tests were done for each of the five incubation periods (the incubation periods cover respectively 27, 59, 112, 224, and 285 days, the table shows the equivalence in moths). Sum of squares (SS), F and p values are shown. **=significant differences at 0.001. The fitness of linear models are presented as R^2.

Source of variation	Incubation period (months)														
	1			2			3			7			9		
	SS	F	p	SS	F	p	SS	F	p	SS	F	p	SS	F	p
LUT	9.27	11.71	<0.001**	3.3	7.7	<0.001**	2.51	7.74	<0.001**	0.83	32.04	<0.001**	0.66	13.86	<0.001**
Litter	13.75	17.37	<0.001 **	14.8	34.02	<0.001 **	11.83	36.47	<0.001**	2.95	80.37	<0.001 **	1.79	31.68	<0.001 **
LUT*Litter	3.67	1.19	0.314	4.04	2.40	0.004 **	1.20	0.93	0.538	0.35	5.71	<0.001 **	0.20	0.97	0.491
Soil- N	0.04	0.19	0.661	0.51	4.89	0.029 **	0.01	0.13	0.719	0.00	0.46	0.498	0.03	2.24	0.138
Soil- P	0.00	0.00	0.961	0.01	0.14	0.708	0.04	0.51	0.477	0.00	0.04	0.849	0.00	0.62	0.432
Soil-pH	0.13	0.63	0.427	0.15	1.39	0.241	0.00	0.06	0.800	0.00	0.28	0.600	0.04	2.84	0.097
Error	18.80			10.20			7.72			0.59			0.88		
Explained variation (R^2)	59 %			69 %			67 %			88 %			76 %		

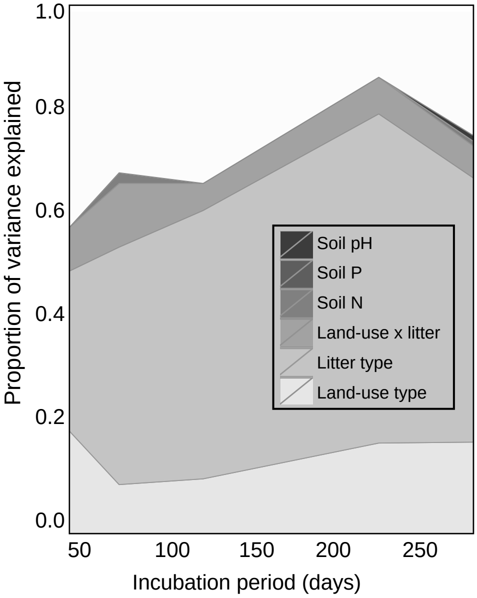


Figure 3. Percentage of litter decomposition variance explained by environmental site characteristics (LUT), litter quality, their interaction and the covariates soil N and P concentration and pH. Results are based on two-way ANCOVA tests for each of the five incubation periods. The summary of the ANCOVAs is presented in Table 3.

tems. The first two axes explained 70% of the variation in litter quality (Fig. 2). In general litter from natural systems was characterized by high levels of concentrations of nitrogen, phosphorus, lignin, tannin, and N:P ratio, whereas litter from cultivated systems was characterized by a high cellulose concentration and a high C:N, and lignin:N ratios (Fig. 2).

A second PCA including only natural systems showed a larger heterogeneity in litter quality from logged forest: higher tannin concentrations for mature forest and higher conentration of lignin and N for logged and secondary forest (Fig. S2).

Environmental site characteristics and litter quality effects on decomposition

Both environmental site characteristics (represented by each LUT) and litter type of the five different LUTs significantly affected decomposition rate, whereas their interaction was only significant after 2- and 7-months of incubation (Table 3). The ANCOVA model explained on average 72 % of the total variation. Across the five harvests, litter type explained 48 % of the variation in decomposition rate, LUT 15 % and their interaction explained 7 % (Fig. 3). The effect of LUT on decomposition rate was stronger at the initial and final part of the incubation period than in-between (Fig. 3). In contrast, the effect of litter type increased through time and slightly dropped at the end of the incubation period (Fig. 3). Soil properties hardly affected decomposition rate; only soil N concentration was significant as a covariate in harvest two (Table 3).

Multiple comparisons amongst the five LUT showed that mature- and logged forest had the fastest decomposition rate, secondary forest an intermediate decomposition rate, and cultivated systems the slowest decomposition rate (Fig. 4a). Multiple comparisons amongst the five litter types showed the opposite pattern; decomposition of litter originating from mature- and logged forest (forest) was the slowest, litter from secondary forest was intermediate, and decomposition rate of litter from cultivated systems was the fastest (Fig. 4b). Except for the first harvest, secondary forest was not significant different from mature- and logged forest.

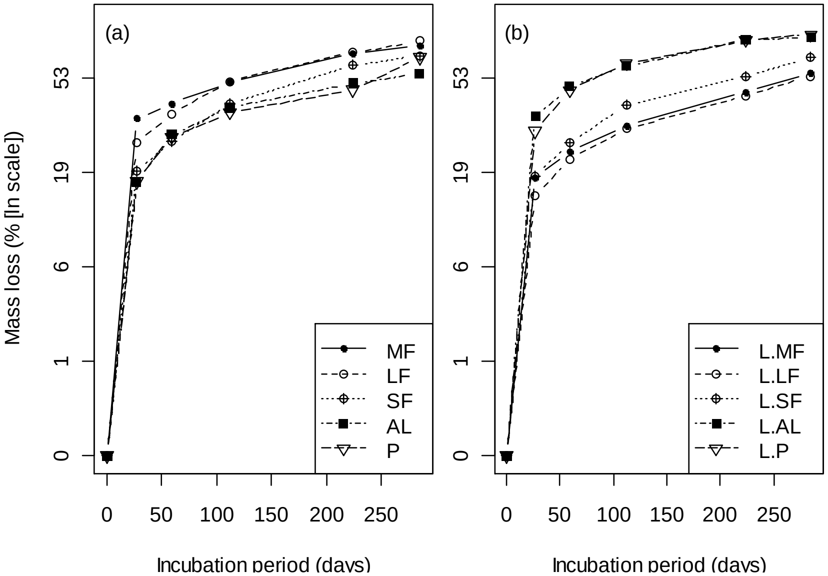


Figure 4. Influence of environmental site characteristics of the five land use type and five litter types on litter decomposition. Litter belonging to each five land use types (mature forest (MF), logged forest (LF), secondary forest (SF), agricultural land (AL) and pastureland (P) were placed in the different land use types in a fully reciprocal litter transplant study. (a) Average mass loss over time for the five land use types. (b) Average mass loss over time for the five litter types (code=L.+ land use type). n=23-25. Data are ln transformed. The superior panels zoom in differences between land use type and litter type.

Actual site-specific decomposition rate

Actual decomposition rate differed significantly among land use types (F4=6.9, p < 0.00012) and incubation periods (F4=29.5, p < 0.00014), but there was no significant interaction between land use type and time (F16=1.9,p =0.39). Actual decomposition in pastureland and mature forest was generally higher than actual decomposition in secondary forest (Fig. 5a). The differences in decomposition rate (g/g day) among land use types of the first phase (1- to 2-month incubation period; Fig. 5b) show the same pattern than the decomposition rate of the overall period (Fig. 5a).

Discussion

To unravel the effects of land use intensification on the litter decomposition process we assessed variation due to differences in environmental site characteristics, litter quality and their interaction across five contrasting land use types. We showed that with land use intensification environmental site characteristics became less favourable for litter decomposition; both decomposition potential (measured with standardized litter) and community litter decomposition decreased with land use intensification (LUI). Litter decomposability, related with litter quality, followed the gradient of land use intensification, it was low for mature

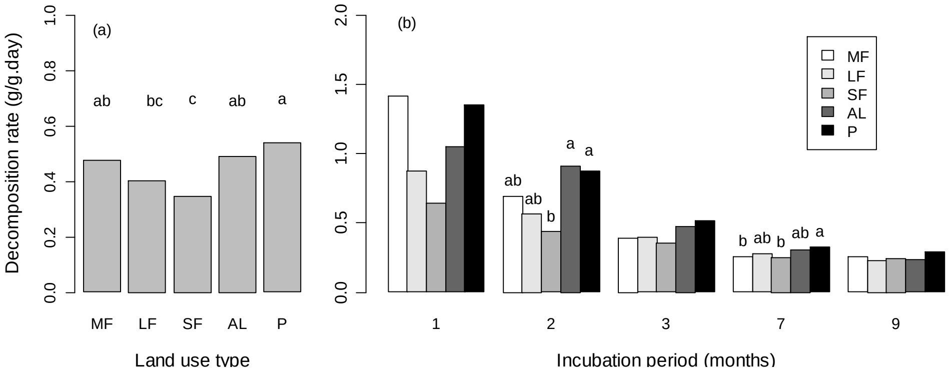


Figure 5. Differences in *actual* decomposition (mass loss) among five land use types (LUT), (a) overall average mass loss, (b) average mass loss per each of the five incubation periods. Mass loss (± SE) of community litter into its own LUT are for mature forest (MF), logged forest (LF), secondary forest (SF), agricultural land (AL) and pastureland (P). Means and standard errors are shown (n = 5). Significant differences among groups were tested in both ways for the overall average mass loss and separately per each incubation period. Bars within treatments accompanied by a different letter are significantly different at $p < 0.05$ (Tukey's HSD test).

and logged forest, intermediate for secondary forest and high for cultivated systems. In general changes in litter quality had a stronger effect on decomposability (explaining 40% of the variation) than changes in environmental site characteristics of the five land use types (explaining 20%). However, the actual decomposition rate was site-dependent showing different patterns of decomposition along LUI. As result of the interaction between site-specific characteristics and litter quality, the actual decomposition in pastureland and mature forest was generally higher than actual decomposition in secondary forest.

With land use intensification environmental site characteristics are less favourable for decomposition

We hypothesized that decomposition of standardized substrates would decrease with land use intensification (from forest to pastureland) because the diversity and activity of decomposer will be reduced as a result of decreased soil organic matter, soil N concentration and pH (Fig. S1), increased harshness of the environment (supra-optimal temperatures, low humidity; Beare et al. 1997) and direct effect of management practices. We indeed found a decrease in decomposition potential as land use is intensified, but modest rather than strong (Table 1, Fig. 1). Contrary to our results, other studies have found higher rates of decomposition potential in human disturbed systems than in undisturbed sites (Visser et al. 1983, Neher et al. 2003, Quested et al. 2007). Higher decomposition rate in disturbed sites was explained by favourable moisture and temperature in recently abandoned semi-natural grasslands compared with long abandoned plots (Quested et al. 2007). Larger heterogeneity in micro-environmental conditions among sites can explain those differences (Tian and Brussaard 1997). It has also found that management practices, such as clearing or burning, can reduce microbial activity and hence decomposition rate (Beare et al. 1997), but others (tillage, planting, fertilization) may enhance microbial activity and lead to increased decomposition in fields compared with forest (Neher et al. 2003).

We hypothesized that soil pH and [N] would have a positive effect on decomposition potential rate, because they determine the type, numbers and activity of microorganisms (de Vries et al. 2012). Our results partially support this relationship. We found indeed that land use types with slow decomposition rate (cultivated systems; Table 1) had also low soil [N], organic matter and pH (Fig. S1), but we did not find direct effects of soil covariates on decomposition (Table 1,3). We also showed that soil [N] and pH increased with land use intensification but the correlation was only significant important for one type of standard litter and for one harvest (Table 1). Similar to our results, Neher et al. (2003) indicated not clear relationship between mass loss and soil pH when undisturbed and disturbed forest have been compared. However, both variables were positively correlated with decomposition rate in disturbed and un-disturbed forest. These results suggest that other environmental factor than soil pH became more important to explain decomposition potential along LUI.

Site-specific factors not measure in this study (e.g. climatic variables, decomposer diversity, management practices) can also explain variations in decomposition potential along LUI (Lavelle et al. 1993). The lower decomposition in our cultivated systems than forest systems may support our hypothesis that it was caused by an increased harshness of environmental conditions as land use change is intensified (field observations). Early studies have showed significant relationship between decomposition rate and temperature or moisture. The direction of this relationship is, however, determined by the range of the site temperature (Waring 2012) because decomposer often have an optima temperature for the enzymatic degradation of specific plant component, (Beare et al. 1997). For instance, Homman and Grigal (1996) showed that decomposition rate increased with temperature at low temperature levels in forest, but decreased at high temperature levels in crop fields.

Pattern of decomposition of our labile (Acalypha communis) and recalcitrant (Stipa eriostachya) standard litter were extensively discussed by Varietti et al. (2005). They found that both litter types had fast weight loss in the first phase (70 days) and slower mass loss in later phases. In our study only labile litter showed such logarithmic mass loss through time (Fig. 1a). This fast decomposition during the first phase is mainly controlled by nutrient concentration, while the slower phase is mainly controlled by the decomposition of cellulose and lignin concentration (Berg 1986). Unexpectedly, recalcitrant litter showed linear mass loss through time (Table 1, Fig. 1b) probably because there was less nutrients and hence, fast nutrient-driven decomposition played a minor role, whereas there was a continuous, constant and slow decomposition of recalcitrant material as lignin. These standard litter types showed the same decomposition patterns in a study comparing tropical forest with different disturbance intensity (García 2009). Decomposition differences between our land use types were most clear after 3 months when most of the labile material (typically cellulose and hemicellulose) was decomposed. This suggests that more recalcitrant compounds can better indicate differences along LUI than labile ones. The fact that differential response of decomposition potential following human disturbance depends on the quality of the standard material was also found for a pine dominated ecosystem (Neher et al. 2003). They additionally found that litter decay models were land use type dependent, while we found that they were material dependent: exponential for labile litter and linear for recalcitrant litter (Fig. 1).

Land use intensification changes litter quality

We hypothesized that litter quality would increase (higher concentration of labile components such N and P and less concentration of recalcitrant components such lignin and tannin; Tian et al. 1995), with land use intensification, because with LUI the plant community shifts from conservative to acquisitive species (Garnier et al. 2004). We indeed found that litter from natural systems was associated with high concentrations of lignin and tannins, which defend plants against herbivores (Coley 1983, Coley and Barone 1996). However, in contrast to our hypothesis, litter from natural systems had as well higher concentrations of N and P than litter from cultivated systems (Table 1). When we zoomed in on our natural systems (Fig. S2) we found that the high N concentration was associated with litter from logged- and secondary forest (cf. García 2009), which is explained because these land use types are dominated by acquisitive pioneer species that have high leaf nutrient concentrations (Fig. S2; Chazdon et al. 2010, Carreño-Rocabado et al. 2012). Besides, low N concentration in litter from cultivated systems was due to both pastureland and agricultural land were dominated by grasses: an exotic forage grass (Brachiaria brizantha) in pastureland and rice (Oriza sativa) in agricultural land (G. Carreño-Rocabado, unpublished data). This is also partly in line with a global meta-analysis (Yuan and Chen 2009) that showed that the litter N concentration of tropical trees is about 50% higher than that of grasses. Besides, the high concentration of cellulose, C:N and lignin:N ratios in litter from cultivated systems suggests as well a grass dominance in these systems (Table 1, Fig.2; Tian et al. 1995, Vaieretti et al. 2005).

