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Medium-term dynamics of tree species composition in response to silvicultural intervention intensities in a tropical rain forest

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ABSTRACT

Managed forests are important landscape components in tropical regions and may contribute to biodiversity conservation. Yet, managing tropical forests sustainably requires an understanding of ecosystem responses to silvicultural interventions. We investigated how silvicultural intervention intensity affects tree species composition and diversity over 30 years in the Brazilian Amazon by comparing them to pre-logging conditions and to an unlogged control. The interventions comprised logging in 1982 and thinning in 1993–1994 and ranged in intensity from 19 to 53% reduction in the original basal area (BA). Trees with a diameter at breast height (DBH) ≥ 5 cm were measured on eight occasions in 41 permanent sample plots of 0.25 ha each. Silvicultural intervention intensity influenced both tree species composition and its trajectory within 30 years. In contrast, tree species diversity was not impaired. High intervention intensities (with BA reduction $> 6.6\ \text{m}^2\ \text{ha}^{-1}$) had a substantial influence on the community of trees (DBH ≥ 10 cm), which did not show signs of return to pre-logging species composition. The reduction of BA through harvesting damage and thinning had a stronger effect on species composition than logging of mature trees itself. Thus, damage should be kept to a minimal level and strong thinning interventions should be avoided. This may enhance ecosystem recovery and maintenance of biodiversity at other trophic levels. Since current permitted harvesting intensities in the Brazilian Amazon are lower than the lowest intensity examined in our study, legal harvesting practices are unlikely to cause substantial, long-term changes in tree species composition.

1. Introduction

Tropical forests are a source of many goods and services, presenting the most complex structures and the highest biological diversity among terrestrial ecosystems (Whitmore, 1998; Ghazoul and Sheil, 2010). The Brazilian Amazon harbors around 20% of the world's species of fauna and flora (Azevedo-Ramos, 2008), and it is estimated that it houses more than 12,000 tree species (ter Steege et al., 2013). Moreover, this region accounts for the largest-continuous area of tropical forest in the world (FAO, 2011). Many anthropogenic processes such as unregulated exploitation and land-use change threaten tropical forest ecosystems and only a small proportion of the biodiversity is contained within protected areas (ITTO, 2009). Thus, conservation strategies will also have to consider forest areas not designated for conservation. Given that logged and secondary forests still harbor a considerable amount of tropical biodiversity (Chazdon et al., 2009; Dent and Wright, 2009; Putz et al., 2012; Burivalova et al., 2014), these anthropogenically disturbed ecosystems are important landscape components for biodiversity maintenance and conservation.

The proportion and identity of species retained in managed forests depend on the applied practices and the ecosystem's resistance and resilience in relation to the disturbance. Considering that managing forests implies manipulating their structures and composition to favor some species and life forms over others, shifts are inevitable (Whitmore, 1998) as well as subsequent impacts on biodiversity (Putz, 2011). Consequently, the intensity and caution employed in silvicultural practices shape the compatibility of timber production and

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conservation (Putz, 2011). The long-term response of forest biodiversity will depend in particular on the question whether anthropogenic disturbances are compatible with the ecological stability of the system (Swanson et al., 1994). Finally, the maintenance of species diversity and composition will support the continuity of provision of goods and services (Thompson, 2010), and the ecosystem's ability to cope with changing environmental conditions (ITTO, 2009).

Therefore, when managing tropical forests, the challenge is to reduce harmful effects while maintaining productivity (Sheil and van Heist, 2000) and provision of other goods and services. To keep biodiversity, resilience and productivity in managed forests, it is essential to have a detailed understanding of these ecosystems, identifying at which level of use and manipulation thresholds might exist, beyond which the system may lose the capacity to recover from interventions (Thompson, 2011). Furthermore, it is crucial to understand the long-term response to management, since the effects may vary according to the time scale that is being considered.

Tree species diversity, measured either as species richness or as a diversity index, is a common response variable used to assess the impact of forest management interventions. In tropical forests, Clark and Covey (2012) reported that logging impaired tree species diversity, whereas many studies found no negative effect (e.g. Yosi et al., 2011; Baraloto et al., 2012; Carreño-Rocabado et al., 2012) or only a slight influence (e.g. Gourlet-Fleury et al., 2013; Duah-Gyamfi et al., 2014a). However, response variables related to species numbers do not represent species identities per se and therefore may not be suitable to identify relevant impacts of forest interventions (Sheil and van Heist, 2000; Putz, 2011; Putz et al., 2012). Although species diversity in general may be little affected, changes in species composition are likely to occur. If compositional changes through management favor post-disturbance dominance of few widespread species at the expense of rare and specialist species, this may lead to a local biotic homogenization (McKinney and Lockwood, 1999). Such a process will probably lead to lower species richness and higher similarity among formerly distinct communities (Olden et al., 2004).

The evaluation of management impacts on species composition and recovery is challenging (van Kuijk et al., 2009), since the effects may greatly vary among and within tropical forests (Ghazoul and Sheil, 2010). Given our limited understanding of forest ecosystems, it is necessary to make use of all available knowledge to support management decisions (Kimmins, 1997). This can contribute to improve techniques and to sustain tropical biodiversity in managed forests (Meijaard et al., 2005). To make management compatible with conservation of original biodiversity, interventions should not lead to substantial or long-lasting changes in plant species composition and dependent diversity at other trophic levels. So far, there is only scant information on possible thresholds of intervention intensity at which such compositional changes might happen in tropical forests.

