Land-use intensification effects on functional properties in tropical plant communities

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Abstract. There is consensus that plant diversity and ecosystem processes are negatively affected by land-use intensification (LUI), but, at the same time, there is empirical evidence that a large heterogeneity can be found in the responses. This heterogeneity is especially poorly understood in tropical ecosystems.

We evaluated changes in community functional properties across five common land-use types in the wet tropics with different land-use intensity: mature forest, logged forest, secondary forest, agricultural land, and pastureland, located in the lowlands of Bolivia. For the dominant plant species, we measured 12 functional response traits related to their life history, acquisition and conservation of resources, plant domestication, and breeding. We used three single-trait metrics to describe community functional properties: community abundance-weighted mean (CWM) traits values, coefficient of variation, and kurtosis of distribution.

The CWM of all 12 traits clearly responded to LUI. Overall, we found that an increase in LUI resulted in communities dominated by plants with acquisitive leaf trait values. However, contrary to our expectations, secondary forests had more conservative trait values (i.e., lower specific leaf area) than mature and logged forest, probably because they were dominated by palm species. Functional variation peaked at intermediate land-use intensity (high coefficient of variation and low kurtosis), which included secondary forest but, unexpectedly, also agricultural land, which is an intensely managed system. The high functional variation of these systems is due to a combination of how response traits (and species) are filtered out by biophysical filters and how management practices introduced a range of exotic species and their trait values into the local species pool.

Our results showed that, at local scales and depending on prevailing environmental and management practices, LUI does not necessarily result in communities with more acquisitive trait values or with less functional variation. Instead of the widely expected negative impacts of LUI on plant diversity, we found varying responses of functional variation, with possible repercussions on many ecosystem services. These findings provide a background for actively mitigating negative effects of LUI while meeting the needs of local communities that rely mainly on provisioning ecosystem services for their livelihoods.

Key words: agriculture; Bolivia; functional diversity; functional traits; land-use intensity; pastureland; plant community; secondary forest; tropical forest.

Introduction

Land-use intensification (LUI) is the main global change driver with the most immediate and strongest

impacts on biodiversity and ecosystem processes and services (MEA 2005, Hooper et al. 2012). LUI impact in the tropics is widespread, occurs at a faster pace than before, and is likely to continue to do so in the future (FAO 2010, Hosonuma et al. 2012). Some types of land use are related to basic human demands (e.g., food), while others, such as logged forest, may be perceived as alternatives to more extreme land-use

changes, such as forest conversion. How functional properties of plant communities change in response to LUI determines whether ecosystem functions and services are preserved or not. Identifying the threshold of maximum LUI modification that maximizes productivity and preserves ecosystem functions is crucial for proper land use (Rockstrom et al. 2009, Johnson 2013). Managing changes in land use requires an understanding of the trade-offs between competing land-use goals. Informing these trade-offs with sound science can contribute to better land-use decisions, and improved mitigation of the negative impacts of those decisions.

The number of studies that evaluate LUI effects on plant functional properties has increased over the last decades as trait-based approaches have been developed. These approaches provide a mechanistic understanding of plant responses to environmental and abiotic filters and to management practices (Mayfield et al. 2010, Garnier and Navas 2012, Conti and Díaz 2013, Gaba et al. 2014), and the effects thereof on ecosystem processes (Díaz et al. 2007). However, in spite of this increased focus on LUI effects, most studies have focused on temperate areas, mainly pasturelands (Garnier et al. 2007, Quétier et al. 2007, Lienin and Kleyer 2011, Garnier and Navas 2012), and others on weed crops (Gunton et al. 2011, Fried et al. 2012, Gaba et al. 2014) rather than on agricultural systems from tropical zones. Studies that evaluated community functional properties in tropical zones have focused on single components (i.e., trait variation; Laliberté et al. 2010) and covered only part of the LUI gradient (Mayfield et al. 2013). With this study, we aim to contribute to a better understanding of the effects of LUI on functional properties of plant communities. We do so by evaluating different land-use types along a gradient of LUI (i.e., from mature forest to introduced pasturelands) in a tropical area in lowland Bolivia, and by discussing the implications for ecosystem services.

There is consensus that plant communities and ecosystem functioning are negatively affected by high levels of LUI (Srivastava and Vellend 2005). At the same time, large differences have been observed in LUI effects (Mayfield et al. 2006, Garnier et al. 2007, Laliberté et al. 2010, Gibson et al. 2011). For instance, functional diversity increases at intermediate levels of LUI (Fédoroff et al. 2005, Quétier et al. 2007), in line with the intermediate disturbance hypothesis (Connell 1978, Bongers et al. 2009), or at higher levels of LUI due to the introduction of "exotic traits" into the regional pool (Mayfield et al. 2005). Differences in plant community responses to LUI may be explained by the spatial scale examined (global vs. local), the length of the LUI gradient and types of land use considered (Fédoroff et al. 2005, Jackson et al. 2009), by threshold effects (Johnson 2013), and by the combination of biophysical factors and management practices that shape LUI.

Levels of land-use intensity depend on three dimensions: inputs and outputs to the production system, and changes of ecosystem properties (Erb et al. 2013). Input intensity is related to practices that increase crop productivity, such as increased cropping frequency per year (in the case of logged forest, the length of the cutting cycle), complemented by the use of technology, and a large amount of capital and other external inputs. The frequency of disturbance events can be used as a proxy for input intensity (Ruthenberg 1980). Output intensity refers to the increase in production per unit area or time. The amount of biomass or energy produced per unit area or time can be used as a proxy for output intensity (Foley et al. 2005). Changes of ecosystem properties are related to ecological patterns and processes such as plant net primary production or diversity; the remaining forest area in relation to the cultivated area can be used as a proxy to understand how much the ecosystem was altered due to LUI (Dayal 1978, Erb et al. 2014). Along the gradient of LUI, both biophysical factors (i.e., light or nutrient availability) and management practices (i.e., the selection of crop species and their spatial and temporal configuration) shape the species assembly of plant communities and, hence, community functional properties (Lienin and Kleyer 2011, Gaba et al. 2014). Whereas the effects of biophysical filters (i.e., resource availability and biotic interactions in different land-use types) have received more attention from ecologists (Weiher et al. 1998, Fukami et al. 2005), the influences of management practices on species assembly and its effects on ecosystem processes have received very little attention (but see Mayfield et al. 2013). Management practices include an historical component of plant domestication, modern breeding techniques, and agricultural practices such as weed control. At the species level, these practices have selected and favored species with certain traits, such as traits conferring high productivity (leaf nitrogen concentration; Sponchiado et al. 1989) and faster decomposition (Cornwell and Cornelissen 2013, García-Palacios et al. 2013). At the community level, management practices affect the species configuration of crop species (i.e., monoculture, polyculture, agroforestry) and the associated weed species (Fried et al. 2012), therefore influencing community functional properties (Garnier and Navas 2012). The relative importance of biophysical filters and management practices for community assembly must be considered to better understand the effects of LUI on diversity and ecosystem processes.