Commonly, litter N- and tannin concentration are negatively correlated (Makkonen et al. 2012) because they are associated with opposite strategies of resources acquisition and conservation in plants (Cornelissen and Thompson 1997). However, against to our expectations, we found a positive correlation between these two chemical litter traits. We suggest that this counterintuitive association is due to the fact that we compared contrasting systems with different life forms: tree-dominated natural systems with high tannin concentration with grass- and herb-dominated systems with low nutrient concentrations.

Effect of litter type and environmental site characteristics on litter decomposition

We hypothesized that site environmental conditions of the different LUTs should have a larger effect on decomposition than litter type because management intensification strongly alters decomposition related factors, such as decomposer diversity and environmental site characteristics. At global scales Makkonen et al. (2012) found that environmental site characteristics among four biomass explain twice variance than litter types (59% versus 34%). However, we found the opposite to be true; differences in litter type explained on average twice as much of the variation in decomposition rate than environmental site characteristics (48% versus 17 %, Fig. 3). A similar pattern has been found at local scales that compares natural habitats or compares undisturbed and disturbed systems (Aerts 1997, Beare et al. 1997, Dent et al. 2006, Quested et al. 2007).

To our knowledge, this is the first study that has tested the relative importance of litter quality and environmental site characteristics along a large gradient of land use intensification in tropical ecosystems. As general pattern we showed that independent of the LUT, litter decomposability increase with land use intensification; litter from mature- and logged forest had low decomposability, litter from secondary forest had intermediate decomposability, and litter from agricultural land and pastureland had high decomposability (Fig. 4b). Garcia (2009) also studied litter from natural systems, and contrary to our results she found that mixed litter from undisturbed forest had faster decomposability than litter from logged forest, and that litter from secondary forest had a similar decomposability as the two other forest types. These difference were not explained with litter quality, suggesting that other physical traits played an important role in explaining difference in litter decomposability. High decomposability of litter produced by dominant species from cultivated systems was also found by Bakker et al. (2011). It suggests that both at the species- and at community level, land use intensification is positively associated with litter decomposability.

Interestingly, the environmental site characteristics effects of the five land use types on litter decomposition was exactly the opposite as the effect of the litter types on decomposability. Mature- and logged forest had better environmental site characteristics for litter decomposition, followed by secondary forest and at the end agricultural land and pastureland (Fig. 4a). This ranking in environmental-driven decomposition was also partially confirmed with our experiment using standard litter types (Table 1, Fig. 1).

Predicting litter decomposability along land use intensification with litter chemical traits

Litter decomposition is a multi-faceted process and depends on a complex of chemical and physical litter traits. It is therefore difficult to disentangle which (combination of) litter traits drive the increase in litter decomposability with land use intensification, as many traits change in concert (Fig. 2). In this study we found that litter N- and lignin concentration were negatively related with decomposition rate, and cellulose concentration, C:N and lignin:N ratios were positively related (Fig. S3). In general, at species level, high litter quality (i.e. low C\N ratio) was related with high decomposability (Tian et al. 1995, Cornwell et al. 2008, Wickings et al. 2011, Makkonen et al. 2012), however our results showed that at community level other physical characteristics of litter can determine litter quality and consequently influence decomposition (Scherer-Lorenzen 2008). Two important methodological considerations that should be taken into account when interpreting our results are a) the small number of litter type (five values that describe litter quality) that limit our predictions, and b) the litter quality only reflexes the most dominant attribute of the litter community, whereas the litterbags incubated represent a larger variation in quality.

Lower decomposability of natural systems litter compared with cultivated systems litter can be explain by their high concentration of recalcitrant components such as tannins and lignin (cf. Tian et al. 1995, Austin and Ballare 2010, Coq et al. 2010, Makkonen et al. 2012), but also due to high nitrogen concentration (Table 1, Fig. 2). Leaf nitrogen has been shown in many studies to be positively related with decomposition rates (Cornwell et al. 2008, Fortunel et al. 2009, Bakker et al. 2011) because decomposers are nitrogen limited, and require high nitrogen concentrations for fast population growth (Vadstein and Olsen 1989). However, empirical studies have showed that the effect of litter nitrogen on litter decomposition are inconsistent, it can vary from positive, negative or non-significant (Sommerville et al. 2004). Negative relationship between litter nitrogen concentration and decomposition rate can also be found in litter that is rich in nitrogen and lignin (such as in secondary forest) because new, stable, and recalcitrant complexes are formed that are difficult to decompose (Neher et al. 2003). Faster decomposability of cultivated systems litter was due to the high concentration of cellulose (Table 1). Cellulose is considered to have intermediate decomposability because it decomposes slower than N and P, but faster than lignin and polyphenols (Minderma 1968). Degradation rate of cellulose can also increases due to photooxidation in open places, such as our agricultural land and pastureland plots (Schade et al. 1999). Besides, differences in physical characteristics between leaves from cultivated and natural systems, such as higher specific leaf area for cultivated systems (results not published), can also explain faster decomposability of litter from cultivated systems (Cornwell et al. 2008, Makkonen et al. 2012). Litter P concentration was not clearly related to decomposition rate, which is in line with a recent meta-analysis (Waring 2012).

Important site-dependent response of actual decomposition

By looking at the decay of each community litter in its own land use type we showed that the effect of land use intensification in the actual decomposition rate depended on the incubation site (cf. Powers et al. 2009). The site independent response has been interpreted as decomposers favouring locally grown litter species over foreign due to long-term adaptation to particular site-specific litter quality (Mikola et al. 2002). As the results are context dependent, it is, therefore, important to evaluate the actual decomposition, which is defined as the in-situ decomposition of litter into its own LUT.

We hypothesized little differences in actual decomposition rate because the increased litter quality of agricultural systems would be offset by the lower decomposability caused by increased harshness of the environment. Nevertheless, we found that actual decomposition rate was highest at the two extremes of the land use gradient (Fig. 5a). Actual decomposition was high in mature forest, perhaps because of the benign environment and large decomposer community. It was also high in agricultural field and pastures, perhaps because of the better litter quality. Contrary to decomposition potential, which tends to decrease as land use is intensified, actual decomposition differed modestly across the land use types, and only secondary forest was lower than the rest (Fig. 5a). High decomposition rate of mature and logged forest litter can also be influenced by the high activity of soil macro fauna in these land use types. During the first harvest some litterbags incubated in mature- and logged forest were damaged per soil macrofauna, although most of those litterbags were eliminated still some influence could remain in our data.

The low decomposition rate of secondary forest cannot be explained with the litter properties that we measured because in multi-dimensional litter trait space (Fig. 2), the litter of mature forest (with high actual decomposition rate) has similar characteristics than that of secondary forest (with low decomposition rates). Other litter traits that we did not measure, such as leaf dry matter content, or leaf toughness, could explain this pattern (data not published; Cornelissen et al. 1999). Differences in actual decomposition amongst land use types occurred mainly during the first three months (Fig. 2b), indicating that especially labile compounds (cellulose in cultivated systems) may cause these LUT differences. Many factors change with land use intensification, management practices strongly influence the site-specific condition and in turn decomposition rate (Tian et al. 1995, Beare et al. 1997). For example, burning in cultivated systems reduces litter cover, and hence the density and diversity of decomposer arthropods, that depend on this microhabitat (Warren et al. 1987).

Conclusions

Effects of LUI on litter decomposition can be driver for a variety of natural and human-induced changes that difficult to determine the overriding factors. Based on a controlled experiment we could separate and explain the relative importance of some of the most important factors that drive decomposition along a large gradient of LUI. The results of this study showed that differences in environmental site characteristics due to LUI lead to a decrease in the rate of decomposition potential, but differences in the litter quality along LUI produced by changes in vegetation lead to an increase in litter decomposability. Furthermore, these changes in litter quality rather than the changes in environment site characteristics are most important in explaining differences in litter decomposition rate across land use types. This result may suggest that LUI-driven shifts in community composition (litter quality) may have large consequences for ecosystem processes and services. However, we showed an important site-depend response, intriguingly, the actual decomposition rates were actually highest in mature forest and in pastureland. These results contribute to understand the relative importance of different factors that influence decomposition with LUI and the potential in manipulating and improving management to maintain ecosystem services such as soil fertility and food production. Our results also indicated that the effects of land use intensification on litter decomposition may negatively affect soil fertility mainly because of the changes in the quality of litter rather than changes in decomposition rates.

Acknowledgements

This research is part of the Long-term Silvicultural Research Program of the Instituto Boliviano de Investigación Forestal (IBIF). We thank the personnel of La Chonta Agroindustria Forestal for permission to work in the concession and for assistance with plot establishment and monitoring. We thank as well the farmers and owners of pasturelands for allowing us to work in their areas (Asencia Uranoi, Choco Mercado, Cornelio Candawiri, Diberato Irapiri, Francisco Bae, Francisco Borins, Herlan Pesoa, Hernan Ativena, Ignacio Egnar, Ivan Avi, Jesus Paz Añez, Jesus Uracoi, Juan Pesoa, Mario Sockock, Matha Severiche, Pascual Iraipi, and Victor Peredo). This study was partly funded by the DiverSus project through Inter-American Institute for Global Change Research (IAI) CRN 2015 and SGP-CRA2015, which were supported by the US National Science Foundation grants GEO-0452325 and GEO-1138881. GCR was funded by DiverSus and by a fellowship from NUFFIC. We appreciate the assistance of field technician Sara Viera and workers, especially Ricardo Mendez. We thank Hans C. Cornelissen for the discussions and valuables comments made on an earlier version of this chapter, and Richard van Logtestijn who assisted us with the chemical analysis of the samples.

Appendices

Table S1. Methods used in the analyses of litter chemical components

Trait	Method
Nitrogen, phosphorus, and carbon	Total carbon and nitrogen were determined by dry combustion with a Flash EA1112 elemental analyses (Thermo Scientific, Rodana, Italy). After digestion in a 1:4 mixture of 37% (by volume) HCl and 65% (by volume) HNO3, phosphorus was measured colorimetrically (Murphy and Riley 1962)
Lignin, cellulose,	After several extraction steps to ensure that only cellulose and lignin made up the composition of the residue of the sample, the C and N concentrations of this residue were used to calculate the lignin concentration, based upon the difference in carbon content between cellulose and lignin (Poorter and Villar 1997).
Tannins	Tannin concentrations were calculated by subtracting the non-tannin phenolics from the total phenolics (Makkar et al. 2003).

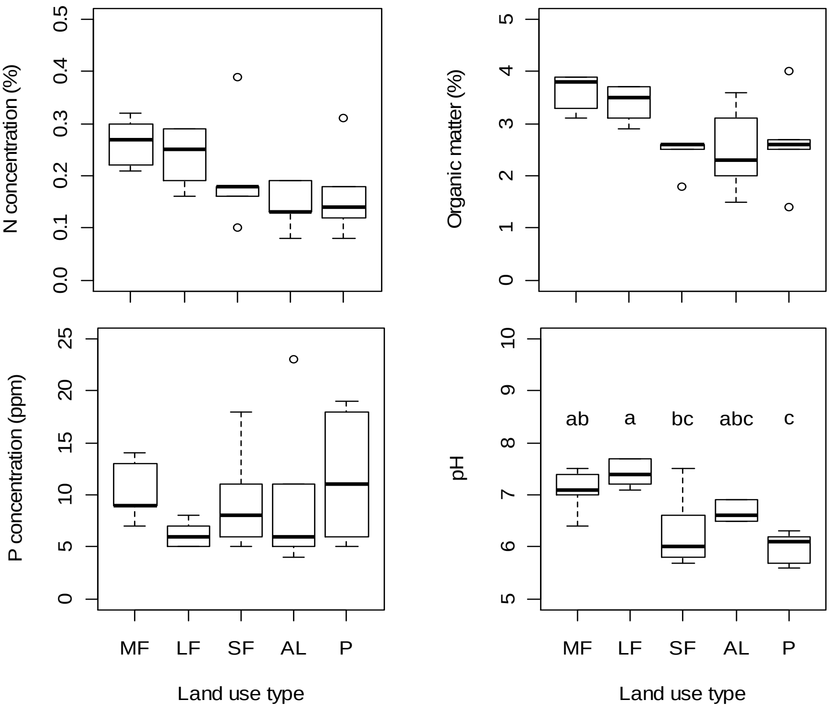


Figure S1. Comparison of soil properties among mature forest (MF), logged forest (LF), secondary forest (SF), agricultural land (AL) and pastureland (P). Different letters indicates significant differences between litter types. Soil properties are nitrogen (N) and phosphorus (P) concentration, organic matter, and soil acidity (pH) (Tukey's HSD test, n =5, α=0.05)

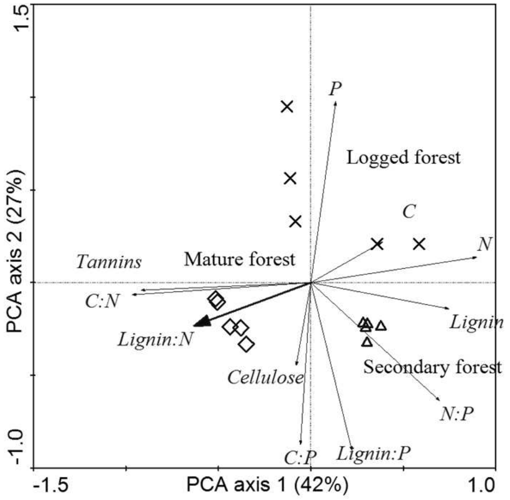


Figure S2. Principal-component analysis of litter type from forest systems (mature forest [diamond], logged forest [x mark], and secondary forest [triangle]) and litter traits, nitrogen (N), phosphorus (P), carbon (C), lignin, cellulose and tannins concentrations, and ratios of N:P, C:N, C:P, lignin:P, and lignin:N. The first axis explains 42 % of the variation and the second axis 27 % of the variation.

