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

Geovana Carreño-Rocabado[1,2]*, Marielos Peña-Claros[1,2], Frans Bongers[1], Alfredo Alarcón[2], Juan-Carlos Licona[2] and Lourens Poorter[1,2]

[1]*Forest Ecology and Forest Management group, Wageningen University, PO Box 47, 6700 AA Wageningen, The Netherlands; and* [2]*Instituto Boliviano de Investigación Forestal (IBIF), PO Box 6204, Santa Cruz de la, Sierra, Bolivia*

Summary

1. 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.

2. A large-scale field experiment was performed in which the dynamics of 15 000 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.

3. 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.

4. In contrast, disturbance intensity affected the *average* plant trait values in the community (the community-weighted mean) for seven 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.

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

6. *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.

Key-words: 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 2005a), and its effects depend strongly on the type, severity, frequency and timing of disturbance (White & Jentsch 2001; Foley *et al.* 2005). Nowhere is land use change occurring more rapidly than in the tropics (MEA 2005b), where it often comes at the expense of the area of tropical forests. Sustainable forest

*Correspondence author. E-mail: gcarreno@ibifbolivia.org.bo

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 & 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; Díaz *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 (Diaz & 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, Mason & Mouillot 2008; Pla, Casanoves & Di-Rienzo 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 & 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 (Poorter & Bongers 2006). 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 (Díaz *et al.* 2004). In forests, the continuum ranges from fast-growing shade-intolerant pioneer tree species with high specific leaf area (SLA), high leaf nitrogen concentrations, high photosynthetic and respiration rates, soft wood and leaves and short leaf life span to slow-growing shade-intolerant species characterized by the opposite suite of traits (Poorter & 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 & Bongers 2006).

The response of tree species to disturbance can follow different trajectories (Flynn *et al.* 2009) depending on disturbance intensity (biomass loss; Pickett & 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 & 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, predefined functional groups, such as pioneers and shade-tolerant species (Finegan, Camacho & Zamora 1999; Gondard & Deconchat 2003) or softwood and hardwood species (Verburg & 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, Bongers & Bongers 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, Bongers & Martínez-Ramos 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: (i) How do taxonomic and functional diversity of response traits change along a disturbance gradient?, (ii) Do the results differ with the type of weighting factor (i.e. abundance or basal area of the species?, (iii) How are those changes driven by underlying demographic processes, such as mortality, survival and recruitment? and (iv) 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: (i) 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 CWM trait values to shift towards high SLA and leaf nutrient concentrations, soft leaves, and a low wood density; (ii) changes in CWM 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; (iii) at higher disturbance intensities those trees that recruit will have on average more acquisitive trait values compared with dead or surviving trees; (iv) the functional diversity of effect traits will increase with disturbance intensity, because a greater trait variation will be found owing 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 1580 mm with 1 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 and 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 S1 in Supporting Information): 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 (owing to a gradual increase in the number of trees harvested, dead trees owing to logging, number of girdled trees and liana cutting), biomass damage (owing to damaged trees during logging operations), opening up of the forest canopy (owing to tree harvesting and tree girdling) and soil disturbance (owing to skid trails and soil scarification). For details on the experimental design see Table S1.

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 remeasured 8 years after disturbance (hereafter T_8). Four 1-ha plots were excluded from the analyses (three for C and one 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 four and seven); 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 these functional traits 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, Bongers & Bongers 2006); WD 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 life span and decomposability (Table S2; Poorter, Bongers & Bongers 2006; Bakker, Carreño-Rocabado & Poorter 2011; Onoda *et al.* 2011).