Community functional properties can be described using metrics that quantify the central tendency, the dispersion, and the distribution of functional traits within the community (Fig. 1; Díaz et al. 2007, Kraft et al. 2008, Shipley 2010). The community-weighted mean (CWM) shows the central tendency of trait values and thereby the functional composition of the
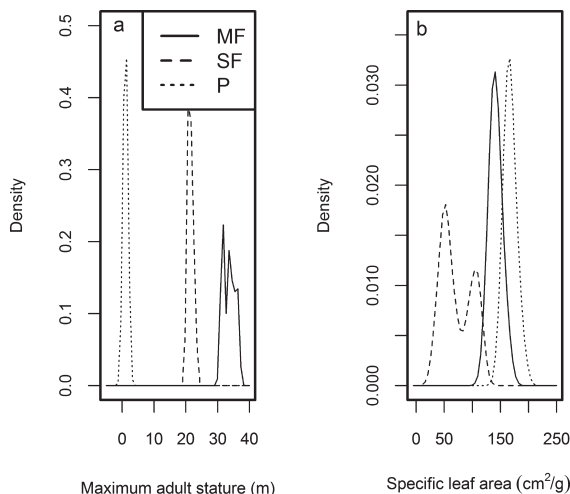
FIG. 1. Examples of community functional properties comparing mature forest (MF), secondary forest (SF), and pastureland (P) in lowland Bolivia. The position of each curve on the *x*-axis is related to the community weighted mean (CWM), the width of each curve is related to the coefficient of variation (CV), and the peakedness of the distribution with the kurtosis (*K*). Panel (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 (LUI) decreases. The same pattern is observed for *K*, but trait variation of mature forest is higher. Panel (b) shows that the CWM, trait variance, and trait distribution of specific leaf area (SLA) 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.

community (Pla et al. 2012); it may indicate what traits are filtered by different constraints (e.g., Lebrija-Trejos et al. 2010, Shipley 2010). Trait dispersion and trait distribution describe the variation of trait values in the community (measured as coefficient of variation and kurtosis of trait distribution; Magurran and McGill 2011). LUI may reduce or increase both the trait mean and the trait variation in the plant community because of strong biophysical filters and management practices.

We evaluate here how community functional properties (CWM, coefficient of variation, and kurtosis) respond to a long gradient of LUI, and how these properties are associated with each other. We compared five important and widespread land-use types: three forest systems (mature forest, logged forest, and secondary forest) and two cultivated systems (small-scale agricultural land and pastureland) that represent a long gradient of LUI in the tropics (Table 1). For the dominant species of each land-use type, we measured 12 functional traits that are related to plant growth, survival (Poorter and Bongers 2006), and productivity, and for crop species, some of these traits are related to human selection pressure (Kendal et al. 2012, García-Palacios et al. 2013; Appendix B: Table B1). We made two predictions: First, we expected forested systems

and cultivated systems would differ in the most abundant plant trait values (i.e., the CWM). Low levels of LUI in mature forest will enhance slow-growing species with conservative trait values, whereas an increase in LUI in logged and secondary forest will enhance establishment of fast-growing species with more acquisitive trait values (sensu Chapin et al. 1993, Lambers and Poorter 2004, Wright et al. 2004, Poorter et al. 2006, Lebrija-Trejos et al. 2010). For cultivated systems, we expected a mixture of acquisitive and conservative trait values due to a combination of fast-growing crop and weed species with high productivity per unit leaf area and slow-growing drought-resistant species that are selected for food provision (Abbo et al. 2012).

Second, we expected that trait variation would increase with increasing land-use intensity to reach a maximum level (i.e., high coefficient of variation and low kurtosis in secondary forest), after which trait variation gradually decreases again in agricultural land and pastureland because these land uses represent highly disturbed, completely changed systems (Fig. 2). Finally, we will discuss to what extent the three metrics used in the study provide complementary information on the functional properties of plant communities or whether they are strongly associated. We end with a discussion how this knowledge can be used to guide a better decision making about LUI in the tropics.

MATERIALS AND METHODS

Study site

This study was conducted in the province of Guarayos, in tropical lowland Bolivia (15° 54′ S, 63°11′ W). Annual precipitation in the area is 1580 mm/yr, with a dry season (<100 mm/month) from April to October. The Guarayos province covers an area of 27343 km². About 60% of this area is covered with mature forest, 32% with crops under slash-and-burn agriculture (with fallow period of 7–15 yr), and 8% with natural and cultivated pasturelands (GMAG 2006).

The mature forest vegetation is classified as semideciduous tropical moist forest (Toledo et al. 2011), with a canopy height of ~27 m, tree species richness of 59 species/ha, density of 368 tree/ha, and basal area of 19.7 m²/ha (all for trees >10 cm diameter at breast height; 1.3 m above ground; 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).

From an economic and social point of view, the most important activities are timber production (88% of Guarayos' forest has been defined as permanent timber production forest), agriculture, and livestock production. More than 10 agricultural crop species

TABLE 1. Description of land-use types used to evaluate the influence of land-use intensification on plant community functional properties in lowland Bolivia.