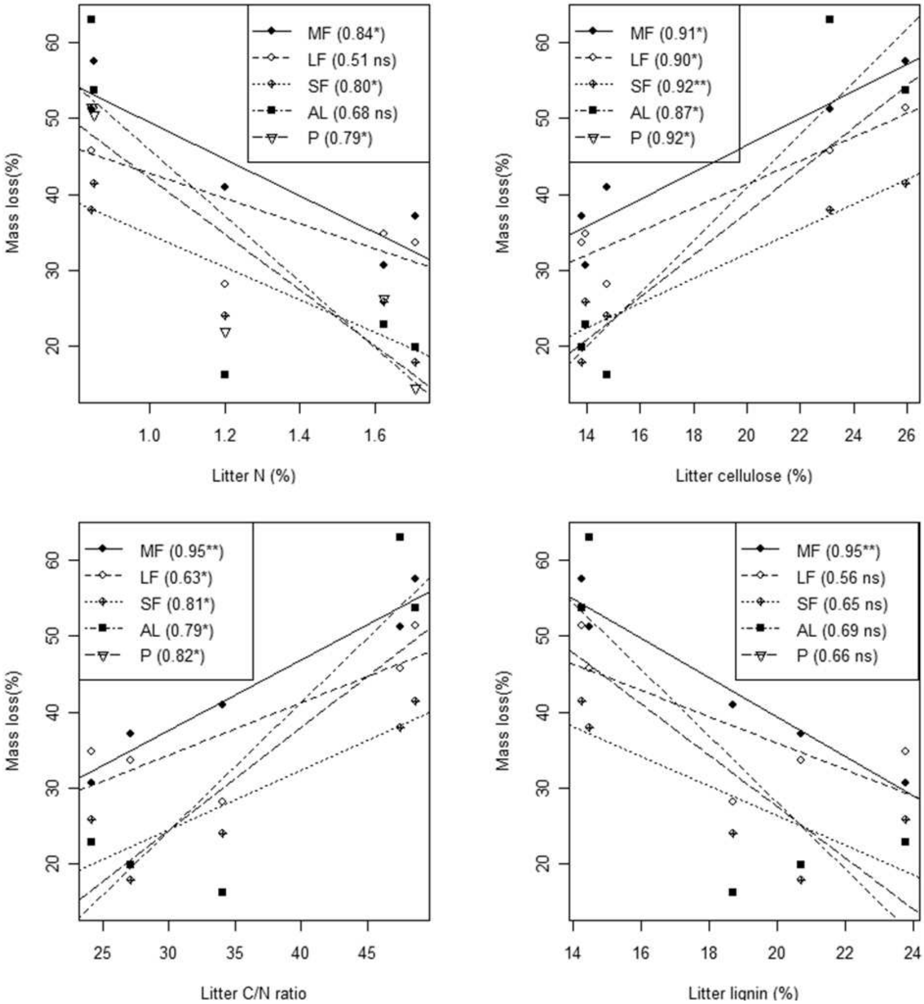


Figure S3. Regression models that predict community litter decomposition rates during the second incubation period (70 days) with litter chemical traits. Mass loss is the mean of five plot per land use type and litter chemical component is the mean of five samples per community litter of each land use type. Land use types are mature forest (MF), logged forest (LF), secondary forest (SF), agricultural land (AL) and pastureland (P). The r2 per and its significance are presented per regression model (*=p<0.05, **=p<0.001, ns=non-significant)

Cusi leaves (palm species, *Attalea speciosa*) used to thatch the roof of a house

Chapter 6

General discussion

Introduction

Land-use intensification (LUI) is one of the major drivers of biodiversity loss and it diminishes the ecosystems' capacity to provide ecosystem processes and services that societies derive from them (MEA 2005; Díaz *et al.* 2007). LUI implies fundamental alterations in biotic and abiotic elements of an ecosystem. Effects of LUI on ecosystems processes can follow different pathways: a) direct effects through changes in environmental conditions, resources, and management practices, and b) indirect effects through changes in properties of the plant community (Laliberté & Tylianakis 2012). I used the framework of *response-and-effect* traits (c.f. Díaz *et al.* 2007; Suding *et al.* 2008) to scale up through the community level the indirect effect of LUI.

Different approaches to analyse LUI effects on plant communities and ecosystem processes have evolved during the last years (Mayfield, Ackerly & Daily 2006). A growing body of literature based on empirical data has shown that LUI affects ecosystems negatively, but that there is also a high heterogeneity of responses to LUI. This heterogeneity is explained by differences in regions, spatial scales, disturbance intensities, taxonomical groups, and response metrics considered (Mayfield *et al.* 2005; Mayfield, Ackerly & Daily 2006; Garnier *et al.* 2007; Laliberté *et al.* 2010; Gibson *et al.* 2011). Differences in LUI effects can even be larger for tropical ecosystems, where biodiversity is high and where the social heterogeneity, and hence the way the land is used and managed, is also large (Chazdon 2003; Stork *et al.* 2009). Uncertainties to predict LUI impacts on ecosystem processes through plant functional traits are a) which traits are more suitable to determine and predict changes in ecosystem processes that at the same time respond to environmental changes and determine ecosystem processes (Lavorel & Garnier 2002), b) what is the relative role of different functional properties (such as mean trait value or trait variation) showing plant response to LUI and affecting ecosystem processes, and c) how trait predictability is influenced by the different scales of evaluation (species or community level; Díaz *et al.* 2007).

LUI effects on plant community assembly are driven by a combination of a) species responses to changes in environmental conditions (biotic and abiotic; *environmental filters)*, and b) management practices that modify species assemblages by constraining some species and introducing other species *(management filters;* Hooper et al. 2005*)*. As a result of these filtering effects, the properties of plant communities (such as community-weighted mean of trait values and trait variation) can be modified. Traditionally, most studies evaluating the response of plant communities to disturbance have focused on taxonomic properties. More recent studies, however, have shown that functional properties have higher sensitivity to disturbance, and more importantly, that functional properties determine the changes in ecosystems processes, rather than taxonomic diversity *per se* (Díaz & Cabido 1997; Vandewalle *et al.* 2010; Lavorel & Grigulis 2012).

In this dissertation I explored the mechanisms through which land-use intensification affects plant community assembly, and ecosystem processes at local scales in the Bolivian lowland tropics. I focused on plant communities because they are responsible for most of the ecosystem fluxes in energy and resources (Grime 1998). I focused on litter decomposition because it is closely related to the nutrient cycle, which is a fundamental ecosystem process for all terrestrial ecosystems (Lavelle *et al.* 1993). This dissertation has three objectives (indicated by the numbers in Fig. 2 , chapter 1) that focus on 1) how plant communities respond to LUI via plant *response*-traits, 2) the effects of plant communities on decomposition via their *effect*-traits, and 3) the relative importance of direct and indirect pathways in explaining LUI effects on ecosystem processes .

Contrasting land use types represent a gradient of land-use intensification

To evaluate effects of land-use intensification (LUI) on plant community and ecosystem processes I used five dominant land use types in tropical lowland Bolivia that represented a long gradient of LUI: mature-, logged-, secondary forest, agricultural land, and pastureland (Table 1, chapter 1). This set of five land use types is further referred to as long LUI gradient. The effects of land-use change on biodiversity and ecosystem processes can be evaluated by using a categorical approach (by comparing different land-use types), or by using a continuous approach (by arranging the different land-use types along a gradient of intensification). In chapters 2 to 5 I analysed LUI effects using a categorical approach, whereas in this chapter I use a continuous approach to link LUI, plant communities, and ecosystem processes.

Land use is characterized by the arrangements, activities and inputs people undertake in a certain land cover type to produce, change or maintain it (Di Gregorio & Jansen 1998). Consequently, land-use type can be described in terms of the management practices applied, and the products the land use type delivers (Watson *et al.* 2000). To rank land use types along a gradient of intensification different parameters that combine natural and human-influence need to be used. In this dissertation I quantified land-use intensification based on five disturbance parameters: intensity given by remaining biomass, total number of disturbance events, disturbance frequency given by the number of disturbance events (e.g., sowing, logging) per year, magnitude as indicated by the percentage of deforested area in 1 km radius, and regeneration time indicating the period since abandonment in which natural regeneration is allowed to occur (Kleyer 1999; Jackson *et al.* 2009). To assess the association between these parameters with the five land use types used in this thesis, I carried out a principal component analysis (PCA; Fig. 1). The first two PCA axes explained 86% of the variation. The first axis was negatively correlated with regeneration time and biomass remaining, and positively correlated with number of disturbance events, frequency of these events and magnitude. This axis separated mature- and logged forest at the left, from agricultural land and pastureland at the right. Secondary forest plots occupied an intermediate position. Hence, this analysis clearly ranked the land use types along a gradient of LUI. From low to high intensification the land use types were mature forest, logged forest, secondary forest, agricultural land, and pastureland.

The five land use types were selected based on their dominance at the local scale (i.e., province of Guarayos), and represent 5 out of the 11 categories of land use type used by FAO's World Census of Agriculture to standardize the several land use types existing over the world (Watson *et al.* 2000). The ranking of the land use types along the PCA axis largely matched the ranking in land use intensity according to the FAO, although FAO considers agricultural land to be more intensified than pastureland. These similarities suggest that, even though my study focuses on local scales, both the five land use types and the LUI gradient could, to some extent, be occurring at global scales.

Especially in the tropics where most of the land use change means deforestation (Lambin, Geist & Lepers 2003), a long gradient of intensification means as well large differences in growth forms (i.e. woody species for forest and grass species for pastureland). However, as many studies have shown, a gradient of land-use intensification can also be represented by the same land use type, but with different degree of management intensification, as it is the case in different levels of management intensity in grasslands (Quested *et al.* 2007; Pakeman 2011a). To evaluate LUI effects that are not driven by differences in growth forms, I zoomed in on a LUI gradient between mature forest and logged forest, using four treatments of disturbance intensity (i.e. unharvested forest as a control, normal logging using reduced-impact logging techniques, normal logging plus light silviculture, and double logging intensity plus intensive silviculture; Table 2, chapter 1). This set of four treatments is referred to as short LUI gradient.

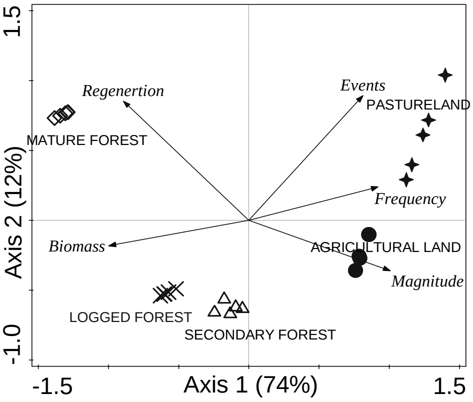


Figure 1. Principal component analysis of five parameters of disturbance associated with five types of land use (mature forest, logged forest, secondary forest, agricultural land, and pastureland). The disturbance parameters are remaining biomass (biomass), total number of disturbance events (events), number of disturbance events (sowing, logging) per year (frequency), percentage of deforested area within a radius of 1 km (magnitude), and time since abandonment in which natural regeneration is allowed to occur (regeneration).

Response of plant communities to LUI

Many studies have shown that LUI reduces plant community diversity and favors species with more acquisitive functional traits, such as high leaf N-concentration or low leaf dry matter content, at cost of species with more conservative traits (Garnier *et al.* 2007; Laliberté *et al.* 2010). However, it has also been reported that there is a large heterogeneity in the response of community assembly. The results of chapters 2 and 3 showed that along both LUI gradients, the functional composition of the plant communities changed from species with more conservative traits to species with more acquisitive traits. These results partially confirm earlier studies that showed that leaf traits involved in the acquisition-conservation trade-off (Grime 2001) are sensitive and respond to LUI (Garnier *et al.* 2007; Laliberté *et al.* 2010). These results suggested as well that changes in functional composition along a long LUI gradient were mainly driven by management filters, while in the case of the short gradient were mainly driven by environmental filters. Two findings support this statement. Firstly, contrary to my expectations, in chapter 2 I found that secondary forest, which has an intermediate position along the long LUI gradient, had more conservative trait values than mature forest (i.e., lower SLA and higher force to punch the leaf) than mature-and logged forest (Table 1, Fig. 2, chapter 2). Normally secondary forests are dominated by fast-growing pioneer species with more acquisitive traits (Van Breugel, Bongers & Martínez-Ramos 2007; Lohbeck *et al.* 2012). However, secondary forests in my study region tend to be dominated by palm species, which have conservative traits. In the region palms are abundant and are facilitated by repeated burning during shifting cultivation. Secondly, in chapter 3 I showed that along the short LUI gradient, different disturbance intensity due to different logging intensity and logging impact leads to an increase in light availability, promoting the recruitment of light-demanding fast-growing tree species with acquisitive traits (i.e. low leaf dry matter content and low leaf toughness; (Fig. 1, 2, chapter 3, cf. Kitajima & Poorter 2010; Onoda *et al.* 2011).

It is important to note that environmental filters constrain species from a regional species pool, whereas management filters also constrains species from a global pool and afterwards introduce those species into a regional pool. The dominant species in cultivated systems were therefore characterized by fast-growing species with acquisitive traits (i.e., high leaf N concentration and low leaf toughness) because the aim of cultivated systems is to produce quickly a large amount of food. However, what is still little discussed by ecologists is that a) depending on the intensification these “new human-modified species assemblages” can also contain an important functional diversity, b) at landscape level this functional diversity can increase the beta component of functional diversity (i.e., the variability in the species functional characters among sampling units in a given area; Ricotta & Burrascano 2008), and c) how at both at the scale of the plot and of the landscape ecosystem processes are being influenced.

Most studies have shown that functional diversity decreases along a LUI gradient. However, in my study I found that along the long LUI gradient, mature forest and logged forest had intermediate functional diversity, whereas secondary forest and agricultural land had high functional diversity (high CV and low K; Table 1, Fig. 2, chapter 2). Ecological processes and management influences explain these differences. Relative-low trait variation in tree communities (individuals ≥ 10 cm of diameter at 1.3 m aboveground) of mature and logged forests suggest that these species have functional traits that are adapted to the local environmental conditions; i.e., only those traits that “have passed through” the different environmental filters are part of these communities (Shipley 2010). High trait variation in secondary forest and agricultural land suggests that management filters increased trait variation through introducing non-native species and/or traits, and through creating more heterogeneity in resources availability in line with the intermediate disturbance hypothesis.

Chapters 2 and 3 also showed that when pre-disturbance functional composition among plots or habitat being compared is large, the “effect” of LUI can only be assessed if functional composition is measured before and after land use change. In chapter 2, plant community response was evaluated based on a control-impact design. The result showed that mature- and logged forest did not differ in their functional composition. However, in chapter 3, plant community response was evaluated using a before-after/control-impact design (Conquest 2000). In this way, differences in functional composition between undisturbed forest and logged forest considered both the natural temporal forest dynamic and the changes due to disturbance. The result showed that mature- and logged forest differed in their functional composition.

Do different functional properties provide complementary or redundant information?