Leaf traits of 45 species come from Rozendaal, Hurtado & Poorter (2006) and Bakker, Carreño-Rocabado & Poorter (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, Poorter & Bongers 2007). Leaf trait variation across species is large compared with variation within species (Rozendaal, Hurtado & Poorter 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 through 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. Leaf fresh mass was measured after leaf hydration in a refrigerator for 12 h. Internode length was measured with a calliper 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: 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 & 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, Bongers & Bongers 2006). For most species, WD (g cm^{-3}) data come from Poorter (2008). For few additional species, wood samples (bark, cambium and wood) were taken for four to five individuals per species (10–30 cm d.b.h.) at 0.5–1-m stem height. Sample volume was measured using the water displacement method, after which samples were oven-dried for at least 48 h at 70 °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, Martínez & Williams 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 of each 1-ha plot). 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 & 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 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, Carreño-Rocabado & Poorter 2011), and net primary productivity (Hmax, WD, SLA, and Nmass; Table S2; Westoby 1998; Falster et al. 2011). Although many traits may codetermine 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 2 to the power of the number of functional traits (Villeger, Mason & Mouillot 2008).

For each group (decomposition rate or net primary productivity), three multivariate functional indices were calculated: FRich quantifies the volume of the multidimensional-functional space occupied by the community, and the algorithm to calculate the convex hull hyper-volume (Cornwell, Schwilk & Ackerly 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, Mason & Mouillot 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 was 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: $\Delta = [T_8-T_0]/T_0*100$. 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 & 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 $0.5 \pm 1.73\%$ and $-3.1 \pm 1.17\%$ (Table 1).

Eight years after disturbance, the treatments had a significant effect on CWM changes for seven of 12 response traits evaluated (Table 2). Seven traits differed significantly when abundance was used as a weighting factor, and four traits differed significantly when basal area was used. Branch density, LDMC, leaf toughness and P concentration showed consistently significant changes, when weighting either by abundance or by basal area. Wood density, SLA 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, WD, leaf toughness and LDMC, but high SLA, 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 for LDMC to 7.7% for P_{mass} (Table 2). Five of seven traits that responded to disturbance intensity showed a gradual change. Only two traits (SLA and WD) showed an abrupt change with an increase in disturbance intensity; that is, the control and normal treatments formed one group, and the light and intensive silvicultural treatments formed another group (Fig. 1).

Individuals that died, survived and recruited during the 8-year period differed significantly in their abundance-weighted CWM for nine functional traits. With an increase in 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 owing to the recruits. The three demographic groups differed also significantly in H_{max} and leaf thickness (Table S3), despite the fact that these parameters did not differ in Δ-CWM among treatments (Table 2).

Table 1. Effects of four disturbance treatments (ranked in increasing order of disturbance) on taxonomic- and functional diversity over an 8-year period

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

Total observed species richness (S) per ha and Jackknife-2 estimated species richness per ha (S') were calculated before (T_0) and after (T_8) disturbance. Means $\pm$ 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 (ML 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 (SLA) and leaf nitrogen concentration, and for decomposition rate were leaf dry matter content leaf chlorophyll, SLA and leaf nitrogen concentration. P-values and means $\pm$ standard errors are shown.

Table 2. Disturbance effects on response traits 8 years after disturbance in a Bolivian tropical moist forest

			Δ-CWM (%)			
Trait	Weighting factor	*P*	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

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 (H_{max}), stem wood density (WD), branch wood density (BD), leaf thickness (LTh), leaf dry matter content (LDMC), Leaf toughness (LTo), Leaf chlorophyll (LCh), N and P concentration per unit leaf mass (N_{mass}, P_{mass}), and N and P content per leaf area (N_{area}, P_{area}). *P*-values from mixed models (ML method) are given (in bold when $P < 0.05$).