In this study, we assessed the effects of different silvicultural intervention intensities on tree species composition and diversity over a period of 30 years. The experiment analyzed here is one of the few long-term studies on forest dynamics following logging and thinning in the Brazilian Amazon or any other lowland tropical rainforest. Specifically, we investigated the medium-term dynamics of tree species composition and diversity compared with the pre-logging condition and to an unlogged control treatment to address the following hypotheses:

(i) Logging, damage and thinning affect tree species composition in comparison to the natural forest;
(ii) Recovery of pre-logging species composition is negatively related to intervention intensity, measured as reduction in basal area;
(iii) Within the range of applied intervention intensities, tree species diversity is not impaired;
(iv) If changes in species composition over time are characterized by higher spatial similarity among managed treatments associated with lower species richness, we expected that a local biotic homogenization will occur.

2. Materials and methods

2.1. Study site

The study was conducted in the Tapajós National Forest, municipality of Belterra, State of Pará, Brazil (3°18′S to 3°19′S, 54°56′W to 54°57′W). The area was originally chosen for the long-term experiment because it represents a typical forest of the region with a low degree of human impacts (Carvalho, 2002). The topography of the region is flat to slightly undulating and the altitude is around 175 m above sea level. The climate is tropical with one dry season and annual rainfall averages 2100 mm. The annual average temperature is approximately 25 °C and the relative humidity is around 86%. The predominant soil type is yellow latosol, which is characterized by a heavy clay texture, deep profile and low fertility and base saturation (Vieira, 1975). The vegetation of the region is classified as ombrophilous dense forest (IBGE, 2012).

2.2. Experimental design and sampling

The experiment is a randomized block design with four replicates (36 ha each). Each silvicultural intensity treatment has 12 permanent sample plots (0.25 ha each) distributed within the four blocks. An area of 36 ha of unlogged forest served as a control. In the logged area, the first assessment of the permanent sample plots occurred in 1981 following liana cutting. Logging was carried out in 1982 and the treatments differed mainly by the minimum felling diameter (Table 1). Directional felling and bucking of trees were performed with chainsaws and the logs were extracted using skidders.

Thinning through poison-girdling was applied between 1993 and 1994 to reduce the basal area to the planned level of the experiment by eliminating non-commercial trees to favor growth and regeneration of commercial species (Oliveira et al., 2006). Thus, intervention intensities comprised logging, damage to trees not harvested (i.e. trees that died as an indirect result of logging) and thinning, together ranging from 19 to 53% of basal area reduction in relation to the original value in 1981 (Table 1).

An accidental fire occurred in the experimental area in 1997, which affected 19 permanent sample plots (Table 1). Although these plots are still being monitored, they were not included in this study. The remaining 41 plots resulted in a coverage of 5.7% of the total experimental area (180 ha). Our design is in accordance with suggestions to capture the heterogeneity among sampling units through many small plots rather than few large plots in tropical forests, with a recommended minimum number of five plots (Bonar et al., 2011). Additionally, the species richness estimation for rarefied and extrapolated samples in the initial census, constructed by using iNEXT (iNterpolation and EXTrapolation) (Chao et al., 2014), indicated a trend towards an asymptote in species richness, and hence a good sampling size to represent the tree species community (see Fig. A1 in Supplementary data).

All trees with a diameter at breast height (DBH) ≥5 cm were sampled in the 41 permanent sample plots and permanently labeled with aluminum tags. Species were identified by their vernacular names by parataxonomists and for the least common species, plant material was collected for identification in the herbarium of Embrapa Amazônia Oriental. The permanent sample plots were inventoried in 1981, 1983, 1987, 1989, 1995, 2003, 2008 and 2012, except for the control area that was not measured in 1981. To permit comparisons with published results and to enable a more detailed analysis, the sampled trees were grouped into two size classes: poles (5 ≤ DBH < 10 cm) and trees (DBH ≥ 10 cm).

Table 1
Silvicultural intervention intensity (treatment) details. C: control; L: logging only; LLTI: logging and light thinning intensity; LMTI: logging and medium thinning intensity; LHTI: logging and high thinning intensity.

Pre-logging interventions (1981)	Treatments				
	C	L	LLTI	LMTI	LHTI
Original basal area ($m^2\ ha^{-1}$)	30.5 ± 2.6[a]	31.9 ± 2.7	31.9 ± 7.9	28.9 ± 6.1	28.8 ± 3.8
Logging (1982)					
Minimum felling diameter (cm)	–	45	55	55	55
Basal area removed through logging ($m^2\ ha^{-1}$)	–	4.6 ± 2.9	5.2 ± 6.4	3.2 ± 2.2	4.9 ± 3.9
Basal area reduction through logging damage ($m^2\ ha^{-1}$)	–	1.5 ± 3.6	0.5 ± 0.8	0.1 ± 0.3	1.2 ± 1.2
Post-logging interventions (up to 2012)					
Thinning of non-commercial trees (DBH ≥ 15 cm) between 1993 and 1994	No	No	Yes	Yes	Yes
Basal area reduction through thinning ($m^2\ ha^{-1}$)	–	–	0.9 ± 0.8	4.7 ± 2.4	9.2 ± 1.8
Percent reduction in basal area through logging, logging damage and thinning	–	19.1	20.8	27.6	53.2
Number of plots not affected by accidental fire in 1997	6	10	7	12	6

[a] Basal area measured in 1983 (first assessment of the permanent sample plots in the control area). Mean and standard deviation are given.

2.3. Data analysis

Dynamics of tree species composition was analyzed using a time-constrained clustering for each treatment to identify whether compositional changes occurred over time. The method considers the sampling sequence and allows only contiguous samples to cluster (Legendre and Legendre, 2012). Time-constrained clustering was applied via multivariate regression trees (MRT) by analyzing the multivariate response matrix using the sample sequence over time as the explanatory variable (Legendre and Gauthier, 2014). Abundances were Hellinger transformed prior to analysis, adjusting species abundance to a range from 0 to 1 (Wildi, 2013). This transformation is recommended because it yields high coefficients of determination for the ecological distance explained by the function and gives low weight to rare species (Legendre and Gallagher, 2001). The cross-validation procedure helped determine the most appropriate number of groups (Legendre and Legendre, 2012). Moreover, indicator species were identified for different periods of species assemblage by calculating the indicator value and its statistical significance following the approach of Dufrene and Legendre (1997).