Little is known about how different community functional properties respond to disturbance. I showed in this dissertation (chapter 2) that metrics that describe the mean trait value (the community-weighted mean), trait variation (the coefficient of variation) and trait dispersion (the kurtosis) captured in a complementary way LUI effects caused by environmental filters and management filters. The importance of using different functional properties is due to the fact that changes in ecosystem processes can be affected not only by the mean community-level trait values, but also by the trait variation or functional diversity (Díaz *et al.* 2007; Lavorel *et al.* 2011; Dias *et al.* 2013). Dias et al. (2013) proposed an experimental framework to identify which community functional property (CWM or functional diversity) is driving decomposition; they concluded that lack of orthogonality between these two attributes does not permit to evaluate the relative importance of them for ecosystem processes. In this dissertation I showed that for the three green leaf traits that better predicted decomposition rate in chapter 4 (leaf N concentration, chlorophyll and leaf dry matter content), CWM and CV were only weakly correlated (i.e., they were more orthogonal), while CWM and K were strongly correlated (i.e. showed less orthogonality; Fig. 2). However, when these metrics were used in a path analysis (see below), then decomposition rate was better explained by CWM in combination with kurtosis, rather than in combination with the coefficient of variation (data no shown). This preliminary analysis suggested that, although CWM and functional diversity (K) were correlated, they could have slightly independent effects on decomposition rate.

Effect traits as predictors of ecosystem processes

In the previous section I discussed how LUI modifies plant communities as a result of

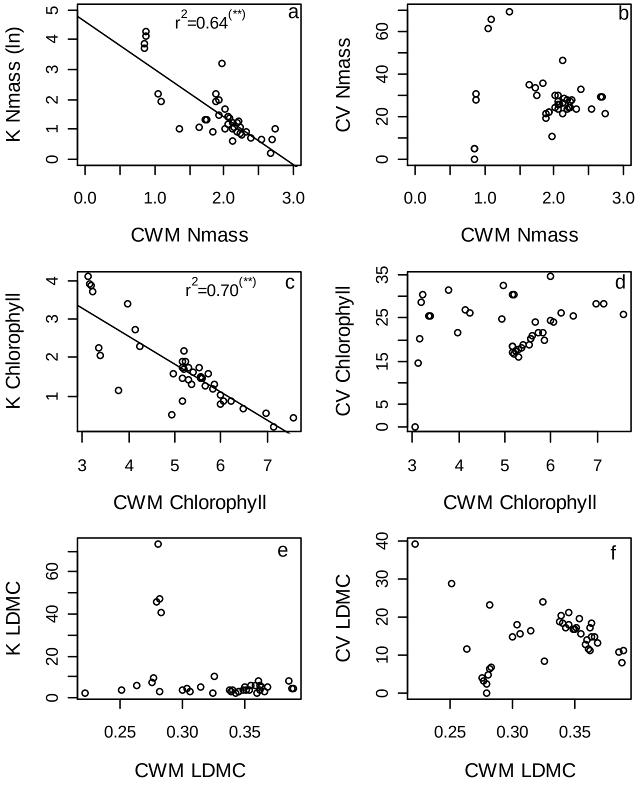


Figure 2. Relationship between community abundance-weighted mean (CWM), kurtosis (K), and coefficient of variation (CV) of plant assemblages belonging to five land use types (n=8, N=40). The relationships are presented for those traits that showed high predictability in decomposition rate: (a, b) leaf percentage of N concentration (N_{mass}), (c, b) leaf chlorophyll content per mass (Chlorophyll), and (e, f) leaf dry matter content (LDMC). The r^2 and its significance are presented in case of statistically significant relationship. (**=P<0.001)

species *response*-traits. In this section I discuss how the "new" plant communities or dominant species affect the litter decomposition rate through *effect*-traits (Lavorel & Garnier 2002).

One of the main drivers of decomposition rate is litter quality (Lavelle *et al.* 1993), which is related with plant strategy (Cornelissen *et al.* 1999). Litter quality is determined by chemical and physical leaf traits, such as N-concentration and leaf toughness. Empirical evaluations of the relationship between litter quality and decomposition rate have shown that, depending on the scale of comparison (global, regional or local scales), the variety of growth forms considered, and the type of disturbance, some traits predict decomposition rate better than others. Two other factors that can influence this relationship are freshness of the leaves (i.e., are traits measured from fresh leaves or from litter) and the scale of analysis (i.e., are species or communities being evaluated). I evaluated the relationship between traits and decomposition both at the species level (chapter 4) and at the community level (chapter 5). For doing this I used a single- and a multi-trait approach.

Which trait is a better predictor of decomposition rate at the species-level and at the community-level along a long gradient of LUI?

In chapter 4 I showed that the interspecific variation in decomposition rate of representative species of mature forest, secondary forest and agricultural land was significant associated with the quality of fresh leaves. Consistent with previous studies, leaf N-concentration and specific leaf area were the best predictors of decomposition rate, and were positively correlated with decomposition (Cornelissen *et al.* 1999; Santiago 2007; Cornwell *et al.* 2008; Fortunel *et al.* 2009). Chlorophyll content was also a good predictor of litter decomposition, perhaps because chlorophyll content is an indirect indicator of magnesium concentration in the leaf. Makkonen *et al*. (2012) found that magnesium is positively correlated with decomposition along a wide range of species at global scales. Magnesium is an essential element in the fauna diet as it is needed in enzymatic reactions, nerve connections, muscle function and skeleton formation (National Research Council 2005). Decomposition rate was also positively correlated with the leaf economics spectrum, indicating that many of the physiological and protective features of green leaves persist through senescence and after shedding (Cornelissen *et al.* 1999; Freschet, Aerts & Cornelissen 2012). Statistically significant correlations between fresh leaves traits and litter traits supported as well this trait persistence. In chapter 5 I looked at decomposition at the community scale, and showed that community litter concentration of N, cellulose and lignin, and C/N ratio were important to predict decomposition rate. Contrary to earlier studies I found that litter N-concentration was negatively correlated, and lignin concentration and C/N ratio were positively correlated with litter decomposition (chapter 5; Cornwell *et al.* 2008; Wickings *et al.* 2011; Makkonen *et al.* 2012).

At both the species- and the community level did litter decomposability increase with LUI, but with different relationship between effect traits and decomposition rate. These differences can be explained by methodological considerations and influences of management practices. At the species level both fresh leaf- and litter N-concentration were measured directly for each of the 24 species being evaluated (16 species from mature forest, 5 species from secondary forest, and 3 species from agricultural land). On the other hand, at the community-level, the N-concentration of fresh leaves was calculated as the community abundance-weighted mean of the most dominant crop species (i.e., peanuts, cassava, rice, and banana), while N-concentration of community litter was measured by pooling the community litter of different plots per land use type. Low N-concentration in litter of agricultural land was due to the high dominance of litter of rice and maize in this land use type (Fig. 3).

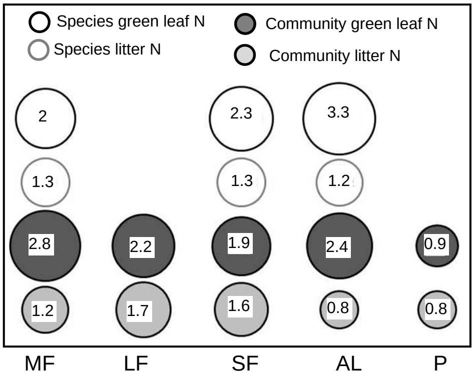


Figure 3. Mean of nitrogen concentration in green leaves and in litter belonging to different land use types (MF=mature forest, LF=logged forest, SF= secondary forest, AL=agricultural land, P=pastureland). The size of the circles is in function of the percentage of N concentration (with actual values given). Open circles are the means based on species characteristics of each land use type (modified from Figure 4a , chapter 4), filled circles are for green leaves the community abundance-weighted mean (data are in Table 1, chapter 3) and for litter the average of a community litter (data are in Table 3 , chapter 5).

Single and multi-trait approach in predicting litter decomposition

Functional diversity can be analysed based on single or on multiple traits. Little is known on how these analyses differ in the ability to predict ecosystem processes along LUI (Butterfield & Suding 2013). The results of this dissertation suggested that both single and multiple trait approaches may give insight in whether and how decomposition rate changes after logging disturbance. In chapters 2 and 5 I showed that functional diversity (estimated using multiple trait indices related with decomposition rate, Villeger, Mason & Mouillot 2008; Pla, Casanoves & Di-Rienzo 2012) did not vary significantly among mature forest and logged forest (the intensive treatment; Table 1, chapter 2). This result suggested that both trait variation, and its effect on decomposition rate, can be maintained after disturbance (Suding et al. 2008; Isbell et al. 2011). Similarly, based on a single trait approach I showed that neither trait variation (coefficient of variation) nor trait distribution (kurtosis) differed between mature forest and logged forest (for specific leaf area, leaf N-concentration and leaf chlorophyll content). Consistently, actual decomposition rate did not differ between mature forest and logged forest (Fig. 5, chapter 5).

Wrapping up; linking LUI, plant communities and ecosystem processes

The effects of LUI in ecosystem processes can operate through direct and indirect pathways. For decomposition rate, it has been found that the direct pathway is important, when undisturbed and human-disturbed systems are being compared (Neher *et al.* 2003; Quested *et al.* 2007). With an increase in LUI, the environmental site characteristics were less favourable for decomposition; mature- and logged forest had better site environmental characteristics for litter decomposition, followed by secondary forest, agricultural land and pastureland (Fig. 4a, chapter 5). These differences in site environmental characteristics explained 17% of the variation in decomposition rate (Table 3, Fig. 3, chapter 5). In contrast, other studies found that LUI could increase the rate of decomposition potential (Visser, Griffiths & Parkinson 1983; Neher *et al.* 2003; Quested *et al.* 2007). Contrasting results can be obtained because studies differ in the land use type being included, or because of large variation in environmental characteristics of the sites (e.g., temperature, soil properties and decomposer communities). Indirect pathway through changes in litter quality is another important factor explaining variation in decomposition with LUI;.

An indirect pathway of the effect of LUI on decomposition goes through shifts in plant functional properties (i.e., litter quality). Differences in litter quality amongst land use types explained more variation (48%) than differences in environmental site characteristics (Fig. 3, chapter 5); with LUI litter decomposability increased (Fig. 4b, chapter 5).

Those traits that are filtered out by LUI have at the same time an important effect on ecosystem processes. In this section I focus on *dual* traits that connect LUI with the litter decomposition through community functional properties. In chapter 4 I showed that traits related to the economics spectrum (LES) can be *dual*-traits: at the species level species characteristic of three contrasting land use types occupied different positions on the leaf economics spectrum (LES; Wright *et al.* 2004), and at the same time I showed that LES was correlated with decomposition rate (as suggested by Suding et al. 2004). Traits related with LES were also identified as *dual*-traits predicting the effect of a long gradient of land-use intensification on primary productivity (Pakeman 2011b).

The role of *dual* traits can be analysed with path analysis, as this analysis is used to examine multiple (direct and indirect) relationships among variables, and allows for the estimation and comparison of effect sizes (Shipley 2009). Using the four traits that better explained decomposition rate at species level (leaf N-concentration, specific leaf area, leaf dry matter content, and leaf chlorophyll; chapter 4), I evaluated different path models (Table S1) to see which model best fitted my data. Since leaf chlorophyll better explained differences in decomposition along LUI, I only show this analysis as a preliminary and potential way to understand the pathway and mechanism in which LUI affects litter decomposition rate. This analysis helps also to illustrate the role of *dual*-traits.

In general, with LUI actual decomposition rate (*in-situ* decomposition, litter decomposed in its own land use type after 70 days of incubation) tended to increase (Fig. 4a). The contribution of the different pathways to this increase was as follow (Fig. 4a): LUI indirectly affected the litter decomposition rate by decreasing CWM of leaf chlorophyll (explained by the high dominance of grasses in cultivated systems), and this led to an increase in the litter decomposition rate (Fig. 5a ,b); LUI directly affected the litter decomposition rate by decreasing soil pH and it led to an increase in decomposition rate; and finally an increase in the index of intensification that grouped other environmental conditions (i.e., factors not measured in this study such as temperature, moist, and decomposers) led to an increase in decomposition rate. The role of kurtosis in the models was not totally clear, although it was an important variable in for fitting the models, mainly due to its correlation with the CWM. Further explorations are necessary to understand the mechanism of the kurtosis influences. The predictability of the path model almost doubled (to R^2=0.70) when decomposition potential (mass loss of standard labile

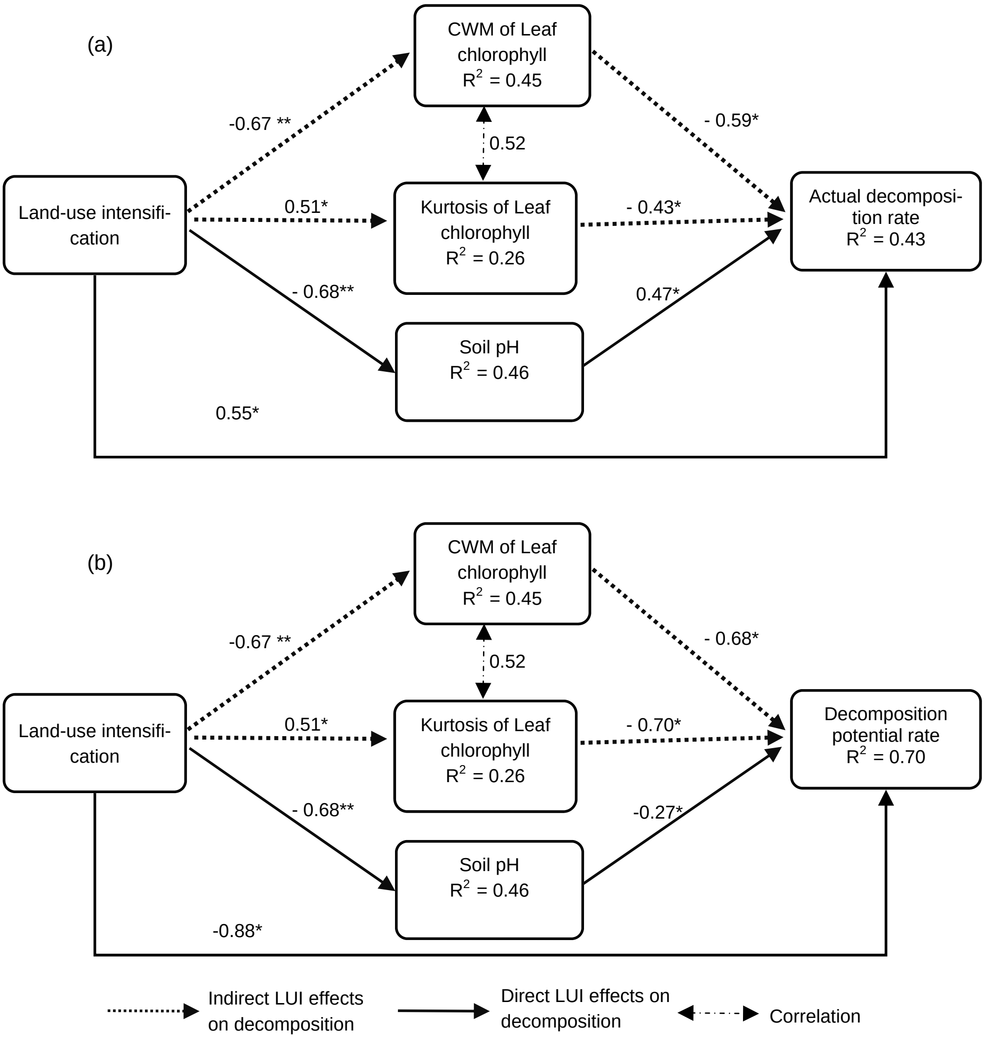


Figure 4. Models that show the direct and indirect pathways in which land-use intensification (LUI) affects ecosystem processes. As a preliminary approach to understand the relative importance of environmental characteristics and community functional properties on decomposition rate different models were fitted using four traits (see Table S1). Here only the models are shown that better fitted the data and were well support as well (x^2=2.397,*df*=2, p=0.302, for both models). Based on an index of LUI, community weighted mean (cwm) and kurtosis (k) of leaf chlorophyll and soil pH the model explain 43% of the variation of (a) actual decomposition rate (*in-situ* decomposition, litter decomposed in its own land use type after 70 days of incubation) and 70% of the variation on (b) decomposition potential (based on decomposition rate of standard labile litter after 70 days of incubation). In this dissertation the direct LUI effects on decomposition rate were studied through soil properties and other environmental site conditions (LUI-decomposition, soil pH-decomposition), while the indirect effect were studied via plant community functional properties (community abundance-weighted mean and kurtosis of leaf chlorophyll). The standardized path coefficients and their statistical significance are presented next to the arrows (**P*<0.05; ***P*<0.001).