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 four trees per ha were logged (Table S1), 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 m² ha⁻¹) of trees >15 cm d.b.h. in a Bornean rainforest (Verburg & 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, Obua & Oryem-Origa 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, Obua & Oryem-Origa 2007; van-Kuijk, Putz & Zagt 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.
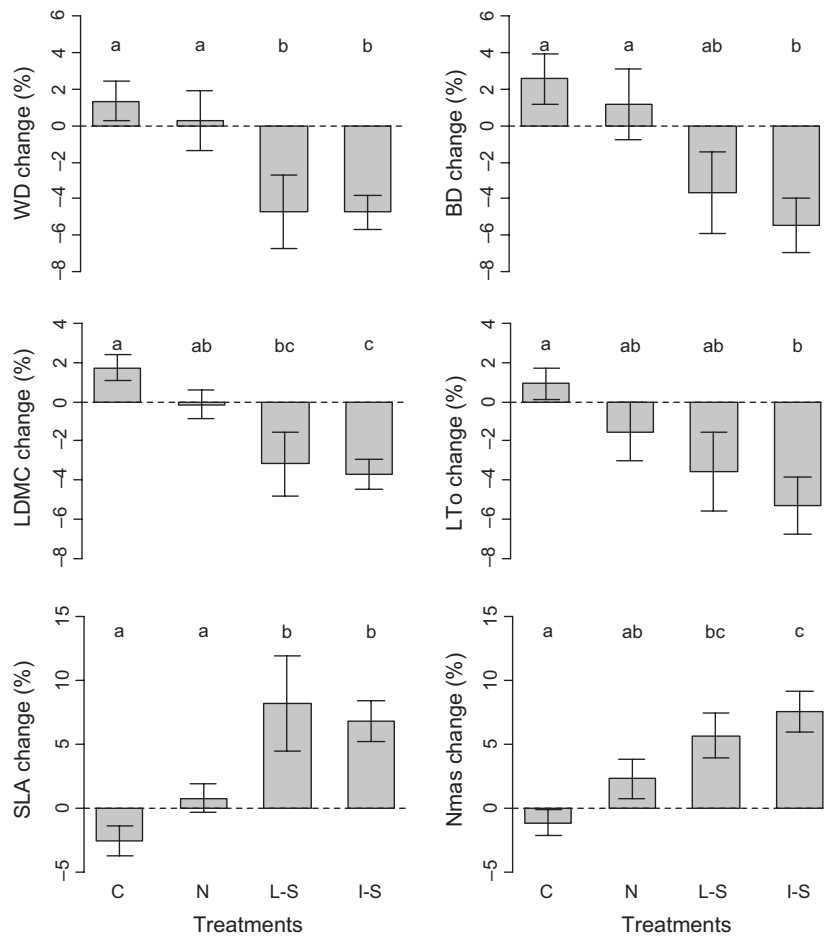
Fig. 1. Disturbance effects on response traits 8 years after the disturbance in a Bolivian tropical moist forest. The relative change in the abundance-weighted community mean of six response traits was compared among Control (C), Normal (N), Light Silviculture (L-S) and Intensive Silviculture (I-S) disturbance 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).

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 LDMC), poorly defended leaves (i.e. low leaf toughness), and short leaf life span (Fig. 1, cf. Kitajima & 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, Poorter & Schieving 2006). As a consequence, these species have high growth rates but die fast as well (Poorter & Bongers 2006). In contrast, low disturbance intensities (i.e. control- and normal logging treatments) promoted species with the opposite suite of traits (Loehle & Namkoong 1987). These results suggest that increased light availability (owing to logging gaps and