Recovery of tree species composition in relation to the initial condition was assessed using the Morisita–Horn index as an abundance-based similarity measure. This index is sensitive to the relative abundance of species and is resistant to under-sampling because it gives higher weight to more abundant species (Jost et al., 2011). The mean similarity per plot between the first and subsequent censuses was plotted for all treatments over time to visualize the reassembly dynamics of species composition (Magurran et al., 2010). To account for the small size of our plots, we repeated this analysis by using Sørenson index and by conducting the analysis at the genus level or excluding species with low density (less than 1 tree ha^{-1}). Since the pattern was consistent, we decided to present here the results based on Morisita–Horn index and at the species identification level. The temporal trajectory of each treatment was investigated using non-metric multidimensional scaling. The results visualize the recovery patterns in a two-dimensional ordination space. Given that differences in initial condition might affect regeneration processes and recovery following interventions, we analyzed compositional differences among treatments by performing a permutational multivariate analysis of variance using distance matrices at the plot level. This compositional comparison was carried out for each measurement in time associated with a measure of among-treatment similarities in order to test our fourth hypothesis.

Species diversity was quantified as species density (number of species) per plot and estimated species richness using Chao's estimator (S_{Chao}) (Maurer and McGill, 2011) correcting to the different number of individuals sampled per treatment. Shannon diversity (H′) and rank abundance distribution curves were also computed to better understand the mechanisms underlying the species composition responses (Dornelas et al., 2011), since they can demonstrate changes in dominance patterns. In addition, species diversity responses were analyzed through comparison of the initial, final, lost, and gained number of species among treatments, from the first to the last census. As data met parametric assumptions, differences among treatments were examined using analysis of variance (ANOVA). In case of a significant treatment effect, a multiple comparison with Tukey's honest significant difference (HSD) test was carried out. For species density, changes over time were tested by using linear mixed effect models taking into account the temporal correlation structure. Student's t-test for paired samples was used to compare the initial with the final number of species for each treatment.

Given that post-disturbance tree turnover may be an important underlying mechanism for the change or recovery in tree species composition, we investigated whether tree turnover predicts species turnover and composition recovery. We analyzed the correlation of tree turnover rate with species turnover rate, rarefied number of species (to the minimum number of individuals found in one plot) and similarity index, taking into account the values per plot over time for each treatment. The relationship between these variables was investigated by computing the Spearman's correlation coefficient.

Annual mortality ($m = (\ln No - \ln St)/t$) and recruitment rates ($r = (\ln Nt - \ln St)/t$) were calculated following the approach used by Condit et al. (1999), where No is the community size at time 0, Nt is the community size at time t, St is the number of survivors at time t and t is the census interval in years. Tree turnover rate was quantified as a mean of mortality and recruitment rates (Phillips et al., 1994). Owing to different lengths of census intervals, the estimates were standardized using $\lambda_{corr} = \lambda * t^{0.08}$, where λ is the rate and t is the census interval in years (Lewis et al., 2004). Species turnover rate was estimated by using $turn = (l + g)/(S * t)$, where l is the number of lost species, g is the number of gained species, S is the total number of species in both censuses and t is the census interval in years (Diamond and May, 1977).

All analyses were conducted separately for the size classes of poles (5 ≤ DBH < 10 cm) and trees (DBH ≥ 10 cm) and employed R version 3.0.3 platform (R Development Core Team, 2014). All packages used in the analyses are cited in the Supplementary data.

3. Results

Over time, 21,595 trees and 319 tree species were recorded. In the natural forest (C: control), no discontinuities in pole and tree species composition occurred over time. In contrast, silvicultural interventions (L: logging only, LLTI: logging and light thinning intensity, LMTI: logging and medium thinning intensity, LHTI: logging and high thinning

Table 2
Time-series response of species composition in poles (5 ≤ DBH < 10 cm) for different silvicultural intervention intensities over a period of 31 years. The clusters identified by MRT are shown and the three species with the highest indicator values are listed for each cluster.