Land-use type	Description	Intensity (%)	System age (yr)	Event frequency (times/yr)	Magnitude (%)	Regeneration (yr)	Species richness
Mature forest (MF)	Forest without signs of large-scale (human) disturbance (recent past).	0	>200	0	0	0	106
Logged forest (LF)	Managed forest 8 yr after logging with reduced-impact techniques, 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 dbh.	14	8	2	<25	8	111
Secondary forest (SF)	Fallow 8–12 yr regeneration after shifting cultivation.	100	8–12	1	>75	8–12	132
Agricultural land (AL)	Small-scale polyculture systems combining two, three species (i.e. corn, peanut, cassava, rice, pineapple, banana). Slash-and-burn with fallow period 8–12 yr. Largest plot < 1 ha (typical size 0.5 ha) surrounded by patches of MF and SF.	100	1–5	8	>75	0	42
Pasturelands (P)	Grasslands with mostly exotic grasses 8–30 yr old. Pastureland area more than 10 ha, in most cases adjacent to other P.	100	20–30	4	>90	0	12

Notes: Land-use types have been arranged from low to high intensification based on five variables describing the disturbance and management activities: intensity, which is given by the percentage of forest cover removed or remaining biomass; age of the current system, which is the number of continuous years under the same system; frequency, which is given by the number of disturbance events (sowing, logging) per year; magnitude, as indicated by the percentage of deforested area in a 1 km radius around the plots; regeneration time, indicating the period since abandonment in which natural regeneration is allowed to occur, and total species richness per land-use type. Quantification of each parameter per land-use type gives a general estimation of intensification.

(e.g., corn [*Zea mays*], rice [*Oryza sativa*], cassava [*Manihot esculenta*], banana [*Musa* sp.], and peanut [*Arachis hypogea*]) 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

LUI gradient.— We selected the five most important land-use types in the region, which cover the whole gradient of LUI. Their management intensity was qualitatively assessed based on six parameters related to input and output of the production system and ecosystem properties (Lambin et al. 2003, Jackson et al. 2009, Erb et al. 2013): management intensity (biomass loss caused by the disturbance events), frequency of management practices (disturbance events), age of current system, magnitude of disturbance (percentage of undisturbed forest in a radius of 1 km), time since disturbance (time for natural regeneration), and overall species richness. Based on these factors, the land-use types could be

ranked from low to high LUI in the following order: mature forest, logged forest, secondary forest, slash-and-burn agricultural fields, and pastureland (see details in Table 1).

Plot design.— To describe species composition and quantify species' relative dominances at the community level, eight plots were established per land-use type. In each land-use type, we sampled the most representative and dominant lifeform for the system, with some exceptions as indicated. For mature and logged forest, data came from the 1-ha plots of the long-term silvicultural research program of Instituto Boliviano de Investigación Forestal (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. [2008*b*]). Within each plot, all trees ≥10 cm dbh were identified and their dbh measured. Ferns and herbs were not included because they present a tiny fraction of aboveground biomass in these systems, and are thought to contribute therefore little to ecosystem processes (c.f. Grime 2001). Data used for this study come from the control and the intensive silviculture plots (i.e., plots

intensively logged and treated with silvicultural treatments), and correspond to measurements made 8 yr after logging. For secondary forest, agricultural land, and pastureland, 0.5-ha plots (50 × 100 m) were established around Ascención de Guarayos. Secondary forest plots were the result of slash-and-burn agriculture, and ranged 8–12 yr 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 × 10 m subplots in each corner of the main plot. Agricultural land consisted of slash-and-burn small-scale nonmechanized agriculture in which a patch of (mature or secondary) forest was slashed and burned. Agricultural fields are typically ~0.5 ha, and are managed using intercropping systems or polyculture systems with seasonal annual crop rotation (i.e., maize, cassava, rice) and perennial species such as banana. These agricultural fields are used for 5–7 yr, after which the area is abandoned for agriculture and is allowed to fallow for a period of 7–15 yr. Pasturelands were at least 10 ha in size and 20 yr old. They consisted of a mixture of native and nonnative grasses, and were grazed 1–2 weeks continuously three to five times per year by cattle and/or sheep. In the agricultural and pasturelands all plants >0.01 m and ≤4 m height (this limit was based on the tallest crop species) were sampled, including trees, shrubs, and herbaceous plants (crops, grasses, and weeds). Using the point intercept 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 tallest individual that intersected the point was identified, and its height was measured.

Because forested and cultivated systems differ strongly in lifeform composition and structure, we used different sizes of sampled areas and different methods to be able to obtain a good estimation of the dominant lifeforms and species in each system. Whereas, in mature and logged forests, it was necessary to sample at least 1 ha to observe a minimum of 85% of the estimated richness of these systems (Carreño-Rocabado et al. 2012), in the agricultural system, we could cover a similar percentage (or even higher for pastureland) with a smaller area (results not shown). Because most of the secondary forest patches were 0.5 ha in size, it was not possible to sample a larger area in secondary forest. Nevertheless, even with a smaller sampled area than other forested systems, secondary forest had an overall higher species richness (Table 1) and higher functional variation compared to the other land-use types. Our sampling procedure therefore allows us to compare these systems in terms of trait composition and trait variation of the most dominant lifeform and species (making up 85–100% of the biomass, depending on the trait considered; Appendix S2: Tables S21 and S22), although we acknowledge that it does not describe the complete trait variation in the community (including smaller and subordinate species).

Traits.— We selected 12 functional traits associated with the response of plants to LUI based on the resource acquisition, resource conservation, and life-history strategies of the species (Aarssen and Schamp 2002). These functional traits not only show the sensitivity of species to changes in resources availability, but also reflect the effect of management on the community trait properties (Appendix S2: Table S21). Maximum adult stature is strongly related with species ability to compete for light (Westoby 1998), and is also closely associated with lifeforms (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, and nitrogen and phosphorus concentration reflect the ability of species to acquire, use, and conserve resources (Poorter and Bongers 2006, Bakker et al. 2011). The force to punch and to tear leaves is closely associated with leaf defense against herbivores and biophysical hazards, and hence, with leaf longevity and resource conservation (Onoda et al. 2011). Leaf slenderness (leaf length divided by leaf width) is related to the cooling of the leaf, and hence, the ability of the species to cope with hot and/or dry conditions. These traits are also related to LUI 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 defenses against herbivores but higher palatability (Lin et al. 2011, Abbo et al. 2012). Methods used for trait measurement follow Pérez-Harguindeguy et al. (2013). See Appendix S1 for detailed descriptions.