gradual death of damaged individuals) is the main factor driving functional responses in the tree community (Finegan & Camacho 1999; Castro-Luna, Castillo-Campos & Sosa 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 & Westoby 2005; Poorter, Bongers & Bongers 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 S3). 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 & 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
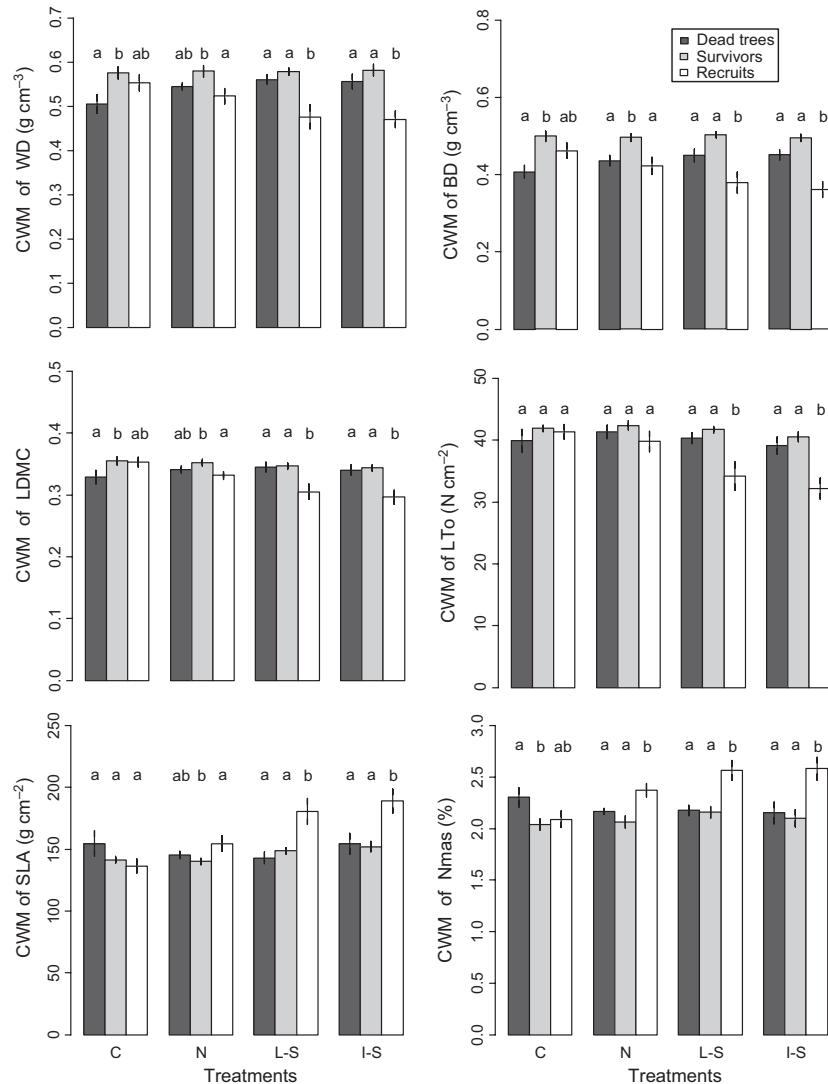
Fig. 2. Differences in the abundance-weighted community mean (± SE) of six response traits among groups of individuals that died, survived and recruited 8 years after the disturbance in a Bolivian tropical moist forest. The treatments are Control (C), Normal (N), Light Silviculture (L-S), and Intensive Silviculture (I-S), and functional traits are branch wood density (BD), stem 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).

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, Bongers & Martínez-Ramos 2007; van-Kuijk, Putz & Zagt 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 S3). 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 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 & Eijk-Bos 2003). In contrast, changes in basal area can be picked up relatively slowly (after 20–30 years, Ghazoul & 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 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 towards 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, Carreño-Rocabado & Poorter 2011).

At high disturbance intensity the CWM of SLA and N_{mass} increased and WD decreased (Table 2, Figs 12and), 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 WD, 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.* 2011, 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 S1). 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

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Supporting Information

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

Table S1. Characteristics of the four disturbance treatments studied.

Table S2. 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'.

Table S3. 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.

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).

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Graphical Abstract

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Disturbances are widespread and may have important effects on community assembly and ecosystem processes. We use a large-scale logging experiment in a tropical forest and show that 8 years after logging, there are little changes in species tree diversity and functional diversity. There were, however, clear shifts in community functional composition towards "fast" species with more acquisitive traits, thus potentially fuelling primary productivity, nutrient- and carbon cycling.