Treatment	Cluster (year)	Species (family)	Indicator value	*P*
L	i (1981–1987)	*Guarea carinata* (Meliaceae)	0.6894	0.001
RE: 0.96[a]		*Paypayrola grandiflora* (Violaceae)	0.5745	0.001
CVRE: 1.02		Sapotaceae	0.5722	0.009
SE: 0.0272	ii (1987–2012)	*Jacaranda copaia* (Bignoniaceae)	0.7537	0.001
		Cordia spp. (Boraginaceae)	0.6648	0.001
		Inga spp. (Fabaceaea)	0.5839	0.001
LLTI	i (1981–1987)	*Maquira sclerophylla* (Moraceae)	0.6141	0.003
RE: 0.95		*Guarea carinata* (Meliaceae)	0.6112	0.003
CVRE: 1.05		Sapotaceae	0.5685	0.049
SE: 0.0306	ii (1987–2012)	*Laetia procera* (Salicaceae)	0.6511	0.001
		Cordia spp. (Boraginaceae)	0.6391	0.001
		Jacaranda copaia (Bignoniaceae)	0.6381	0.002
LMTI	i (1981–1987)	Sapotaceae	0.4090	0.001
RE: 0.93		*Guarea carinata* (Meliaceae)	0.4071	0.002
CVRE: 1.00		*Licaria cannella* (Lauraceae)	0.3925	0.005
SE: 0.0109	ii (1987–2003)	*Cecropia distachya* (Urticaceae)	0.7462	0.001
		Cecropia spp. (Urticaceae)	0.5310	0.001
		Jacaranda copaia (Bignoniaceae)	0.4282	0.001
	iii (2003–2012)	*Xylopia nitida* (Annonaceae)	0.4794	0.001
		Inga rubiginosa (Fabaceae)	0.4426	0.001
		Siparuna decipiens (Siparunaceae)	0.4247	0.001
LHTI	i (1981–1987)	*Guarea carinata* (Meliaceae)	0.4646	0.001
RE: 0.88		*Eugenia* spp. (Myrtaceae)	0.4112	0.002
CVRE: 1.03		*Maquira sclerophylla* (Moraceae)	0.4007	0.003
SE: 0.0241	ii (1987–2003)	*Cecropia distachya* (Urticaceae)	0.7176	0.001
		Jacaranda copaia (Bignoniaceae)	0.5534	0.001
		Cecropia spp. (Urticaceae)	0.4445	0.004
	iii (2003–2012)	*Inga auristellae* (Fabaceae)	0.6111	0.001
		Virola michelii (Myristicaceae)	0.5453	0.001
		Pouteria reticulata (Sapotaceae)	0.4900	0.002

See Table 1 for treatment abbreviations.

[a] General statistics from MRT: residual error (RE), cross-validated error (CVRE) and standard error (SE).

intensity) changed species composition in both size classes (see Fig. A2 in Supplementary data).

For poles, logging, harvesting damage and thinning caused a shift in species assemblage. The first discontinuity was recognized five years after logging (1987) in all treatments and the second became apparent nine years after thinning (2003), however, only for the treatments with medium and high follow-up thinning intensity (LMTI and LHTI) (Table 2). For trees, two homogeneous subgroups were found in each logged treatment. While the discontinuity in species composition showed up in 1987 for the two lower intervention intensities, i.e.

Table 3
Time-series response of species composition in trees (DBH ≥ 10 cm) for different silvicultural intervention intensities over a period of 31 years. The clusters identified by MRT are shown and the three species with the highest indicator values are listed for each cluster.

Treatment	Cluster (year)	Species (family)	Indicator value	*P*
L	i (1981–1987)	Sapotaceae	0.5928	0.002
RE: 0.94[a]		*Carapa guianensis* (Meliaceae)	0.5097	0.019
CVRE: 1.00		*Amaioua guianensis* (Rubiaceae)	0.4999	0.035
SE: 0.0204	ii (1987–2012)	*Cecropia* spp. (Urticaceae)	0.9304	0.001
		Cecropia distachya (Urticaceae)	0.7636	0.001
		Jacaranda copaia (Bignoniaceae)	0.7627	0.001
LLTI	i (1981–1987)	Sapotaceae	0.5526	0.024
RE: 0.97		*Neea floribunda* (Nyctaginaceae)	0.5243	0.033
CVRE: 1.07		*Sagotia racemosa* (Euphorbiaceae)	0.5000	0.001
SE: 0.0198	ii (1987–2012)	*Jacaranda copaia* (Bignoniaceae)	0.7501	0.001
		Cecropia spp. (Urticaceae)	0.5966	0.001
		Cecropia distachya (Urticaceae)	0.5000	0.001
LMTI	i (1981–2003)	Sapotaceae	0.6853	0.001
RE: 0.94		*Eschweilera coriacea* (Lecythidaceae)	0.5614	0.001
CVRE: 0.99		*Sagotia racemosa* (Euphorbiaceae)	0.4426	0.001
SE: 0.0144	ii (2003–2012)	*Inga alba* (Fabaceae)	0.7064	0.001
		Jacaranda copaia (Bignoniaceae)	0.5863	0.001
		Laetia procera (Salicaceae)	0.5749	0.001
LHTI	i (1981–2003)	Sapotaceae	0.6710	0.001
RE: 0.90		*Diospyros* spp. (Ebenaceae)	0.6545	0.001
CVRE: 0.99		*Rinorea guianensis* (Violaceae)	0.6032	0.002
SE: 0.0163	ii (2003–2012)	*Inga alba* (Fabaceae)	0.8085	0.001
		Jacaranda copaia (Bignoniaceae)	0.7439	0.001
		Bellucia grossularioides (Melastomataceae)	0.7129	0.001

See Table 1 for treatment abbreviations.

[a] General statistics from MRT: residual error (RE), cross-validated error (CVRE) and standard error (SE).