With these measurements we calculated the following morphological traits: specific leaf area (SLA; leaf area/leaf dry mass, cm^2/g), leaf dry matter content
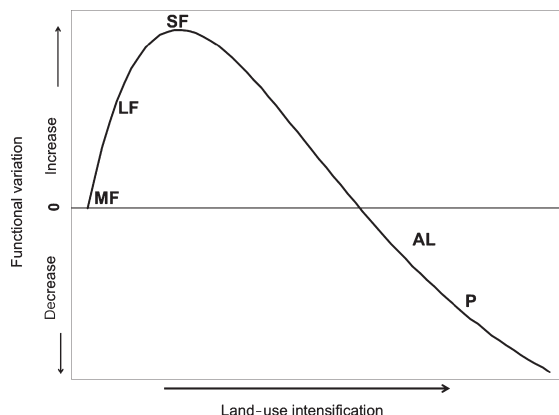

FIG. 2. Potential response of functional variation to increasing land-use intensity. Land-use types are as described in Fig. 1, with the addition of logged forest (LF), and agricultural land (AL).

(LDMC; leaf dry mass/leaf fresh mass, g/g), leaf toughness (LTo; force/leaf lamina area, N/cm^2), maximum adult stature (H_{max}, m), wood density (WD; g/cm^3), and leaf chlorophyll content estimated with a SPAD meter (Konica Minolta, Tokyo, Japan). The SPAD value was converted to chlorophyll concentration per unit leaf area (Chl, $\mu mol/m^2$) using a mean of the regression equations for six temperate herbaceous species ($Chl_{area}= 13.9 \times SPAD - 112.9$, $\mu mol/m^2$; Anten and Hirose 1999), The nitrogen (N_{mass}, percentage dry mass) and phosphorus concentration per leaf dry mass (P_{mass}, percentage dry mass) were determined for a pooled leaf plus petiole sample per species.

Trait coverage.— Traits were collected for the most dominant species in each community, as they indicate how the community in general responds to the environment, and because the traits of the dominant species have the strongest impact on ecosystem processes. H_{max} was determined for all species. The forest 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 communities of agricultural and pastureland, dominant species were selected based on a dominance index that combines species cover (number of points with species presence) and the height of each individual plant. We had functional trait data for 85–97% of the dominance per plot, depending on the trait considered (Appendix B: Table B1). We acknowledge that, by omitting rare species, we do not describe the complete trait variation in the community (including smaller and subordinate species). Omitting rare species could have an effect in detecting differences between land-use changes in community trait variation. The effect could have been larger for secondary forest since these communities have a high temporal turnover in species composition (Lohbeck et al. 2014). However, in our study, we were able to detect higher trait variation in secondary forest, which suggests that omitting rare species had little influence in our comparisons.

Metrics describing community functional properties.— Using the non-transformed trait values, we calculated three single-trait metrics of community functional properties: the central tendency based on the community-weighted mean (CWM), and functional variation based on the coefficient of variation (CV), and the kurtosis of trait distribution (K). It has been shown that single-trait metrics perform well for linking environmental gradients and ecosystem processes (Butterfield and Suding 2013). The CWM of plant traits was calculated as the mean trait value per community (Garnier et al. 2004, Díaz et al. 2007), weighting species contribution into a community by their relative basal area/dominance index and by their abundances. The CV shows the extent of variability of traits in relation to the CWM. Trait variation could be described using the standard deviation or range, with the advantage that they are expressed in the original trait

units, and can therefore inform us more directly about plant strategies and ecosystem function. We prefer to use CV and K instead, because CV expresses the trait variation in percentages, and therefore allows comparison of different (trait) variables that are expressed in different units and scales. The K of trait distribution shows how acutely trait value distribution peaks around the CWM, and is more informative about trait variation than the trait range, which depends on only two measurement points (the minimum and the maximum), and can therefore be strongly affected by outliers. The K is a very intuitive and straightforward metric, successfully applicable to detect shifts in the relative importance of different processes driving species dominance in secondary succession (Lohbeck et al. 2014) and assembly processes in tropical forest (Cornwell and Ackerly 2009, Kraft and Ackerly 2010). Both CV and K considered species abundances because they were calculated based on all individuals of the dominant species per plot. To be consistent with the three metrics, all evaluations were done with abundance-weighted metrics. However, as originally trait cover had been calculated for the dominant species based on their basal area for trees and dominance index for crops and grasses, we evaluated the correlation per land-use type and functional trait between CWM weighted by basal area/dominance index and weighted by abundance. Functional measures based on basal area or abundance weighting were significantly (all tests were significant at $P < 0.05$) correlated in 50 out of 53 measures ($r > 0.8–1$), only three correlations were ≤0.35 (Appendix S2: Table S23).

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 nonnormal distribution). We did not do Bonferroni corrections in the pairwise Wilcoxon test in order to reduce the Type II error when differences between land-use types were tested. Relationships among the three aspects of community functional properties were analyzed with Pearson correlations, pooling all land-use types ($n = 40$ plots). To explore relationships between functional properties (CWM, CV, and K) of the 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 we carried out three series of principal components analysis

(PCA). First, to evaluate the complementarity and sensitivity of the metrics to land-use type, we carried out three independent PCAs, one for each metric (i.e., CWM, CV, and K) considering all traits and land-use types. Second, to understand how trait covaried within each metric and within land-use types, a single PCA was done including all metrics, traits, and land-use types. Third, to further explore