litter across all five land use types after 70 days of incubation) was used as dependent variable instead of actual decomposition rate (Fig. 4b). This suggested that CWM and kurtosis could also be indicators of differences in site environmental conditions: with LUI decomposition potential decreased indicating site environmental characteristic were less favourable for decomposition independently of the litter quality (Fig. 5c,d). Functional diversity was also found to be positively correlated with decomposition potential (measured with standard material), possibly because high functional diversity provided a more heterogeneous micro-environment and a larger range of litter quality, both factors influencing the community decomposer (Scherer-Lorenzen 2008). Although the models fitted the data and explained a considerable part of the variation in decomposition, the mechanism through which effect traits were influencing decomposition was not clear. Additional traits, such as leaf toughness, may need to be included in the model to account for other leaf characteristics than the chemical ones.

Relevance for ecosystem services and conclusions

The rapid increase in land-use intensification and its negative impact on ecosystem services (MEA 2005) provides challenges and opportunities to ecologists to apply ecological principles, and to explain how communities and ecosystem processes respond to human disturbance (Meyer & Swank 1996). Decomposition of organic matter is a key process in biogeochemical processes because it releases carbon and nutrients from organic material and it is, therefore, directly linked to ecosystem services such as maintenance of soil fertility (Wood et al. 2009). To my knowledge, this dissertation is one of the first to use a response-and-effect traits framework, to understand how LUI affects community assembly and ecosystem processes in tropical ecosystems.

I showed that LUI does not necessarily lead to low functional diversity and low decomposition rate. My results indicate that the impacts of LUI on plant community and ecosystem processes are highly variable at local scales. The results of this dissertation can be relevant for applied issues such as ecosystem restoration, the length of the fallow cycle that permits soil regeneration, increasing crop productivity while maintaining soil fertility, and for increasing carbon stocks in logged forest and secondary forest.

The results of this dissertation suggest that ecosystem processes, such as primary productivity and litter decompositions, are at the medium term not influenced by different intensities of selective logging and silvicultural treatments because species diversity and functional diversity are maintained. However, at the long term, a high disturbance intensity (through the application of light and intensive silvicultural treatments) may increase primary productivity and increase decomposition rate because the community shifts toward species with more acquisitive traits. Similarly, I found that increasing LUI resulted in community-level dominance of plants with acquisitive leaf trait values. Finally, my results indicate that LUI has both direct and indirect effects on ecosystem processes. While I showed that changes in litter quality due to LUI are more important in

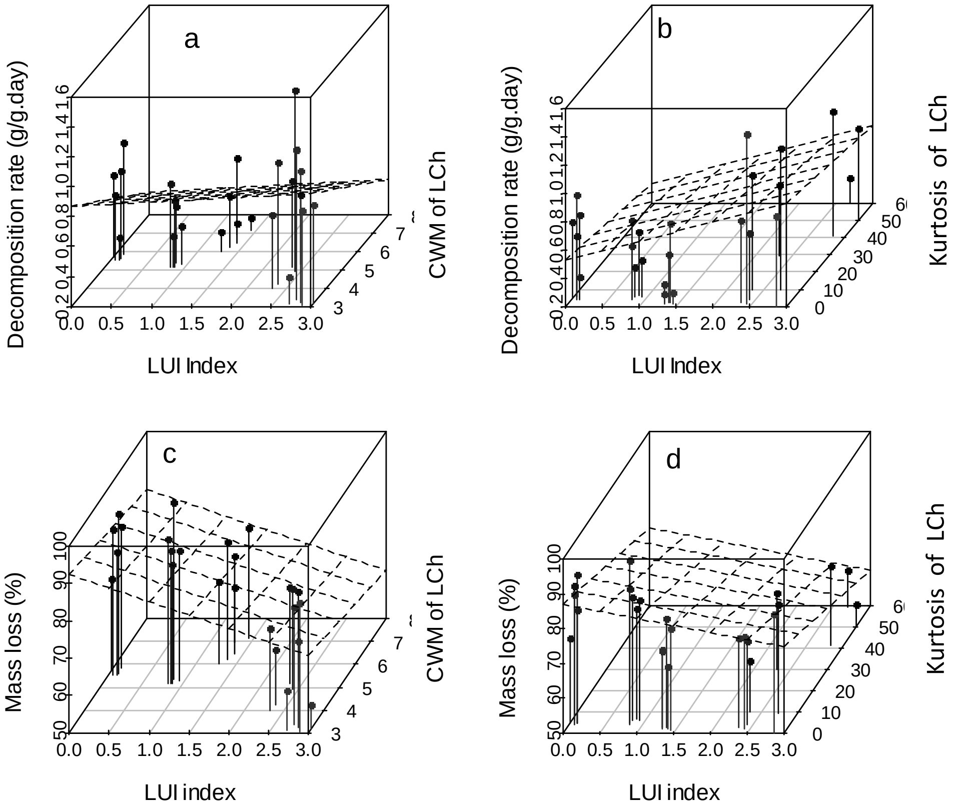


Figure 5. Relationship between land-use intensification, community functional properties (community weighted mean [CWM], and kurtosis) and litter decomposition after 70 days of incubation period. Figures a and b show the rate of the actual decomposition (*in-situ* decomposition, litter decomposed in its own land use type) and figures c and d showed the decomposition potential (mass loss of standard labile material along all plots) (N=40).

explaining litter decomposition rate than changes in site environmental conditions, the actual decomposition rate was influenced by both drivers because litter with high decomposability (litter from pastureland) incubated in the land use type with low decomposition potential (pastureland plot) had generally the same decomposition rate as litter with low decomposability (litter from mature forest) incubated in the land use type with high decomposition potential (mature forest plot).

This dissertation showed that, depending on the gradient of LUI, it is possible to provide ecosystem services such as timber production, while at the same time maintaining the capacity of the ecosystem to provide other ecosystem services such as decomposition. I also showed that with a long gradient of LUI, the management of human-modified systems may have a strong impact on diversity conservation, ecosystem processes and services. Finally, in landscapes highly modified by human disturbance the mix of cultivated systems and natural systems can increase functional diversity and reduce the negative LUI impacts on ecosystem processes.

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Canopy in secondary forest after 12 years of regeneration

Summary

Land-use intensification (LUI) is one of the main global drivers of biodiversity loss with negative impacts on the ecosystems processes and services to human society. To evaluate and predict those impacts, it is necessary to study a LUI gradient that includes natural systems and human-disturbed systems. Because LUI implies fundamental alteration in both, environmental conditions and biotic elements, its effects on ecosystem processes go through two pathways; a direct pathway, via changes in environmental conditions, and an indirect pathway, via changes in the plant community. It is expected that an increase in LUI a) results in dominance of species with acquisitive traits (fast-growing species) over species with conservative traits (slow-growing species), b) a decrease of functional diversity, and c) an increase in decomposition rate and primary productivity due to dominance of acquisitive species. Since the mechanisms and relative importance of each pathway are poorly understood for tropical ecosystems, in this dissertation I explored how land-use intensification affects plant community assembly and ecosystem processes in the Bolivian tropical lowlands. Using a functional *response-and-effect* framework I evaluated 1) how plant communities respond to LUI (chapters 2 and 3), 2) the effects of plant communities on decomposition (chapters 4 and 5), and 3) the relative importance of direct and indirect pathways in explaining LUI effects on ecosystem processes (chapters 5 and 6).

I used two gradients of LUI: a long gradient, including five contrasting land use types that differed in life forms (mature forest, logged forest, secondary forest, agricultural land, and pastureland), and a short gradient of disturbance intensity represented by four experimental treatments in managed forest (mature forest, and forest subject to one of three levels of logging intensity and application of silvicultural treatments). Plant community response to LUI was evaluated based on species diversity and community functional properties. The effects of LUI on ecosystem processes were evaluated based on differences in litter decomposition rate among land use types. Community functional properties were evaluated as the *mean* trait value of the community (i.e., functional composition, described using the community-weighted mean) and functional *diversity* based on single-trait metrics of variation and dispersion (coefficient of variation and kurtosis) and indices based on multi-traits (functional richness, evenness, and divergence). I evaluated litter decomposition at the species level and at the community level using three experiments: a) a common garden experiment with 23 dominant plant species that evaluated differences among species, b) a standard litter incubated across different land use types that evaluated the effect of environmental factors, and c) a fully reciprocal litter transplant experiment (community litter of each land use type incubated in all land use types) that evaluated the relative importance of environmental conditions and litter quality. Change in plant community and decomposition rate along the long LUI gradient were compared at a single moment in time, whereas for the short LUI gradient, plant community response was evaluated in terms of temporal changes in functional properties. I also used path analy-

sis and structural equations to test the causal effect of LUI in plant community and decomposition.

In chapter2, I found that increasing LUI resulted in community-level dominance of plants with acquisitive leaf trait values. These results partially confirm earlier studies that showed that leaf traits involved in the acquisition-conservation trade-off, such as specific leaf area, leaf dry matter content, nitrogen and phosphorus concentration are sensitive and respond to LUI. However, secondary forests had more conservative trait values (i.e., lower SLA and higher force to punch the leaf) than mature-and logged forest. Besides, systems with an intermediate position along the LUI gradient (i.e., secondary forest and agricultural land) had higher functional diversity (high CV and low K) than systems at the extremes of the gradient. Both, differences in CWM and functional diversity across land use type, were the result of environmental and management filters.

In chapter 3, I found that with an increases in LUI plant communities shift from conservative species towards species with more acquisitive trait values. With an increase in disturbance intensity due to logging and application of silvicultural treatments, the composition of the dominant species changed from species with high leaf construction costs (i.e. high leaf dry matter content), well-defended leaves (i.e. high leaf toughness), and a long leaf lifespan to species with the opposite suite of traits. These changes were driven by recruitment (of individuals that reached 10 cm diameter at 1.30 m above ground 8 years after disturbance) rather than by growth of surviving individuals. These results suggest that environmental filters, rather than management filters, mainly influenced the plant communities: increased light availability (due to logging gaps and death of damaged individuals) was the main factor driving functional responses in the tree community. Although functional diversity changed along the long LUI gradient, the three functional diversity indices calculated based on traits related to primary productivity and decomposition rate did not respond to the short LUI gradient.

In chapter 4, I found that at the species level decomposition was high for species characteristics of agricultural fields, followed by species from secondary forest and mature forest. The 23 species studied belonged to different functional groups, and occupied different positions on the leaf economics spectrum (LES). Nearly half of the leaf- and litter traits were significantly correlated across species. Nutrient concentrations of green leaves and litter were correlated, this means that the ranking of the species based on nutrient concentration is largely the same before and after leaf senescence. Interspecific variation in decomposition rate was significantly associated with the quality of fresh leaves. Multiple regression analysis showed that leaf N- concentration, specific leaf area, and chlorophyll content per unit leaf area had positive effects on decomposition, explaining together 65–69% of the variation. Species position on the LES and regeneration light requirements were also positively related to decomposition.

In chapter 5, I found that LUI affected litter decomposition via direct and indirect pathways. Difference in litter quality along LUI had a stronger effect on decomposability (explaining 48% of the variation) than difference in site environmental characteristics (explaining only 17% of the variation). With LUI litter decomposability increased due to changes in litter quality; litter from forest systems was characterized by high concentrations of lignin, tannin and nitrogen, whereas litter from cultivated systems had a high concentration of cellulose. Conversely, with LUI *decomposition potential* decreased (measured as mass loss of standard litter incubated in all land use types) due to environmental site characteristics became less favourable. Since soil properties only weakly affected decomposition, management practices, decomposer community, and climatic conditions were the main drivers of the direct effects of LUI on decomposition potential. Although litter quality explained more variation in decomposition rate across the LUI gradient than environmental site characteristics, the *actual* decomposition rate (*in-situ* decomposition of litter community into its own land use type) was site-dependent, determined by both drivers, and they compensated each other. Thus, litter with high decomposability (litter from pasture land) incubated in the land use type with low decomposition potential (pasture land) had generally a similar decomposition rate as litter with low decomposability (litter from mature forest) incubated in the land use type with high decomposition potential (mature forest).

To link land-use intensification, plant communities, and ecosystem processes under the framework of *response-and-effect* traits, those traits related with the leaf economic spectrum (leaf nitrogen concentration, specific leaf area and leaf chlorophyll) may act as *dual* traits, connecting LUI, plant communities, and decomposition rate, both at species level and at community level. These traits drive both plant community response to LUI, and the decomposition rate of the litter produced by the responding community. Based on path analysis I showed that both the direct and indirect pathways explained variation in decomposition rate due to LUI. However, to understand the mechanisms explaining how different functional properties influence these pathways further research is necessary.