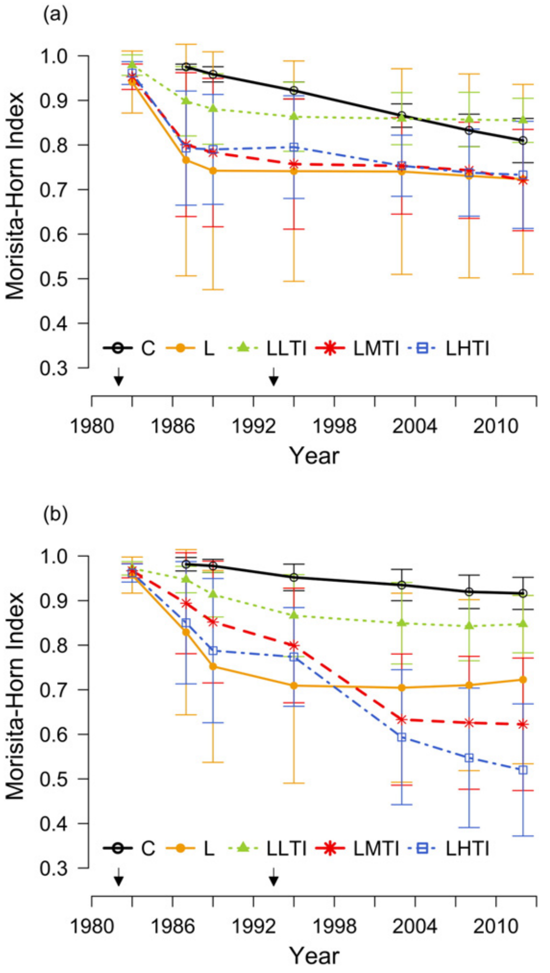

Fig. 1. Similarity (mean and standard deviation per plot) of species composition to initial conditions for each treatment (C: control, L: logging only, LLTI: logging and light thinning intensity, LMTI: logging and medium thinning intensity, LHTI: logging and high thinning intensity): (a) poles and (b) trees. Interventions of logging (1982) and thinning (1993–1994) are shown by downward arrows above the time axis.

logging only (L) and logging followed by light thinning intensity (LLTI), for the two higher intervention intensities (LMTI and LHTI) the discontinuity became apparent in 2003 (Table 3).

The indicator species analysis for each homogeneous subgroup (cluster) demonstrated that pioneer species increased in their importance following silvicultural interventions (see Table A1 for information on ecological group of indicator species). For pole-sized trees, post-intervention compositions were characterized by an increased importance of species such as *Jacaranda copaia* (Aubl.) D. Don (Bignoniaceae) and *Cecropia* spp. (Urticaceae) (Table 2). For trees, the pioneer species *J. copaia*, *Cecropia* spp. and *Inga alba* (Sw.) Willd. (Fabaceae) increased in abundance and were frequent indicator species following interventions (Table 3).

Species composition similarity in relation to initial conditions (1981/1983) showed a comparable response for poles across all treatments over time (Fig. 1a). However, species composition of trees ≥10 cm was substantially influenced by silvicultural intervention intensity. The most pronounced and lasting reductions in similarity were observed for the treatments with high basal area reduction through harvesting damage and thinning (Fig. 1b). The treatment LLTI maintained the most similar composition to pre-logging conditions. Similar results were obtained when carrying out the analysis at the genus level, by excluding species with low density (less than 1 tree ha^{-1}) and by using the Sørenson index. Given that trees ≥10 cm DBH underwent the most substantial changes in species composition, we further investigated for this size class the dynamics of each treatment following interventions. In the logging only treatment (L), a trend for recovery in species composition could be observed, whereas the composition in the two most intensive treatments (LMTI and LHTI) clearly continued to move further away from its original condition and showed no signs of return (Fig. 2). In contrast, the tree species composition in unlogged forest (C) and the logged forest followed by a light thinning (LLTI) experienced, respectively, only a marginal and slight change over time (Fig. 2).

The analysis on compositional differences indicated significant differences in composition among treatments, in all measurements for poles ($P < 0.01$) (see Fig. A3a and b). Species composition in tree-sized dimension did not differ before logging ($P = 0.09$), but from 1983 on, significant differences were found ($P < 0.001$) (see Fig. A3c and d). For trees, this indicates that treatments followed different trajectories after interventions. The compositional similarity between unlogged forest and treatments decreased over time, particularly for treatments LMTI and LHTI (Table 4).

Although species diversity, measured as either species density or S_{Chao}, decreased immediately after logging, it increased over time in all treatments and recovered to or even surpassed the pre-logging level (Fig. 3 and see Fig. A4). A significant change in species density over time was observed for poles and trees (result from linear model, $P < 0.05$). The unlogged forest kept approximately the same species density over time, and this parameter under disturbed conditions did not differ from the control, except for poles in years 2003, 2008 and 2012 ($P < 0.01$).

For both size classes, a slight decrease in the Shannon diversity was observed after logging for all silvicultural intervention intensities, followed by an increasing trend over time (see Fig. A5). For trees, no treatment effect occurred in any of the inventories. However, for pole-sized trees, a significant effect was detected in 1983, when C differed from L and LLTI ($P < 0.05$), and in 1995, 2003, 2008 and 2012 ($P < 0.05$), when LLTI was significantly lower than LMTI. The slope of the rank abundance distribution became shallower over time mainly in the treatments L and LMTI, indicating a trend to increased evenness over time (see Fig. A6).

For poles, the final number of species was significantly higher in LMTI and LHTI. For trees, the number of species lost from plots was significantly higher in the most intensive treatment (LHTI). Species recruitment led to significantly higher numbers of gained species in the two most intensive treatments (LMTI and LHTI) in both pole and tree dimensions (Table 5). The comparison of the initial to the final number of species (Student's t-test) for each treatment, demonstrates that for poles the species density significantly increased in the treatments L, LMTI and LHTI. For trees, a significant increase occurred only in the LMTI treatment (Table 5).

Tree turnover rates were strongly and significantly correlated with species turnover rates in both size classes and for all treatments (Table 6). Turnover rates were higher in the initial period following logging and this effect lasted until 1989. Nevertheless, the rates returned to lower levels over time, except for LMTI and LHTI, where thinning caused an increase in species and tree turnover rates between 1995 and 2003 (see Fig. A8). There was no clear pattern for the relationship between tree turnover rates and rarefied number of species or similarity index (Table 6).

4. Discussion

For the community comprising tree-sized individuals (DBH ≥ 10 cm), the species composition was substantially affected by basal area reduction greater than 6.6 m^2 ha^{-1}. This change in composition may lead either to a longer recovery time or to a different state. Conversely, species diversity (species richness and Shannon diversity) was not impaired under disturbed conditions relative to the natural forest and pre-logging conditions, irrespective of intervention intensity.