differences between less-contrasting land-use types, three PCAs were done, in which each time plots belonging to the most disturbed system were excluded (i.e., a PCA for only forest systems, a PCA with only mature forest and logged forest, and a PCA for only agricultural systems). All PCAs were based on correlation matrices. Analyses of variance, Wilcoxon rank-sum tests, and correlations were done
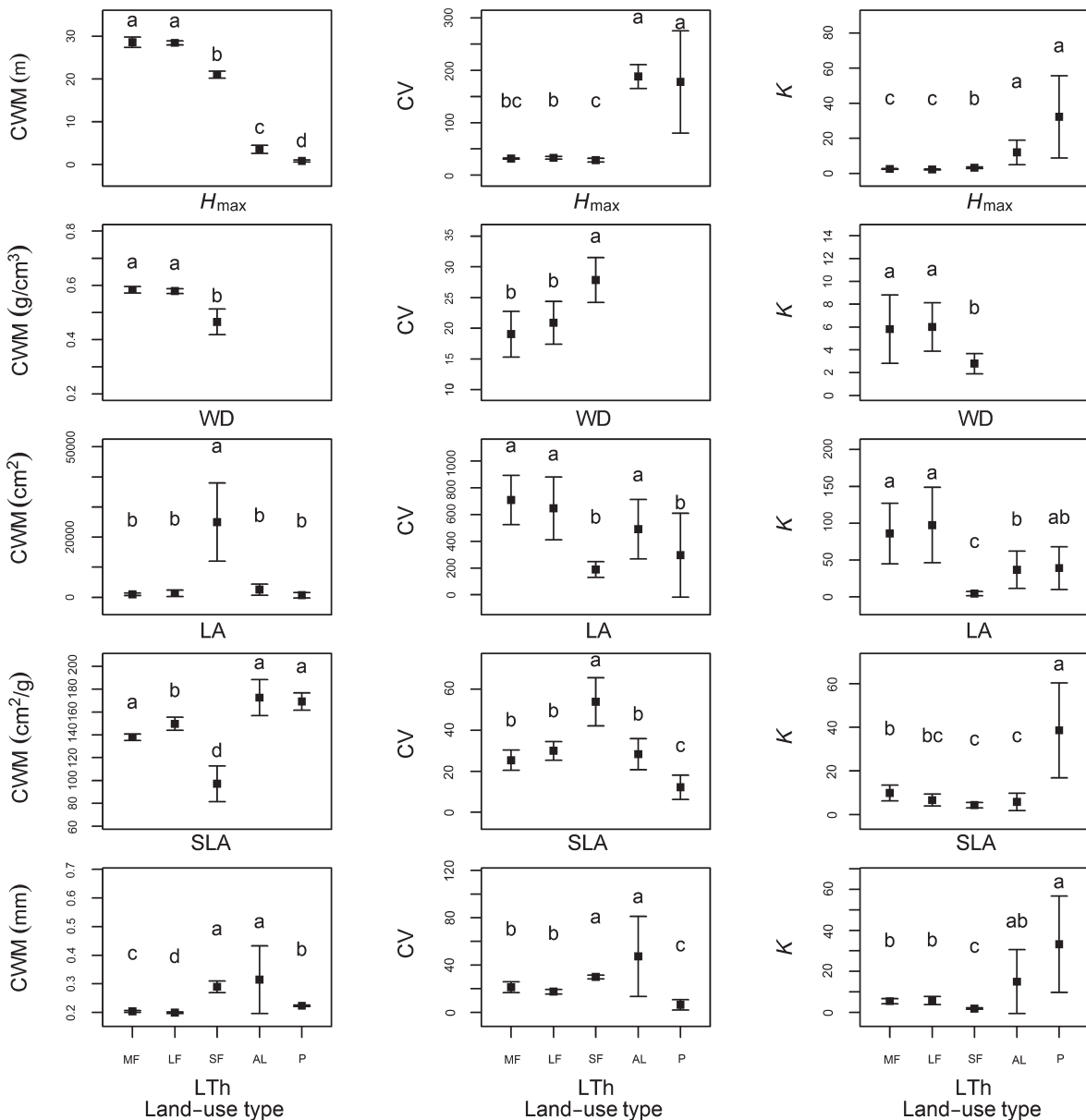
FIG. 3. Differences of three elements of community functional properties along a long gradient of LUI: land-use types are as in Table 1. The CWM, CV, and K (Fig. 1) of 10 functional traits are shown. The traits are maximum adult stature (H_{max}), wood density (WD), leaf area (La), specific leaf area (SLA), leaf thickness (LTh), leaf dry matter content (LDMC), force to punch (Fp), leaf chlorophyll per area (LCh), and N and P concentration per unit leaf mass (N_{mass}, P_{mass}); for more detail on traits, see Appendix B. Means and 95% 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).
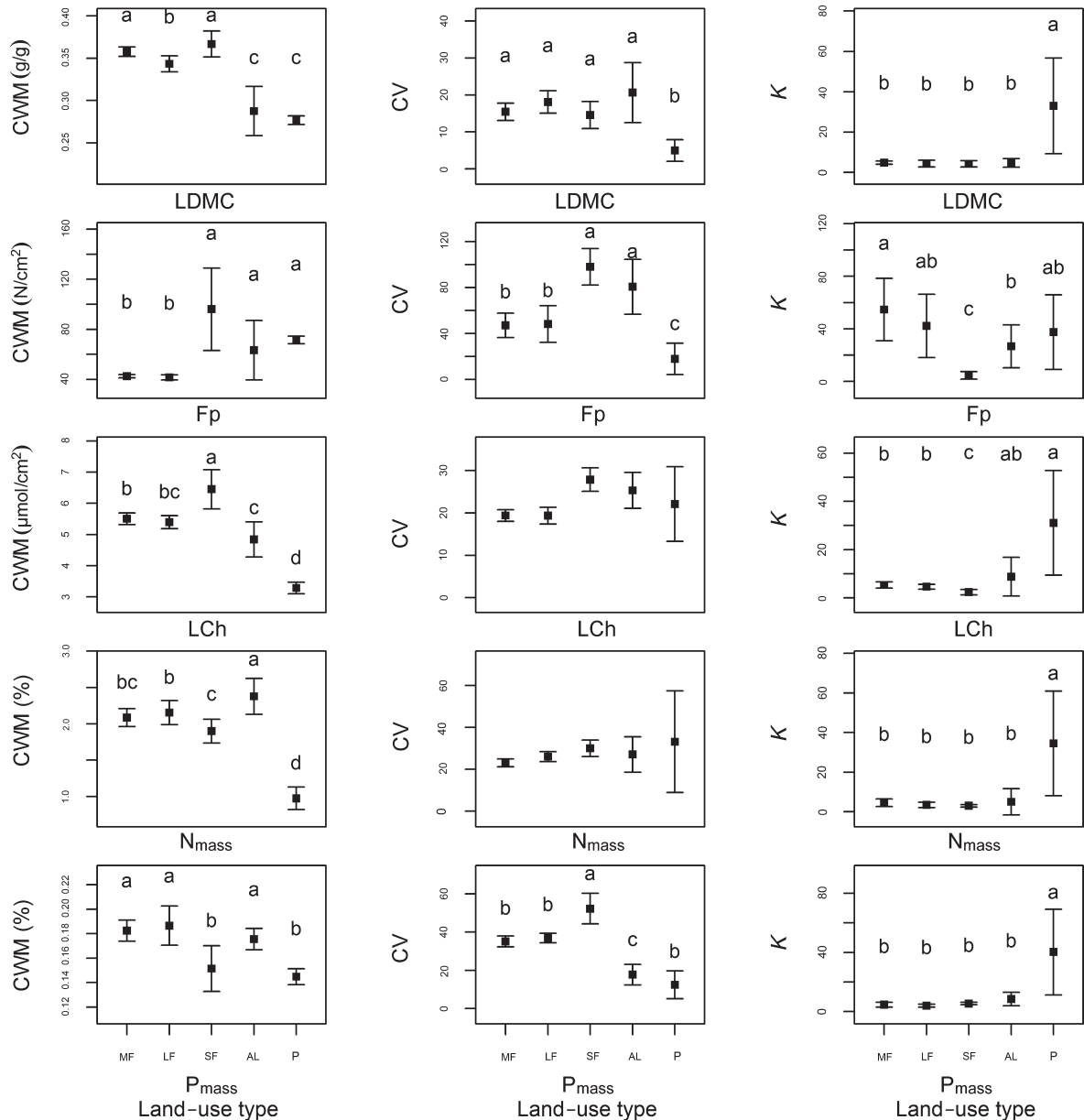
FIG. 3 Continued.