Land-use intensification effects on plant communities and ecosystem processes can have cascading effects on ecosystem services. For instance, plant community responses to disturbance caused by logging and silvicultural treatments, suggest that ecosystem processes, such as primary productivity and litter decomposition, will not change at the mid-term. At the longer term, however, primary productivity and decomposition rates may increase because the community is changing towards trees with more acquisitive trait values. Secondary forest and agricultural land are characterized by high functional diversity, which can have a positive effect on maintaining diverse ecosystem services, such as seed dispersion or crop pollination. My results also suggest that the negative effect of LUI on soil fertility of agricultural land is mainly caused by changes in litter quality (and the amount of litter produced) rather than by changes in decomposition rates (since there was not a clear difference in decomposition rate between mature forest and agricultural land).

Tropical ecosystems are not only very diverse in species, they are also diverse in their responses to human disturbance. I conclude that LUI has important effects on plant community properties and ecosystem processes. The extent and the pathways of these effects, however, contrast with some predictions of current ecological theory. High intensification of land use does *not necessarily* lead to low plant functional diversity, and less favourable environmental conditions for decomposition do *not necessarily* lead to low decomposition rates. Instead, the multiple factors related with management decisions at local scales cause a large heterogeneity of ecosystem responses. Consequently, depending on the management decisions taken, the negative effect of LUI could be mitigated.

Resumen

La intensificación del uso del suelo (IUS) es una de las principales causas de pérdida de biodiversidad con consecuencias negativas para los procesos y servicios ecosistémicos. Para evaluar y predecir estos impactos es necesario estudiar un gradiente amplio de IUS que incluya tanto sistemas naturales como sistemas antrópicos. Dado que la IUS causa al mismo tiempo alteraciones en los factores abióticos y bióticos, los efectos en los procesos ecosistémicos pueden producirse a través de dos vías: una vía directa, a través de cambios en las condiciones ambientales, y una vía indirecta, a través de cambios en las comunidades vegetales. Se espera que un incremento en la IUS a) favorecerá a especies de estrategias adquisitivas (especies con crecimiento rápido) en perjuicio de especies con estrategias conservadoras (especies de crecimiento lento), b) disminuirá la diversidad funcional, y c) aumentará la tasa de descomposición y productividad primaria debido al aumento de especies adquisitivas. Dado que se conoce poco sobre estos mecanismos en esta tesis investigué cómo la intensificación del uso del suelo afecta al ensamblaje de las comunidades vegetales y los procesos ecosistémicos en las tierras bajas tropicales de Bolivia. Usando el marco conceptual de caracteres funcionales de *respuesta* y de *efecto* evalué: 1) cómo la comunidad vegetal responde a la IUS (capitulo 2 y 3), 2) el efecto de la comunidad vegetal sobre la descomposición de hojarasca (capitulo 4 y 5) ?, y 3) la importancia relativa de los efectos directos e indirectos de la IUS en los procesos ecosistémicos (capitulo 5 y 6).

Para alcanzar estos objetivos usé dos gradientes de IUS: un gradiente amplio que incluyó cinco usos de suelo que difieren en las formas de vida de las comunidades vegetales (bosque maduro, bosque aprovechado, bosque secundario, cultivo y pasturas) y un gradiente estrecho que incluyó cuatro niveles de perturbación causados por el aprovechamiento forestal y aplicación de prácticas silviculturales (bosque sin aprovechamiento, y tres bosque sujetos a uno de los tres niveles de intensidad de aprovechamiento y prácticas silviculturales). La respuesta de la comunidad vegetal a la IUS fue evaluada en base a la diversidad de especies y las propiedades funcionales de la comunidad, mientras que el efecto en los procesos ecosistémicos fue estudiado en base a diferencias en la tasa de descomposición de la hojarasca (perdida de biomasa, en adelante denominado descomposición). Para medir las propiedades funcionales de la comunidad evalué la composición funcional usando la media ponderada de la comunidad (MPC) y la diversidad funcional usando métricas de variación y dispersión de caracteres individuales (coeficiente de variación y curtosis), e índices calculados usando caracteres múltiples (índice de riqueza, equidad y divergencia funcional). La descomposición fue mediada a nivel de especie y a nivel de comunidad usando tres experimentos: una cama de descomposición común donde se incubó hojarasca de 23 especies de plantas características de tres tipos de uso de suelo, material estándar incubado en los diferentes usos de suelo para evaluar el efecto de diferencias en factores ambientales, y un experimento de trasplante reciproco incubando hojarasca de cada tipo de uso de suelo en todos los diferentes usos de suelo para

evaluar la importancia relativa de factores ambientales y calidad de hojarasca en la descomposición. Los cambios en la comunidad vegetal a los largo del gradiente amplio de IUS y los efectos en la tasa de descomposición fueron evaluados comparando los usos de suelo después de la perturbación antrópica, mientras que los cambios a lo largo del gradiente estrecho de IUS fueron evaluados como la diferencia relativa entre antes y después de la perturbación. Finalmente, hice un análisis de rutas y ecuaciones estructurales para determinar el efecto causal de la IUS en las propiedades funcionales de la comunidad vegetal y en la tasa de descomposición.

En el capítulo 2 encontré que al incrementar la IUS, la comunidad vegetal fue dominada por especies con caracteres funcionales adquisitivos. Estos resultados confirman parcialmente otros estudios que encontraron que los caracteres relacionados a la estrategia de uso y adquisición de recursos de las plantas, como el área foliar específica, el contenido foliar de materia seca, la concentración de nitrógeno y fósforo foliar, son sensibles y responden a la IUS. Sin embargo, también encontré que el bosque secundario, que se encuentra en una posición intermedia en el gradiente de IUS, tuvo caracteres más conservadores (ej. baja área foliar específica y alta fuerza física de las hojas) que el bosque maduro. Además tanto el bosque secundario y los cultivos, tuvieron mayor diversidad funcional (alto coeficiente de variación y baja curtosis) que los sistemas en los extremos del gradiente (bosque maduro y pasturas). Los resultados sugieren que tanto las diferencias en la MPC como en diversidad funcional fueron el resultado de filtros ambientales y de manejo.

En el capítulo 3 encontré que al incrementar la IUS la comunidad vegetal cambió de especies dominantes con caracteres funcionales conservadores a especies con caracteres adquisitivos, es decir la comunidad arbórea cambió de especies que invierten más recursos en la construcción de hojas (altos valores en contenido de materia seca foliar), hojas bien defendidas (altos valores en fuerza física de las hojas) y hojas con larga persistencia a especies con características opuestas. Estos cambios fueron mayormente influenciados por el reclutamiento de nuevos individuos (individuos que alcanzaron 10 cm de diámetro ocho años después de la perturbación) más que por el crecimiento de los individuos sobrevivientes. Estos resultados sugieren que los cambios en la comunidad vegetal son el resultado de filtros ambientales como el incremento en la disponibilidad de luz debido a los claros de aprovechamiento y a la muerte de árboles dañados a lo largo del tiempo. A pesar que la diversidad funcional cambio a lo largo del gradiente amplio de IUS, ninguno de los tres índices calculados con caracteres funcionales relacionados a la productividad primaria y la descomposición de hojarasca respondieron a las intensidades de perturbación a lo largo del gradiente estrecho de IUS.

En el capítulos 4 encontré que la tasa de descomposición a nivel de especie fue mayor para especies características de cultivos, seguidas por especies características de bosque secundario y bosque maduro. Las 23 especies estudiadas pertenecen a diferentes grupos funcionales y ocuparon diferentes posiciones a lo largo del gradiente de balance económico de la hoja (LES por sus siglas en inglés). Esta variación estuvo asociada a la calidad de las hojas frescas. Más de la mitad de los caracteres funcionales de las hojas frescas y hojarasca estuvieron correlacionados entre si (ej. la concentración de nutrientes de las hojas), lo que significa que la posición que las especies ocupan en un gradiente de concentración de nutrientes es el mismo antes y después de la senescencia de las hojas. Los análisis de regresión múltiple mostraron que la concentración de nitrógeno foliar, el área foliar específica y el contenido de clorofila por unidad de área tuvo un efecto positivo en la tasa de descomposición, explicando entre el 65 a 69% de la variación en la tasa de descomposición. La posición de las especies a los largo del LES y los requerimientos de luz influyeron también positivamente en la tasa de descomposición.

En el capítulo 5 encontré que tanto las diferencias a los largo del gradiente de IUS en condiciones ambientales (efecto directo) y en la calidad de hojarasca (efecto indirecto) influyeron en la tasa de descomposición. El efecto indirecto fue más importante en la tasa de descomposición (explicando un 48% de la variación) que el efecto directo (que explicó solo un 17% de la variación). Con un incremento en la IUS las condiciones ambientales fueron menos favorables para la descomposición potencial (medida como la perdida de biomasa de material estándar); en consecuencia la tasa de descomposición potencial fue mayor en el bosque maduro y el aprovechado, seguido por el bosque secundario y al final los cultivos y las pasturas. Dado que las propiedades del suelo influyeron poco en la descomposición, es posible que el efecto directo de la IUS en la descomposición potencial se dio a través de diferencias en las prácticas de manejo, comunidad de descomponedores, y otros factores climáticos no medidos.. La IUS también influyó en la calidad de hojarasca. La hojarasca perteneciente al bosque maduro, al bosque aprovechado y al bosque secundario tuvo altas concentraciones de lignina, taninos y nitrógeno, mientras que la hojarasca perteneciente a los cultivos y pasturas tuvo alta concentración de celulosa. Como consecuencia, la descomponibilidad de la hojarasca aumentó con la IUS. Aunque la calidad de la hojarasca explicó más variación en la descomposición que las condiciones ambientales, no hubo diferencias en la descomposición real (descomposición de hojarasca en su propio sitio) entre los extremos del gradiente de IUS. Este resultado mostró un efecto de compensación entre las condiciones ambientales y la calidad de hojarasca. Es decir la tasa de descomposición de hojarasca de rápida descomposición incubada en ambiente no favorable (hojarasca de pasturas incubada en este uso de suelo) es similar a la tasa de descomposición de hojarasca de lenta descomposición incubada en ambiente favorable (hojarasca de bosque maduro incubada en bosque maduro).

Para relacionar el efecto de la IUS, comunidades vegetales y procesos ecosistémicos se puede utilizar el marco conceptual de "caracteres funcionales de *respuesta* y de *efecto*", en el cual los caracteres funcionales relacionados con el LES (concentración de nitrógeno foliar, área foliar específica y contenido de clorofila) son considerados como caracteres *duales*. Estos caracteres duales influyen tanto en la respuesta de la vegetación a la IUS como en la tasa de descomposición de la hojarasca producida por esta misma vegetación. Con el análisis de ecuaciones estructurales encontré que tanto la influencia directa como la indirecta determinan cambios en la tasa de producción de hojarasca debido a la IUS. Sin embargo, para explicar los mecanismos mediantes los cuales las propiedades funcionales de la comunidad influyen en la tasa descomposición es necesario realizar más investigaciones.

Los efectos de la IUS en las comunidades vegetales y procesos ecosistémicos pueden tener efectos de cascada en los servicios ecosistémicos. Por ejemplo, la respuesta de la comunidad vegetal a la perturbación debido al aprovechamiento forestal y tratamientos silviculturales sugirieron que los procesos ecosistémicos como la productividad primaria y la descomposición de la hojarasca no son afectados a mediano plazo. Sin embargo, a largo plazo ambos procesos ecosistémicos pueden incrementar porque la comunidad vegetal será dominada por especies con caracteres más adquisitivos. Asimismo la alta diversidad funcional en el bosque secundario y los cultivos puede tener un efecto positivo para el mantenimiento de los diversos servicios ecosistémicos como la dispersión de semillas y la polinización de los cultivos. Finalmente, la IUS puede tener efectos negativos en la fertilidad de los suelos debido a los cambios en la calidad de hojarasca más que debido al cambio en la tasa de descomposición (dado que no hubo diferencias entre la tasa de descomposición del bosque maduro y los cultivos).

Los sistemas tropicales no sólo tienen una alta diversidad de especies, sino que también muestran una diversidad de respuestas a perturbaciones antropogénicas. En base a los resultados de esta tesis concluyo que la IUS tiene importante consecuencias para la comunidad vegetal y los procesos ecosistémicos. Sin embargo, el alcance de estas consecuencias contradicen algunas de las afirmaciones de teorías ecológicas actuales. Así, los incrementos en la IUS *no necesariamente* significan baja diversidad funcional en la comunidad vegetal, y condiciones ambientales menos favorables para la descomposición de hojarasca *no necesariamente* significan bajas tasas de descomposición. En vez de ello, diversos factores relacionados con las decisiones de manejo que ocurren a escala local causan una variedad de respuestas de los ecosistemas a la IUS. Esto hace posible que decisiones de manejo pueden mitigar los impactos negativos que la IUS tiene en los procesos ecosistémicos.

Samenvatting

De intensivering van landgebruik is een van de voornaamste oorzaken van wereldwijd verlies van biodiversiteit. Dit heeft negatieve gevolgen voor ecosysteemfuncties en -diensten. Om deze gevolgen te kunnen evalueren en voorspellen is het nodig om de intensivering van landgebruik te bestuderen, gebruik makend van een gradiënt van natuurlijke ecosystemen, naar meer door de mens verstoorde ecosystemen. Intensivering van landgebruik leidt tot fundamentele veranderingen in zowel milieucondities als biotische elementen. De effecten van landgebruik op ecosysteemfuncties zullen daarom via twee trajecten verlopen; een direct traject, middels veranderingen in milieucondities en een indirect traject, via veranderingen in de plantengemeenschap. Ik verwacht dat intensivering van landgebruik resulteert in a) dominantie van soorten die investeren in het verkrijgen van hulpbronnen (snel groeiende soorten) ten koste van soorten die investeren in bescherming van plantmateriaal (langzaam groeiende soorten), b) een afname van de functionele diversiteit en c) een toename van de decompositie en primaire productie door de dominantie van de soorten die investeren in het verkrijgen van hulpbronnen. Omdat de mechanismen en het belang van beide trajecten nog slecht begrepen zijn voor tropische ecosystemen, heb ik in dit proefschrift onderzocht hoe de intensivering van landgebruik de samenstelling van de plantengemeenschappen en ecosysteemfuncties beïnvloedt in het tropisch laagland in Bolivia. Ik heb door middel van een “functionele respons-en-effect raamwerk” geëvalueerd 1) hoe plantengemeenschappen reageren op intensivering van landgebruik (hoofdstuk 2 en 3) , 2) wat de effecten van de plantengemeenschap zijn op natuurlijke afbraak (hoofdstuk 4 en 5), en 3) het belang van directe en indirecte trajecten voor de verklaring van het effect van intensivering van landgebruik op ecosysteemfuncties (hoofdstuk 5 en 6).