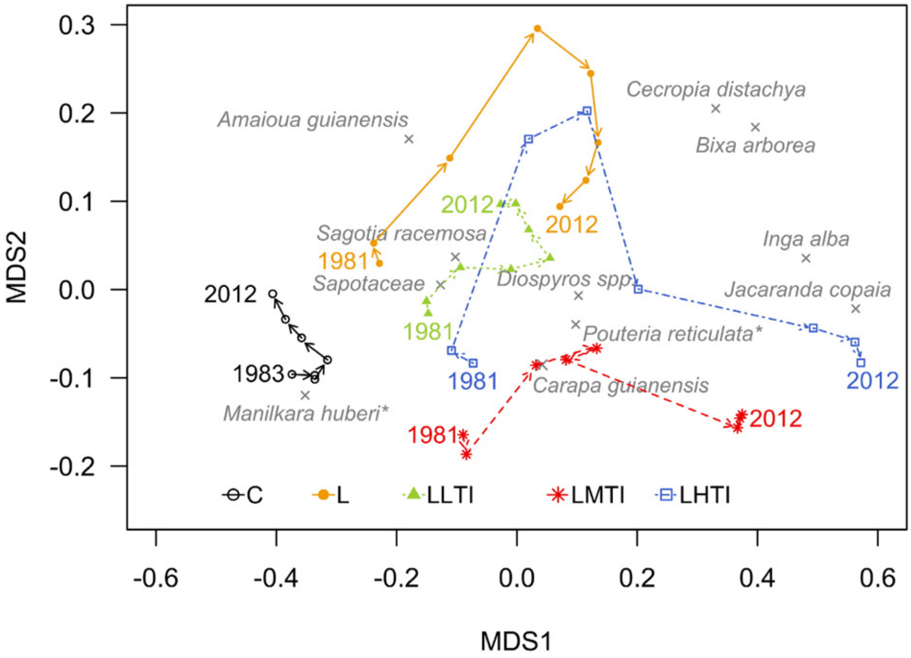

Fig. 2. Non-metric multidimensional scaling diagram of 1st and 2nd axes for trees ≥10 cm (stress: 0.1246), considering each treatment (C: control, L: logging only, LLTI: logging and light thinning intensity, LMTI: logging and medium thinning intensity, LHTI: logging and high thinning intensity) and measurements over 31 years. Species pointed out in the ordination space are indicator species identified for different periods of species assemblage (Table 3). Species followed by asterisk are indicator species for the unlogged forest.

4.1. Dynamics of tree species composition

The natural forest did not vary in composition over time, but silvicultural interventions affected species composition and stimulated recruitment of pioneer species, supporting our first hypothesis. The discontinuities in species composition did not become apparent immediately after silvicultural intervention, but showed a time lag, similar to logged subtropical forests in Australia (Kariuki et al., 2006). This phenomenon was attributable to subsequent, post-intervention mortality and recruitment. Immediately after logging and thinning, mortality was high due to damage, poison-girdling and the inability of sensitive and rare species to cope with the new conditions, which were probably characterized by increased light availability, higher temperatures and wind speed (Laurance et al., 2006). Following this phase of increased mortality, recruitment increased and was high in 1983, 1987 and 2003, leading to a shift in species composition. Similarly, floristic changes during two decades after fragmentation of an Amazonian forest were mainly driven by high mortality associated with dispersion and species recruitment (Laurance et al., 2006).

Variations in species composition following disturbances are associated with changes in the relationship between species and environmental conditions (Legendre and Gauthier, 2014). Manipulation of forest structure leads to changes in resource availability, for instance through modification of light penetration, decomposition and mineralization of nutrients held in organic matter (Canham and Marks, 1985), and tree species in their different life stages will be favored or disadvantaged to different degrees. The increased light penetration and temperature in the forest understory creates opportunities for species recruitment. Consequently, regeneration of pioneer species that were dispersed or may have been in the soil seed bank was triggered, e.g. *Cecropia*, whose seeds can persist in the seed bank for many years (Dalling, 2002). The change towards increased importance of pioneer species after logging, as was also observed in our study, is a common phenomenon in tropical rain forests (e.g. Yosi et al., 2011; Carreño-Rocabado et al., 2012; Hawthorne et al., 2012; Gourlet-Fleury et al., 2013).

The short-lived genus *Cecropia* increased dramatically in abundance in managed forests, but remained very infrequent in the unlogged forest. Other pioneer species, such as *J. copaia*, *I. alba* and *Bixa arborea* Huber also increased substantially in abundance following logging. The non-pioneer species *Eugenia* spp., *Guarea carinata* Ducke, *Sagotia racemosa* Baill. and members of the Sapotaceae family were substantially reduced in abundance in managed forests over time. These species were affected either by damage to remaining trees through logging operations or by thinning. *Licaria cannella* (Meisn.) Kosterm was logged in 1982 and considerably reduced in abundance in treated forests, but a decreasing trend in abundance for this species was also observed in the natural forest. As clearly shown by species indicator analysis (Tables 2 and 3), species-dominance patterns changed in silviculturally treated forests, since indicator species changed between the pre- and post-intervention periods. Nevertheless, detailed inferences on species changes are difficult, since species exclusion or recruitment may have been driven not only by management interventions but also by natural dynamics. Where it is difficult to quantify changes in the abundance of individual species, changes in functional trait composition would be informative for understanding the relationship between compositional changes and ecosystem processes.