using R 2.12.1 (R Development Core Team 2011), whereas PCA analyses were done using CANOCO (ter Braak and Šmilauer 1998).

RESULTS

Differences in community functional properties

Community weighted mean.— For all 12 evaluated traits, the CWM differed among land-use types (one-way ANOVA or Kruskal-Wallis test, $P < 0.001$, Fig. 3; Appendix S2: Table S24). 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 six out of 11 traits). Mature and logged forest had, compared to other land-use types, the highest adult stature, leaf 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 (Fig. 3). 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 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 (Fig. 3).

Functional variation (CV and K*).*— Variation in trait values within each community was described with the coefficient of variation (CV) and kurtosis of trait distribution (K). For the 480 plot-trait combinations (i.e., 40 plots × 12 traits), CV averaged 38% and ranged between 14% and 69%. The CV differed significantly (ANOVA or Kruskal-Wallis test $P \leq 0.001$, Fig. 3) among 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 pastureland (with the exception of CV of H_{max}, which was highest in pastureland, Fig. 3; Appendix S2: Table S24).

Trait distribution within each community was described by K; a high K indicates a narrow trait distribution. The K of all evaluated functional traits differed significantly among land-use types (ANOVA $P \leq 0.03$ or Kruskal-Wallis test $P < 0.005$, Fig. 3; Appendix S2: Table S24). Mature forest, logged forest, and pastureland had the highest K for leaf area, and force to punch and tear; cultivated systems had the highest K for adult stature; and pastureland had the highest K for the other seven leaf traits (leaf slender, specific area, thickness, dry matter content, chlorophyll, N_{mass}, and P_{mass}). Contrarily, secondary forest had in general the lowest K for the similar set of leaf traits (except dry matter content, N_{mass}, and P_{mass}; Fig. 3).

To explore the ability of metrics to distinguish and describe different land-use types, we did a separate PCA per metric (CWM, CV, and K). The PCA based on the CWM explained 74% of the variation in trait values among plots with the first two axes (Appendix C: Fig. C1). This PCA clearly separated forested systems from cultivated systems, although it made a less clear distinction between mature and logged forest. The natural systems at the right were characterized by high leaf chlorophyll content and leaf dry matter content; the cultivated systems were characterized by high leaf slenderness and specific leaf area. Secondary forest was separated from mature and logged forest due to high leaf force to punch and leaf area. For the PCA based on CV, the first two axes explained 60% of the variation. Using the CV, the agricultural land was clearly separated from other land-use types due to high variation in maximum adult stature and leaf chlorophyll content, but some plots of pastureland were not distinct from mature forest and agriculture land. (Appendix S3:

TABLE 2. Correlations between community weighted mean (CWM), coefficient of variation (CV), and kurtosis (K) of five land-use types for 12 functional traits, in lowland Bolivia.

Metric pairs	H_{max}	WD	N_{mass}	P_{mass}	LDMC	Fp	SLA	LCh	La	LTh	LSl	Ft
CWM, K	−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, K	0.79**	−0.69**	−0.25	−0.56**	−0.54**	−0.44**	−0.60**	−0.09	0.75**	−0.02	−0.40*	0.02

Notes: 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), and N and P concentration per unit leaf mass (N_{mass}, P_{mass}); $n = 40$ plots, but 24 plots for WD.

* $P < 0.05$; ** $P < 0.01$.

Fig. S32). For the PCA based on K, the first two axes explained 90% of the variation; using K, pastureland was clearly separated from the other land-use types with high values in all traits, but force to punch and leaf area separated mature and logged forest from the other land-use types (Appendix C: Fig. C3).

Association among metrics and with LUI

The three metrics (CWM, CV, and K) with which functional properties were described were often significantly correlated with each other; CWM was correlated with K for 10 traits, CWM vs. CV for six traits, and CV vs. K for eight 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).

To evaluate how the three metrics were associated, and to what extent they were able to distinguish different land-use types, we did a complete PCA, including all three metrics, all traits, and all five land-use types (Fig. 4). The first two PCA axes explained 60% of the variation (Fig. 4a). The first axis separates 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. All axes from PCAs with a single metric ordered the plots along a gradient of LUI, which was also obtained with the PCA that included all three metrics (see following paragraphs; Fig. 4).

The first axis was strongly positively associated with K (Fig. 4b) of all traits, and negatively associated with the CWM and CV (Fig. 4b) of some traits. The forested systems at the left were characterized by high CWM of N_{mass}, LDMC, and H_{max}, and high CV of P_{mass} and LDMC. The cultivated systems at the right were characterized by high K 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 K of leaf area, and high K 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. 4b).

To zoom in to more subtle differences among less contrasting land-use types, we removed step-by-step the plots with the most intense land-use type. Only PCA results that provided extra information are shown. A PCA that considered only forest systems showed that mature forest tends to have low variation in SLA and N_{mass} (high K) and more tall and conservative species (high CWM of SLA and H_{max}) compared to

logged and secondary forests (Appendix S3: Fig. S34). Secondary forests were mainly characterized by high CV for most of the traits. A PCA with only mature and logged forest showed that logged forest tended to have more acquisitive species (high CWM of SLA) and more variation of N_{mass} (high CV; Appendix S3: Fig. S35). A PCA with only agricultural land and pastureland showed that these two systems were mainly separated by CWM and K (Appendix S3: Fig. S36), with similar values or high CWM for (i.e., leaf thickness, leaf N_{mass} and P_{mass}) and high K for pastureland (i.e., leaf slenderness, specific area, thickness, dry matter content, chlorophyll, N_{mass}, and P_{mass}).