Ik heb gebruik gemaakt van twee gradiënten voor intensivering van landgebruik: een lange gradiënt waarin vijf contrasterende landgebruiks-typen voorkomen die verschillen in vegetatie (volgroeid bos, gekapt bos, secundair bos, landbouwgrond en grasland) en een korte gradiënt van verstoringsintensiteit waarin vier experimentele behandelingen in beheerd bos worden onderzocht (volgroeid bos en bos onderhevig aan één van de drie niveaus van kap intensiteit en soorten bosbehandelingen).

Het gevolg van intensivering van landgebruik op de plantengemeenschap is geëvalueerd aan de hand van soortendiversiteit en functionele eigenschappen van de gemeenschap. Het gevolg van intensivering van landgebruik op ecosysteemfuncties is geëvalueerd gebaseerd op verschillen in natuurlijke afbraak van bladstrooisel tussen landgebruikstypen.

Functionele eigenschappen van de gemeenschap zijn berekend als de gemiddelde waarde van de eigenschappen voor de gemeenschap (m.a.w. functionele compositie, beschreven door de community-weighted mean, CWM) en van de functionele diversiteit gebaseerd op één enkele eigenschap van variatie en dispersie (variatiecoëfficiënt en kurtosis) en indices gebaseerd op meerdere eigenschappen (functionele rijkdom, gelijkmatigheid en divergentie).

Drie afbraakexperimenten zijn uitgevoerd om de decompositie op soorts- en op gemeenschapsniveau te evalueren: a) Het bladstrooisel van 23 dominante plantensoorten werd geplaatst in een speciale afbraak-tuin om verschillen tussen soorten te kunnen evalueren, b) Transplantatie van standaard materiaal in de verschillende landgebruikstypen en c) een volledig wederkerig bladstrooisel transplantatie experiment waarin het bladstrooisel van de bomengemeenschap van 5 landgebruikstypen werd geïncubeerd in alle andere landgebruikstypen om de relevantie van omgevingsfactoren en bladstrooiselkwaliteit te bepalen. Verschuivingen in plantengemeenschappen en afbraaksnelheid over de lange landgebruiksgradiënt van intensivering werden vergeleken in een momentopname, terwijl in het geval van de korte gradiënt de respons van de plantengemeenschap is geëvalueerd in termen van veranderingen in functionele eigenschappen door de tijd heen.

In het tweede hoofdstuk zet ik uiteen hoe de toenemende intensiteit van landgebruik resulteert in een toename van dominante boomsoorten met een snelle groei strategie. Deze resultaten bevestigen eerdere studies die lieten zien dat bladeigenschappen die betrokken zijn bij de trade-off tussen opbouw enerzijds en bescherming van plantmateriaal anderzijds (zoals dichtheid, droge stof-, stikstof- en fosforconcentratie) belangrijk zijn voor het verklaren van plantreacties na intensivering van landgebruik. Desalniettemin had secundair bos meer eigenschappen typerend voor een optimale bescherming van plantmateriaal dan volwassen of gekapt bos. Ook hadden bossen met een tussenliggende positie op de gradiënt van intensivering in landgebruik (secundair en gekapt bos) een hogere functionele diversiteit (hogere variatiecoëfficiënt en lagere kurtosis) dan systemen op de extremen van de gradiënt. Zowel verschillen in CWM als functionele diversiteit tussen landgebruikstypen waren het resultaat van milieu - en management filters.

In hoofdstuk 3 laat ik zien dat met een toename in intensivering van landgebruik de plantengemeenschap verschuift van soorten die investeren in bescherming van plantenmateriaal naar soorten die investeren in het verkrijgen van hulpbronnen. Dus met intensere vormen van landgebruik door houtkap en toepassing van bosteeltkundige ingrepen veranderde de eigenschappen van de dominante soorten van ‘dure bladeren’ (bv hoge droge stof gehalte van het blad), met betere afweer (bv hoge taaiheid van het blad) en langere levensduur, naar soorten met tegenovergestelde eigenschappen. Zulke veranderingen worden veroorzaakt door individuen die zich nieuw hebben gevestigd in de plantengemeenschap (dat zijn de individuen die 8 jaar na verstoring minimaal 10 cm stamdiameter hebben bereikt) en niet door de groei van overlevende individuen. Deze resultaten suggereren dat milieufilters een belangrijkere rol spelen dan beheers filters in het bepalen van de plantensamenstelling: de toename in beschikbaarheid van licht (vanwege een opener bladerdak door kap-activiteiten en het afsterven van beschadigde bomen) was de voornaamste factor die de functionele respons van de bomengemeenschap veroorzaakte. Hoewel functionele diversiteit (gebaseerd op meerdere effect-eigenschappen) veranderde met de lange landgebruiksgradiënt, veranderde deze niet met de korte landgebruiksgradiënt.

In hoofdstuk 4 laat ik zien dat op soortsniveau, decompositie hoog was voor soorten die voorkomen op landbouwgrond, gevolgd door soorten uit secundair bos en volgroeid bos. De 23 onderzochte soorten behoren tot verschillende functionele groepen en hebben verschillende posities langs het *'blad-economisch spectrum'* (Leaf Economics Spectrum, LES). Bijna de helft van de blad en bladstrooisel eigenschappen zijn gecorreleerd tussen soorten. Nutriënten concentraties van vers blad en bladstrooisel zijn gecorreleerd, wat betekent dat de rangschikking van de soort op basis van nutriënten concentratie grotendeels hetzelfde is voor en nadat bladeren van de boom vallen. Variatie in afbraaksnelheden tussen de soorten was significant geassocieerd met de kwaliteit van de verse bladeren. Multipele regressie analyse liet zien dat blad N- concentratie, specifiek blad oppervlak en chlorofyl inhoud per bladeenheid een positief effect hebben op afbraak snelheid, deze verklaren 65-69% van de variatie. De positie van de soorten langs het blad-economisch spectrum en lichtbehoefte gedurende de regeneratie-fase waren ook positief geassocieerd met afbraak.

In hoofdstuk 5 bestudeer ik het effect van de intensivering van landgebruik op bladstrooisel afbraak in de vijf landgebruikstypen. Landgebruiksintensivering beïnvloedt strooisel afbraak op directe en op indirecte wijze, waarbij verschillen in strooiselkwaliteit een groter effect hebben op de afbraak (verklaarde 48% van de variatie) dan verschillen in milieuomstandigheden (verklaarde 17% van de variatie). Met de intensivering van landgebruik nam de decompositie snelheid toe door veranderingen in strooiselkwaliteit; bladstrooisel van bos ecosystemen heeft hogere concentraties van lignine, tannine en stikstof terwijl bladstrooisel van gecultiveerde systemen een hoge concentraties cellulose heeft. Aan de andere kant is landgebruiksintensivering minder bevorderlijk voor potentiele afbraak (gemeten door gewichtsverlies van standaard afbraak-materiaal geincubeerd in alle landgebruikstypen) vanwege minder geschikte milieucondities. Van deze milieucondities hadden bodemeigenschappen slechts een gering effect hadden op de afbraaksnelheid en waren beheer van het land, biota verantwoordelijk voor afbraak, en klimaatomstandigheden de voornaamste aandrijvers van de directe effecten van intensivering op potentiele afbraak. Hoewel de kwaliteit van bladstrooisel meer variatie verklaarde in *potentiele* afbraak langs de gradiënt in landgebruiks-intensivering dan milieucondities, was de *werkelijke* afbraak (de afbraak van bladstrooisel op de plaats van herkomst) plot-afhankelijk en werd bepaald door zowel de strooiselkwaliteit alswel de milieucondities. Dus bladstrooisel dat *potentieel* makkelijk afbreekbaar is (uit grasland) had over het algemeen een vergelijkbare afbraaksnelheid dan bladafval dat *potentieel* moeilijker afbreekbaar is (uit volgroeid bos) wanneer het geïncubeerd werd in, resepctievelijk, land met en hoge (volgroeid bos) en lage (grasland) decompositie potentie.

Door het linken van landgebruiksintensivering, plantengemeenschappen en ecosysteem functies binnen het raamwerk van respons-en-effect eigenschappen, blijkt dat eigenschappen gerelateerd aan het blad-economisch spectrum (blad stikstof concentratie, specifiek blad oppervlak en blad chlorofyl) kunnen fungeren als *tweevoudige* eigenschappen: deze koppelen landgebruiksintensivering, planten gemeenschappen en bladstrooisel-afbraak, zowel op soortsniveau als op het niveau van de gemeenschap. Deze eigenschappen bepalen zowel de respons van de plantengemeenschap op intensivering van landgebruik als de afbraaksnelheid van bladval geproduceerd door de gemeenschap. Gebaseerd op pad-analyse laat ik zien dat zowel de directe als de indirecte trajecten variatie verklaren in afbraaksnelheden als gevolg van landgebruiksintensivering. Echter, meer onderzoek is nodig om te begrijpen hoe verschillende functionele eigenschappen deze trajecten beïnvloeden.

De gevolgen van intensivering van landgebruik op plantengemeenschappen en ecosysteem functies kunnen een domino effect hebben op ecosysteemdiensten. Bijvoorbeeld, de respons van een plantengemeenschap op houtkap en bosbouw activiteiten suggereert dat ecosysteem functies zoals primaire productiviteit en afbraak niet zullen veranderen op de middellange termijn. Op de lange termijn zullen de productiviteit en afbraaksnelheid echter kunnen toenemen vanwege de sneller groeiende bomen in de gemeenschap. Secundair bos en landbouwgrond worden gekarakteriseerd door hoge functionele diversiteit, wat een positief effect zal kunnen hebben op het onderhoud van diverse ecosysteemdiensten, zoals zaad verspreiding en bestuiving. Mijn resultaten laten verder zien dat het negatieve effect van de intensivering van landgebruik op vruchtbaarheid van landbouwgronden voornamelijk komt door veranderingen in de kwaliteit van het bladstrooisel (en de hoeveelheid geproduceerd bladstrooisel) en niet door veranderingen in afbraaksnelheden (aangezien er geen duidelijke verschillen waren in afbraaksnelheden tussen volgroeid bos en landbouwgrond).

Tropische ecosystemen zijn niet alleen soortenrijk; ze zijn ook rijk in hun respons op verstoring door mensen. Ik concludeer dat de intensivering van landgebruik belangrijke gevolgen heeft voor de eigenschappen van plantengemeenschappen en voor ecosysteemfuncties. De mate van deze gevolgen en de trajecten waarin deze verlopen contrasteren echter met enkele voorspellingen binnen de huidige ecologische theorie. Sterke intensivering van landgebruik leidt niet noodzakelijkerwijs tot lage functionele diversiteit van de plantengemeenschap, en minder bevorderlijke milieuomstandigheden voor natuurlijke afbraak leiden niet noodzakelijkerwijs tot lagere afbraaksnelheden. In plaats daarvan zorgen de verscheidene factoren gerelateerd aan beheersbeslissingen op lokale schaal voor grote heterogeniteit in ecosysteem reacties. Als gevolg daarvan kunnen de negatieve effecten die samenhangen met de intensivering van landgebruik worden gereduceerd door de juiste beheerbeslissingen te nemen.

Acknowledgements

Humans are social creatures, and we do become more social when we face challenges. Indeed, this PhD was a challenge for me, but I have been very well accompanied and supported along all its process. I need and I want to thank all those people (and groups/institutions) who made this challenge more difficult and more easy.

I thank the financial support of the Netherland Fellowship Program (NFP), and the DiverSus project, unquestionably without these supports this project would not have been possible.

This thesis is part of the Nucleo DiverSus led by Sandra Diaz, and composed by many researchers from different institutions and countries. I would like to say thank you to all the DiverSus members for their ideas, discussions and advices. I thank Sandra Diaz, Marcelo Cabido, Bryan Finegan, Hans Cornelissen, Marielos Peña-Claros, Lourens Poorter, Laura Pla, Syndonia Bret-Harte, Peter M. Ray, Fernando Casanoves, Laura Pla, Natalia Pérez Harguindeguy, Carlos Urcelay, Florence Baptist, Fabien Quétier, Lucas Enrico, Georgina Conti, Pedro Jaureguiberry, Anibal Cuchietti, Valeria Falczuk, Soledad Pérez, Daniel Cáceres, Pablo Rodriguez-Biella, Felicitas Silvetti, Esteban Tapella, Beatriz Salgado, Fernando Férnandez, Leda Lorenzo, and Marcel Caritá. I specially thank Laura Pla and Fernando Casanoves for their statistical advices, Hans Cornelissen and Natalia Pérez Harguindeguy for the discussions for the chapter that evaluates litter decomposition.

I want to thank my local institution in Bolivia, the Instituto Boliviano de Investigación Forestal (IBIF), for all the support during the field work, and during the long processes to find and get a grant to come to the Netherlands. I thank the different executive directors of IBIF: Bonifacio Mostacedo, Zulma Villegas, Marisol Toledo, and Nataly Ascarrunz. I thank as well my colleagues Alfredo Alarcón, Juan Carlos Licona, Emma Nuñez, Laly Dominguez, Jackeline Tapia, Karina Muñoz, Sandra Velasco, Lars Markesteijn, and Israel Ibañez for their help that made my work easier; and my colleagues with whom I shared findings and doubts Joseph Veldman, Margot Stoddard, Marlene Soriano, Betty Flores, Carlos Pinto, José Luis Santivañez, Turian Palacios, Mayra Maldonado, and Danaë Rozendaal. I thank the many students who help me in different phases of my field work, Guisela Languidey, Janett Juarez, Viviana Suarez, Peter Van Buuren, Benoit Chevallier, Shirley Arana, Eddy Cambará, Shirley Pérez, and Rosali Padilla. I am grateful to Maartje Bakker for her help establishing the first plots, measuring leaf traits and doing some of the decomposition experiments; I am also grateful to Sara Viera who coordinated the last two harvests of the decomposition experiment.

Sin duda el apoyo de las empresas La Chonta Ltda. en Guarayos e INPA Parket Ltda. in Concepción fue muy importante para mi trabajo de campo. Agradezco tanto a las personas que las dirigen (Pablo Antelo Gil y Paul Rozenboom respectivamente) como a su personal. Especialmente agradezco al personal de La Chonta por ayudarnos con el pontón para cruzar el rio y por proveerme de alimento y alojamiento cuando ni con pontón se cruzaba el rio. Situaciones parecidas ocurrieron a la entrada de INPA, gracias a Daniel Velázquez por su socorro.