Following silvicultural interventions, recovery will, over time, typically lead the system back to an approximation to its former state, unless resilience is impaired (Perry et al., 2008). In our study, species composition of trees ≥10 cm DBH moved away from the original composition after high silvicultural intervention intensities (LMTI and LHTI) and did not show a recovery trend (Fig. 1). This finding lends support to our second hypothesis and raises the question whether there may be a threshold in intervention intensity beyond which the species assemblages will take much longer to return to a similar pre-logging composition or may not return at all. To our knowledge, we have shown the first experimental evidence of a possible transition to a new forest composition caused by high silvicultural intervention intensity in selectively cut rainforests. Basal area reduction through harvesting damage and thinning appeared to be the major factors that decreased the compositional similarity in relation to initial conditions. In contrast to our results, a study in Central Africa reported little impact of thinning through poison girdling of all non-commercial trees with DBH≥50 cm on tree species composition, since genus composition

Table 4
Compositional similarity (Morisita–Horn index) among treatments in each measurement, taking into account tree-sized individuals (DBH ≥ 10 cm).

Comparison	1981	1983	1987	1989	1995	2003	2008	2012
C to L	–	0.91	0.83	0.74	0.74	0.75	0.76	0.78
C to LLTI	–	0.85	0.84	0.81	0.79	0.78	0.77	0.79
C to LMTI	–	0.82	0.81	0.77	0.81	0.64	0.63	0.62
C to LHTI	–	0.81	0.76	0.70	0.72	0.55	0.50	0.48
L to LLTI	0.93	0.92	0.88	0.86	0.85	0.85	0.86	0.88
L to LMTI	0.91	0.88	0.88	0.87	0.84	0.80	0.81	0.81
L to LHTI	0.92	0.92	0.93	0.93	0.79	0.78	0.77	0.76
LLTI to LMTI	0.92	0.89	0.88	0.88	0.89	0.78	0.77	0.77
LLTI to LHTI	0.93	0.93	0.89	0.88	0.91	0.76	0.70	0.68
LMTI to LHTI	0.93	0.9	0.90	0.90	0.88	0.92	0.92	0.91

See Table 1 for treatment abbreviations.

remained similar to the unlogged forest (Ouédraogo et al., 2011). The discrepancy may be explained by different thinning practices applied in each study.

The community of pole-sized trees remained rather similar to prelogging conditions over time, probably owing to the fact that the rapid growth of pioneer species quickly recovered the canopy layer thus creating proper conditions for recruitment of species that were part of the original assemblage. A study on seedling regeneration following harvesting in Ghana also indicated a high level of similarity with undisturbed conditions already after 3 years (Duah-Gyamfi et al., 2014b). The pattern observed in our study may be an indication that species composition in tree-sized dimensions may still recover through recruitment from pole-sized trees in the longer term. A trend for recovery in species composition from young life stages towards late-successional forests was observed in secondary forests in Costa Rica (Norden et al., 2009). The authors reported that dispersal and establishment of mature forest species associated with the presence of old-growth forest remnants were crucial for the resilience of species composition. In our study area, both conditions of recruitment and closeness to mature forest are favorable. Nevertheless, it remains an open question, how long recovery may take under high disturbance intensities.

Silvicultural intervention intensity did not impair species diversity (e.g. species density and Shannon diversity) (Figs. 3 and A5), supporting our third hypothesis. The decrease in species numbers soon after logging may be attributed to the removal or death of species with low density (Montagnini and Jordan, 2005). The complete recovery of species density is in accordance with other studies that reported steady or even increased species richness following silvicultural interventions (Cannon et al., 1998; Zagt et al., 2003; Smith et al., 2005). Evenness increased over time as the slope of the rank abundance distributions became shallower (Fig. A6). This may be explained by the replacement of species with low density by abundant pioneer species, which prompted an increase in the evenness and thus higher Shannon diversity. Therefore, tree turnover was a good predictor for species turnover in this species-diverse forest, but not for recovery of species composition. This indicates that stem recruitment was attributable mainly to species new to the tree community. If the tree turnover was driven by autochthonous and already dominant species, then species turnover would have been lower (Chazdon et al., 2007).

An increased species turnover rate following interventions was likely triggered by the change in environmental conditions created by logging and thinning. These changes did not foster the recruitment of species from the original composition, but caused the elimination of species and replacement by new ones. Consequently, species diversity can be higher, since species of different successional stages may coexist (Chesson and Huntly, 1997). Thus, despite the positive relationship between tree turnover and species turnover, it did not lead to species composition recovery but rather changed species assemblage towards increased importance of pioneers. Similarly, a transition in functional composition from slow-growing to fast-growing species was observed in logged forests in Bolivia (Carreño-Rocabado et al., 2012) and French Guiana (Baraloto et al., 2012).

Considering the decrease in compositional similarity among treatments and the steady or even increased species richness following interventions, our results do not support our fourth hypothesis. Although the composition changed with higher importance of pioneer species at the expense of non-pioneer and infrequent species, there is no evidence for a local biotic homogenization, except for the two highest intervention intensities, which maintained a high within-plot similarity over time and followed comparable trajectories (Table 4). In these treatments (LMTI and LHTI), the pronounced decrease in similarity to the unlogged forest following thinning corroborates the strong effect of this intervention on species composition. This might be expected since the high disturbance intensity is likely to lead to a composition dominated by generalist species that may cope with the new adverse conditions. This finding reinforces the detrimental effects of the two highest disturbance intensities, which should be avoided in selection management with the joint objective to conserve biological diversity.