Fig. 4. Principal-component analysis (PCA) of metrics of community functional properties: CWM, CV, and K of 10 functional traits (traits are as in Fig. 3, with the addition of the leaf slenderness index, LSl [cm/cm]; WD and Fp were not included because not all land-use types had woody species in their composition and the trait was highly correlated with force to tear). (a) Loading metrics of community-trait structure in the first (explained variation is 40%) and second axes (explained variation is 18%). (b) Loading plots of land-use types on the first and second axes: mature forest (diamond, MF), logged forest (x, LF), secondary forest (triangle, SF), agricultural land (circle, AL), and pastureland (star, P).

Discussion

We evaluated changes in plant community functional properties along a gradient of LUI. Using five land-use types, we analyzed the central tendency (CWM), the variation (CV), and the distribution (K) of single traits within plant communities of each land-use type. Here, we discuss our main results of differences among land-use types, correlations between the three metrics, association and/or complementarity between metrics along the LUI gradient, and implications for the conservation and provision of ecosystem services in a tropical LUI context.

Response of CWM to LUI

We measured differences in functional composition and functional variation among land-use types (at local spatial scale) via CWM of 12 functional traits. These functional traits clearly responded to LUI (Fig. 3). Our results partially confirmed our hypotheses and results of earlier studies that leaf traits involved in the acquisition–conservation trade-off (Grime 2001), such as SLA, LDMC, and leaf N_{mass} and P_{mass}, 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 trait values, such as high SLA and low LDMC. However, other acquisitive leaf trait values such as N_{mass} and P_{mass} did not show a clear directional pattern. We also hypothesized that CWM would clearly separate our forested systems from cultivated systems, going from conservative to acquisitive CWM. This hypothesis was supported for some traits when forested 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 (Fig. 3). 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 polyculture systems or intercropping in the sampled agricultural land plots. Intercropping to some extent resembles forested systems where species, through complementary traits, have a complementary resource use, leading to an overall higher productivity (Coolman and Hoyt 1993, Denevan et al. 1995). For example, polyculture systems may combine perennial species with less acquisitive traits (pineapple or cassava) and seasonal and fast-growing species with more acquisitive traits (rice, maize, and peanuts; e.g., Ewel 1999).

In contrast to our expectations, within forested systems, only CWM of three leaf traits (specific leaf area, leaf dry matter content, and leaf thickness; Fig. 3) responded to LUI and an opening up of the forest canopy (logging and silvicultural treatments). The most disturbed communities were dominated by fast-growing species with more acquisitive trait values. The lack of response in the other nine traits can be attributed to a short recovery time after the disturbance (8 years), a large heterogeneity among plots, or because these traits do not respond to logging in tropical forest. Such lack of logging effects was reported earlier (Mayfield et al. 2010): functional diversity of leaf area and maximum adult stature did not respond to logging disturbance in temperate forest 50 years after logging. However, a more consistent and clear response to disturbance intensity of logged forest toward more acquisitive species has been shown when the initial functional properties of the community (pre-logging) were taken into account (see Carreño-Rocabado et al. [2012] for this approach). Counterintuitively, secondary forests had more conservative trait values (i.e., lower SLA and higher force to punch and tear) than mature and logged forest (Fig. 3). 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 trait values (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. These species might have become abundant due to repeated burning in the region. Their large, strong, and heavy leaves have led to conservative CWM values (Fig. 3). 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 (Fig. 3).

Within cultivated systems, we expected consistent differences between agricultural land and pastureland because of the obvious differences in species composition with peanut, banana, cassava, and rice 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 other traits we did not find significant differences (Fig. 3).

Whether or not the leaf economic spectrum and functional traits related to plant performance are related to LUI largely depends on local or regional land-use management practices. For instance, whereas Garnier et al. (2007) indicated a strong and consistent response of functional traits to increasing land-use intensity, at the community level, this resulted in dominance by plants with more acquisitive leaf trait values. Our study shows that the system with intermediate levels of intensification (i.e., secondary forest) may have less acquisitive trait values than systems with low levels of intensification. Perhaps our study shows different results because it covers a larger range of LUI and strikingly different land-use types. Hump-shaped functional responses along a gradient of LUI have also

been found in other, different, contexts and LUI gradients (Fig. 4 in Laliberté et al. 2010). No major explanation for these different responses has been articulated yet. Also, the nature of the land-use type itself has an effect here (Jackson et al. 2009). For instance, large-scale oil palm plantations and soybean fields are both intensively managed land-use types, but oil palms have very conservative trait values while those of soybean are very acquisitive.

Response of functional variation among land-use types: trait variation and trait distribution

We described functional variation as the extent of trait variability to the mean measured here as the CV and the trait distribution measured as the K (Shipley 2010, Magurran and McGill 2011). Supporting previous studies, our result showed that response of functional variation to LUI is trait dependent (Mayfield et al. 2005, Laliberté et al. 2010). Thus, our expectation that functional variation increases in secondary forest and decreases in cultivated systems (Fig. 2) was only registered for P_{mass}. The common trend among the different traits was an increase in functional variation for secondary forest, and no differences in functional variation between agricultural land and mature forest (Figs. 2 and 3). In our study, we only found a reduction of functional variation in the most extreme end of the gradient of LUI (i.e., pastureland). However, species richness may influence this result; high functional variation at high LUI (i.e., agricultural systems) may be related to low functional redundancy due to far fewer species representing traits at this level of intensification.

In general, early studies did find that functional variation (measured as functional response and redundancy) decreases with increase in LUI (see Laliberté et al. 2010, Pakeman 2011). However, at the same time they also showed that at local scales and depending on the functional traits evaluated, functional variation can increase with LUI (Laliberté et al. 2010). Differences among studies in functional diversity metrics, the large heterogeneity of land-use types, range of LUI, and the range of variations in the environmental factors makes a general conclusion about the effects of LUI difficult (Wright et al. 2005). Based on our results, we showed that even with high disturbance intensity where the whole system was drastically changed (i.e., agricultural land system), functional variation can be maintained by a combination of biophysical filters and management practices. It is, however, important to indicate that for forested systems we only sampled trees, whereas for cultivated systems we sampled different lifeforms (shrubs and herbs), influencing functional variation (Díaz and Cabido 2001).