No habrían ecólogos de campo sin la ayuda de la gente local, los asistentes de campo que nos enseñan y ayudan durante la toma de datos. Quiero expresar mi gran aprecio, admiración y gratitud a las personas que me apoyaron durante el trabajo de campo; muchas gracias a José Chuviña, Ricardo Méndez, Angel Méndez, José Iraipi, Don Juancito Alvarez y muchos otros más. También agradezco mucho a los dueños y encargados de las propiedades donde trabajé: Asencia Uranoi, Choco Mercado, Cornelio Candawiri, Diberato Irapiri, Francisco Bae, Francisco Borins, Herlan Pesoa, Hernan Ativena, Ignacio Egnar, Ivan Avi, Jesus Paz Añez, Jesus Uracoi, Juan Pesoa, Mario Sockock, Matha Severiche, Pascual Iraipi, y Victor Peredo.

In The Netherlands I have had the fortune to be part of a wonderful research group, the Forest Ecology and Forest Management group (FEM). I want to thank all the staff for their professionalism, their friendship, and all the opportunities to discuss ideas and build dreams. Thanks to Frits Mohren, Frans Bongers, Britta Eilmann, Leo Goudzwaard, Jan den Ouden, Marielos Peña-Claros, Lourens Poorter, Ute Sass-Klaassen, Peter Schippers, Frank Sterck, Ellen Wilderink, Patrick Jansen, Pieter Zuidema, and Hans Polman and the guest researchers Stefan Schnitzer, Esron Munyanziza, José Quero, Noelia González, Cesar Perez-Cruzado, and Bryan Finegan. I especially thank Yoshiko Iida for her help with my R-codes, it encouraged me to use and abuse R. Many thanks as well to my PhD colleagues Abeje Eshete, Ana Catarina Jakovac, Corneille Ewango, Emiru Hizikias, Estela Quintero, Gabriel Muturi, Gustavo Schwartz, Jean Ndyambaje, Kwame Oduro, Lucy Amissah, Lars Markesteijn, Marlene Soriano, Madelon Lohbeck, Marisol Toledo, Masha van der Sande, Mart Vlam, Meenakshi Kaul, Mathieu Decuyper, Monique Weemstra, Motuma Tolera, Paul Copini, Peter Groenendijk, Peter van der Sleen, Tefera Mengistu, and Yosias Gandhi for sharing their victories, defeats, knowledge, ignorance, and especially their jokes and good mood that make life nicer and better. Similarly, I would like to thank Frank Sterck and Peter Schippers for their advises in statistical issues and the analysis of structural equations for the last chapter of my thesis. An especial thanks to Joke Jansen who help me a lot during my time in FEM.

I also thank the other staff of Wageningen University, Patricia Meijer , Karin van der Goot , Marion Rodenburg, Petra Cornelissen, Claudius van de Vijver, and Carmen Carcelen for all the administrative, academic and logistical support during my stay in Wageningen. MY acknowledgements also go to colleagues from other groups for the nice discussions on diverse topics that in some way have contributed to this dissertation: William van Dijk, Alejandra Tauro, Kyle Tomlinson, André van Proosdij, and Christian Seiler. I thank “my translation team” who helped me with the translation and the editing of the summary: Alejandra Tauro, Cristina Casavecchia, Madelon Lohbeck, Masha van der Sande, William van Dijk, Jeroen Houdijk, Peter van der Sleen, and Ricardo Stanoss. My participation in various discussion groups gave the opportunity to meet other PhD candidates and discuss diverse topics more than functional diversity. I thanks to the organizer Ep Heuvelink, Marije Kuiper, and André van Proosdij.

When I participated in the PE-RC weekend together with other PhD candidates I heard a parody about the relationship between the PhD candidate with the (co) promotors. The “official” first part of the parody states that to do a PhD is like driving a car in which the PhD candidate is the driver and the (co)promotors go in the backseat advising how to drive. The second part clarifies that the (co)promotors go in the backseat *strangling* the PhD candidate. In some way both parts are true. I am very grateful to my promotor Professor Frans Bongers, and my co-promotors Lourens Poorter and Marielos Peña-Claros for giving me the opportunity to know the “functional word”, and help me to drive this car and reach this goal without serious accidents. Special thanks to Frans for all his unlimited energy, positivism, and comprehension during all this time; to Marielos for her friendship and constancy to keep working in Bolivia; and to Lourens for listening to my ideas, for thinking with me along all the chapters, and for encouraging me (sometimes strongly) when I needed it. I want to say that there was not one day in which I needed advice and there was not at least one of my supervisors to help; that is a luxury for any PhD candidate.

I thank to the Systems Ecology lab at VU University Amsterdam (Richard van Logtestijn), and in Bolivia the Centro de Investigación Agrícola tropical, CIAT-Bolivia (Carlos Herrera) for the foliar and soil analyses. I thank the Museo de Historia Natural Noel Kempf Mercado and several people for their help in taxonomic identification of plants (Ezequiel Chávez, Marisol Toledo, Daniel Villarroel and Daniel Soto).

Along this process many friends helped me in many ways such as teaching me how to enjoy the weather and lunch without a warm soup (sopita caliente) in The Netherlands. Thank you very much Gera Dendikken, William van Dijk, Linda Kool, Bart Krops, Madelon Lohbeck. También agradezco infinitamente la amistad y apoyo de Marisabel Vargas, Tatiana Villarroel (la kity), Alejadnra Tauro, Zulma Villegas, Marlene Soriano, Cristina Casavecchia, Andrea Casselli, Miguel Rosas Munguia, Rodrigo Soria, Daniela Aguirre, Claudia Coca, David Ortiz y Elena Prieto. I am highly grateful to my paranymphs Madelon and Tatiana.

Quiero agradecer de manera especial a un gran amigo y maestro, Peter Feinsinger, por enseñarme a ser crítica y usar mi sentido común (el menos común de los sentidos, según el) a lo largo de todo el proceso de diseñar y realizar una investigación. Yo soy una de decenas de investigadores latinoamericanos que emprendieron sus carreras de posgrado gracias a la motivación y apoyo de Peter (y el pollo!!).

Finally my deepest gratitude goes to both of my families. In Bolivia agradezco a mi mamá la señora Martha Rocabado Balderrama quien me ha trasmitido y dado la fuerza y constancia para perseguir un objetivo y alcanzarlo; a mi papá Don Eduardo Carreño Lora por todo su amor y continuo apoyo; y a mi hermano Crystian y su familia Deysi y la pequeña Camilita, por quererme y estar ahí para mí. Gracias también a la familia Jancko-Rocabado, especialmente a mi prima Patricia por cuidar a mi mamá y papá mientras estoy lejos.

In Nederland maak ik deel uit van de families Houdijk en van Olst, erg vriendelijke,

vrolijke en eerlijke, warme mensen die me thuis doen voelen in dit mooie, goed georganiseerde en voor 80% van de tijd koude Holland. Heel erg bedankt Oma Houdijk (die niet meer onder ons is), Paul, Mariëtte, Thijs, Maaike, Oma van Olst, Willy, Ria, Ivanka en Dunja. Ik ben in het bijzonder dank verschuldigd aan Willy, omdat zij met veel zorg en liefde op Inat heeft opgepast, dat heeft mij enorm geholpen om dit proefschrift af te ronden, zonder haar hulp zou het 100 keer lastiger zijn geweest. Tot slot wil ik Jeroen Houdijk en Inat bedanken.

Aan Jeroen als echtgenoot en vriend, bedankt dat je zo lief bent en voor al je steun, advies en zorg; aan Inat voor het geven van extra energie en een reden om mijn proefschrift tot een eind te brengen, deze prestatie is zonder twijfel te danken aan ons drieën. *Finalmente, quiero agradecer a Jeroen por ser mi esposo y mi amigo, gracias por ser tan dulce, por todo tu apoyo, tus consejos y cuidados; y a Inat por darme una extra energía y razón para terminar la tesis, indudablemente este logro es de los tres*.

Short biography

Inés Geovana Carreño Rocabado was born on the 21th January 1974 at Potosí, Bolivia. She completed high school in 1991 at the Colegio Nacional Cástulo Chávez in Santa Cruz, Bolivia. In 1992 she started to study agronomy at the Universidad Autónoma Gabriel René Moreno in Santa Cruz, Bolivia. During her studies she did an internship implementing kitchen gardens within the project of Development of small scale agriculture in Santa Cruz, Bolivia. Under the supervision of Dr. Timothy Killeen she carried out a thesis research to determine the age of two species of tree ferns and their demographic structure in a cloud forest of Amboró National Park (ANP). The thesis was granted by the environmental monitoring program of ANP. She obtained her degree of agronomic engineer in 2000. From 2000 to 2002 she worked at the Museo Noel Kempff Mercado as a GIS technician on projects related with land use management and conservation.

In 2002 she founded Rescate en tus Manos (REMA) a NGO committed to work in education, local capacity building and training. Between 2002 and 2004 she was the executive director of REMA. During this period she also gave workshops for a wide range of stakeholders in Bolivia, Chile, Panama, Argentina, and Ecuador. She is member of the Latin American EEPE Network that encourages to teach ecology in the schoolyards.

In 2004 she began the Master Program of Ecology and Natural Resources Management at the Instituto de Ecologia, A.C. of Xalapa, Mexico. The master was supported by the scholarship of the Secretaria de Relaciones Exteriors of Mexico. Under the supervision of Dr. Klaus Mehltreter she carried out a thesis study that evaluated the role of forest fragments for ferns diversity conservation in shadow coffee plantations in Veracruz, México. She graduated in 2006.

Back in Santa Cruz she worked for two years at the Instituto Boliviano de Investigación Forestal in Santa Cruz, Bolivia, as a researcher in the DiverSus project. DiverSus project focuses on the design and implementation of a new interdisciplinary framework to analyze and compare field studies of land use change across the Americas. This project was the framework of this PhD thesis, and the field work along those two years provided most of the data used in this PhD thesis. In September 2009 she started her PhD program at Wageningen University, the Netherlands. During the program she continued her contribution for DiversSus project. Her PhD program was interrupted for four months of maternity leave. In May 2013 she finished this PhD.

As plant ecologist she is interested in both fundamental and applied ecology. Specifically she is interested to understand the effects and consequences of human disturbances in biodiversity and ecosystem processes. As educator she wants to empower local people to ask questions about the natural history of their surroundings and to answer these through hands-on scientific inquiry. Her long-term goal is to integrate both approaches to increase the knowledge of the Bolivian natural history and to facilitate the integration of Bolivian researchers into the international community of ecologists.

Publications

Peer review papers

Carreño-Rocabado, G., M. Peña-Claros, F. Bongers, A. Alarcón, J.-C. Licona, and L. Poorter. 2012. Effects of disturbance intensity on species and functional diversity in a tropical forest. Journal of Ecology **100**:1453-1463.

Bakker, M. A., G. Carreño-Rocabado, and L. Poorter. 2011. Leaf economics traits predict litter decomposition of tropical plants and differ among land use types. Functional Ecology **25**:473-483.

Books and chapter books

Feinsinger, P., S. Álvarez, G. Carreño, E. Rivera, R. L. Cuéllar, A. Noss, F. Daza, M. Figuera, E. Lanz, and L. García. 2011. 18 Local People, Scientific Inquiry, and the Ecology and Conservation of Place in Latin America. The Ecology of Place: Contributions of Place-Based Research to Ecological Understanding. 403 p.

Rivera E. and G. Carreño. 2007. Guía del facilitador Enseñanza de la Ecología en el Patio de la Escuela. Santa Cruz, Bolivia. 64 p.

Chiné M., G. Carreño y E. Rivera. 2006. Medioambiente. Módulo 6 del Programa de Formación e Innovación Institucional y Académica dirigido a los Institutos Normales Superiores (INS). Versión online, Universidad de Barcelona Virtual.

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PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (4.5 ECTS)

- Land use change effects on functional diversity and ecosystem processes in lowland Bolivia; presented in the Third Project Workshop of DiverSus group; CATIE, Turrialba, Costa Rica (2010)

Writing of project proposal (4.5 ECTS)

- Land use change effects on functional diversity and ecosystem processes in lowland Bolivia (2010)

Post-graduate courses (7.7 ECTS)

- What's up in tropical forest community ecology?; PE&RC (2009)
- Measuring Functional biodiversity; CATIE (2010)
- Multivariate analysis; PE&RC (2010)
- Mixed linear models; PE&RC (2011)
- ALTER-Net Summer school: biodiversity and ecosystem services; ALTER-Net (2011)

Laboratory training and working visits (0.3 ECTS)

- Land use change and litter decomposition; University Amsterdam (2012)

Invited review of (unpublished) journal manuscript (1 ECTS)

- Functional Ecology: species assembly (2012)

Competence strengthening / skills courses (2.1 ECTS)

- PhD Competence assessment; Lang.Serv.WUR (2009)
- Scientific writing; Lang.Serv.WUR (2011)
- PE&RC Annual meetings, seminars and the PE&RC weekend (1.8 ECTS)
- Seminar of land use changes (2009)
- PE&RC Day: intelligent communication: on the origin of communication (2009)
- PE&RC Weekend (2010)
- PE&RC Day: innovation for sustainable: what are the neighbours doing? (2011)

Discussion groups / local seminars / other scientific meetings (5 ECTS)

- Frontier Literature in Plant Physiology (FLOP) (2009-2010)
- Wageningen Evolution and Ecology seminar (2009-2012)
- Mathematics, statistics and modelling in Production Ecology and Resource Conservation (Maths & Stats) (2010)
- Ecology theory and application (2011)
- Symposium of Tropical Ecology in the Netherlands Presentations current PhD research (2011)
- R-Group (2011)

International symposia, workshops and conferences (6.6 ECTS)

- Third project workshop of DiverSus group in CATIE, Costa Rica (2010)
- International meeting of the ATBC in Tanzania (2011)
- Third national Ecological meeting in Bolivia (2011)

Lecturing / supervision of practical's /tutorials (2.2 ECTS)

- Centre of ecosystems young scientists research symposium (2010)
- Course of basic statistics (2010)
- Disturbance and functional ecology (presented in the monthly lectures organized by IBIF, Bolivia) (2010)
- Land use change and ecosystem processes (presented in the monthly lectures organized by IBIF, Bolivia) (2011)
- Data base management in R (2011)
- Symposium of Tropical Ecology in the Netherlands Presentations current PhD research in the frame of the course (2011)

Supervision of a MSc student (3 ECTS)

- Maarje Bakker: Connecting the lifecycle's loose ends (2010)

The fellowship was funded by the Netherland Fellowship Program (NFP) , and by DiverSus project through the Inter-American Institute for Global Change Research (IAI) CRN 2015 and SGP CRA 2015, which were supported by the US National Science Foundation grants GEO-0452325 and GEO-1138881.

The partial financial support from Wageningen University for printing this thesis is grateful acknowledged.

The thesis layout and the cover was designed by G. Carreño-Rocabado

Pictures were taken by G. Carreño-Rocabado

Printed by Gildeprint Drukkerijen