High trait variation in secondary forest can be both the result of a high environmental heterogeneity (which leads to differences in plant strategies; Lebrija-Trejos et al. 2010) and traditional management practices that enrich or enhance secondary forest with species of subsistence and with 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 (see also Lasky et al. 2014). The large trait variation in agricultural land can be attributed to intercropping systems (Coolman and Hoyt 1993). Slash-and-burn management techniques can maintain a number of species and functional diversity (Altieri 2004, Chazdon et al. 2009). High K in pastureland suggests that dominant nonnative grass species suppress plant diversity and that a high level of management disturbance (like continuous grazing by domesticated livestock) can hinder the establishment of other species (Quétier et al. 2007).

Association between the three aspects of community functional properties

Community functional properties have been described with parameters that measure the mean 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, it still has not been assessed how these parameters behave and how much they are associated in different plant communities. 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, Fig. 4) and partly independent. We hypothesized and found that large differences in CWM among land-use types also result in large differences in CV and K. This result is consistent with other studies that evaluated a LUI gradient, and showed that some traits are more sensitive to land-use changes than others are (Mayfield et al. 2006, Garnier et al. 2007). A clear example was adult stature, for which all three metrics were correlated (Fig. 3). At the community level, a reduction in adult stature and an increase in K with LUI indicates that management practices are at play, as intensified systems are, in general, dominated by small fast-growing species such as rice, wheat, maize, and potatoes (FAO 2014) that result in high biomass yields per unit area and time (Boehmel et al. 2008). However, these relationships between functional properties may change in the case that a low-intensified system represented by a mature forest is compared with a high-intensified system represented by oil plantation instead of pasturelands.

Half of our traits showed negative correlations between CV and K, and the other traits showed positive or no correlation. We believe that high correlation between metrics (e.g., CWM, CV or CV, K) does

not mean redundancy in the capacity to detect LUI effects on functional trait properties, but indicates complementarity; whereas one metric is sensitive to species response to biophysical filters (i.e., CWM), another metric is sensitive to management practices (Ricotta and Moretti 2011). This is also supported by the fact that using only one metric is not enough to distinguish among the five land-use types (Appendix C: Figs. C1–C3), whereas an overall PCA using all three metrics (Fig. 4) separated the three forest systems based on CWM and CV, and the cultivated systems based on K.

Biophysical filters and management practices drive community assembly along the LUI gradient

We found that changes in community functional properties due to LUI were driven by both environmental and management practices (Jackson et al. 2009, Conti and Díaz 2013); we expected biophysical filters to be more important at low levels of LUI, and management practices to be more important at high levels of intensification. Within our forested systems, an increase in LUI resulted in an increase in CV and a decrease in K (Appendix S3: Figs. S34 and S35), 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 LDMC in logged forest compared with mature forest also suggests that increased light availability drives functional response of the tree community (Castro et al. 2010, Carreño-Rocabado et al. 2012).

Responses to both biophysical filters and management practices were found in secondary forest. It is well-documented that biophysical filters play a strong role in community assembly during secondary succession (Lebrija-Trejos et al. 2010). Both the influence of biophysical filters and management practices and how farmers tend to favor the establishment of timber and/or fruiting tree species (i.e., *Cordia alliodora*, *Guazuma ulmifolia*, *Sapium glandulosum*, *Mangifera indica*) may be an influence (van Breugel et al. 2013). The occurrence of more conservative traits in secondary forest (i.e., low CWM of SLA; Fig. 3) was explained by the high palm abundance, which is probably due to the use of fire for land clearing, the ability of palms to survive fires, and management decisions (i.e., large single-stemmed palms are difficult to cut without a chainsaw and are commonly left standing in agricultural fields).

All three metrics were able to distinguish the different cultivated systems (Fig. 4). High CV in agricultural systems and high K for pastureland indicate a strong influence of management practices as (1) an increase in trait variation is likely to be due to the introduction of exotic species with possibly different functional traits into a regional species pool, and (2) a peakedness in trait distribution is related to increasing yields from cultivation through practices such as weed control or soil fertilization. In both processes, response traits reflect targeted species (for agriculture) but also the native species that survive and persist and form part of the agricultural fields (i.e., weeds). Our results suggest that the three metrics have a large potential to detect the effect size of different types of filters (i.e., biophysical filters and management practices). Although further research is needed to test their consistency across other land-use types, our results show that they can be used to assess the functional response of some ecosystems to LUI, and build a link between changes in community composition (deliberate or not) and the response of ecosystem-level processes and services, following the methods of Díaz et al. (2007, 2011).

CONCLUSIONS

There is a consensus that LUI has a negative effect on plant diversity and ecosystem processes, but at the same time, there is empirical evidence that there is a large heterogeneity in the responses. We found that, along a long gradient of land-use intensity in the tropics, community assembly is driven by both biophysical filters and management practices that filter trait values. However, against our expectations, systems with high land-use intensity and strong management practices also had high functional variation. As land use intensifies, plant communities tend to shift toward smaller plants with shorter lifespans and more acquisitive leaf traits. Functional variation changed in a hump-shaped way along a gradient of land-use intensity, at first as a result of increasing environmental variation in line with the intermediate disturbance hypothesis, and later with the introduction of nonnative species (and their different trait values) into the local species pool. It peaked not only for secondary forest but also for agricultural land. Our results on the high functional variation of secondary forests also contribute to the broader debate on the value of these forests, their current value based on their capacity to provide a variety of ecosystem services, as well as their potential for restoration and enhanced service provision (Chazdon 2013, Elias 2013). We used three simple and straightforward metrics (CWM, CV, and K) to describe community functional properties, and have shown that they are able to distinguish, functionally, the different land-use types. Our results showed that different human-modified systems can be similar in their functional properties or even become more functionally diverse than conserved forest. These results highlight the complexity of the functional response of ecosystems to land-use intensity. The metrics selected to assess functional variation enabled a quantitative, process-based analysis of these responses. Such approaches are particularly important to address the consequences on biodiversity and ecosystem services

of multiple ecological trajectories driven by tropical LUI (Brown et al. 2013, Ziter et al. 2013), including novel ecosystems emerging out of new species assemblages (Hobbs et al. 2006). They can also contribute to solving the conundrum of conserving biodiversity and providing ecosystem services in productive landscapes (Melo et al. 2013), and even restoring such landscapes (Chazdon et al. 2009).

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1890/14-0340.1/suppinfo

Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.2c2d2