4.2. Implications for management and conservation

In the Brazilian Amazon, a polycyclic silvicultural system is employed, based on a felling cycle of 25–35 years with a maximum

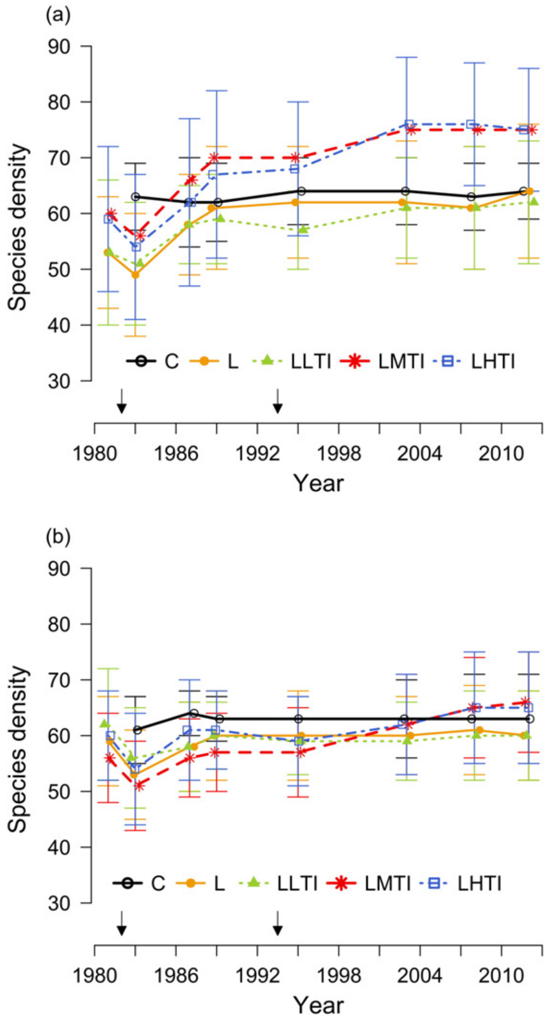

Fig. 3. Species density (mean and standard deviation per plot) over time for each treatment (C: control, L: logging only, LLTI: logging and light thinning intensity, LMTI: logging and medium thinning intensity, LHTI: logging and high thinning intensity): (a) poles and (b) trees. Interventions of logging (1982) and thinning (1993–1994) are shown by downward arrows above the time axis.

Table 5
Number of initial, final, lost and gained species per plot (mean and standard deviation) between the first (1981/1983) and the last census (2012) for each treatment. *F*-statistic values follow analysis of variance for the effect of treatment on each variable.

Treatment	Poles				Trees			
	Initial	Final	Lost	Gained	Initial	Final	Lost	Gained
C	63 ± 6	64 ± 5b	18 ± 3	19 ± 7b	61 ± 6	63 ± 8	12 ± 4b	13 ± 6b
L	53 ± 10*	64 ± 12b	20 ± 6	30 ± 10ba	59 ± 8	60 ± 8	17 ± 5b	18 ± 5b
LLTI	53 ± 13	62 ± 11b	20 ± 7	29 ± 13ba	62 ± 10	60 ± 8	16 ± 3b	14 ± 2b
LMTI	60 ± 9***	75 ± 8a	22 ± 4	36 ± 8a	56 ± 8***	66 ± 9	17 ± 5b	28 ± 7a
LHTI	59 ± 13***	75 ± 11a	23 ± 7	39 ± 4a	60 ± 8	65 ± 10	25 ± 3a	30 ± 6a
F	1.36	3.71*	0.97	4.97**	0.95	0.97	6.32***	14.60***

See Table 1 for treatment abbreviations. Values accompanied by different letters indicate significant differences between treatments (Tukey's HSD test). Asterisks in the column of the initial number of species indicate the result of the Student's t-test between initial and final number of species for each treatment.

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

harvesting volume of 30 m^3 ha^{-1} (MMA, 2006). Harvesting intensities in our study were on average two times higher (61.1 m^3 ha^{-1}) than the maximum accepted by current legislation. Hence, we can presume that under current logging prescriptions such substantial changes in species composition as reported in our study will not occur. Under high intervention intensities (basal area reduction > 6.6 m^2 ha^{-1}), the increased importance of pioneer species and the lack of recovery in composition will affect the delivery of goods and services by these ecosystems. For example, timber provision will possibly shift towards tree species with lower wood density and thus reduce the value of the growing stock in these forests in relation to the first harvest. A change in those tree species composing the growing stock after the first harvesting has been also observed in other tropical forests (e.g. Yosi et al., 2011; Hawthorne et al., 2012; Duah-Gyamfi et al., 2014b).

Logging effects were to a large extent associated with damage to remaining trees during felling and removal. Harvesting damage affected the highest number of species per unit of basal area reduced (18.5 species m^{-2}), followed by thinning (3.7 species m^{-2}) and logging (1.1 species m^{-2}) ($P < 0.001$) (Fig. A7). This observation reinforces the importance of reduced impact logging for easing the negative influence of harvesting on species diversity and composition (Putz, 2011). Additionally, in the selection system, recruitment and growth of selected species are typically favored through post-logging silvicultural treatments such as elimination of competing trees, in particular those of non-commercial species or poor shape. Although this activity aims to influence forest structure and species composition in favor of commercial species, its long-term effects in tropical forests are still largely unknown (Putz et al., 2001; Ouédraogo et al., 2011). Our results indicate that basal area reduction through thinning more than 4.7 m^2 ha^{-1} strongly affected species composition of trees ≥ 10 cm DBH, since species reassembly was clearly constrained after this silvicultural intervention in the most intensive treatments (LMTI and LHTI) (Fig. 1).

The culling of unwanted species typically places emphasis on the current timber value, and the largely unknown ecological importance of thinned trees (Sheil and van Heist, 2000) or the future merchantable value of certain species is often not taken into consideration. Therefore, this activity needs careful planning to minimize ecological and silvicultural risks. The effect of this intervention to improve and sustain timber production will be addressed in a subsequent study. Our results further suggest that deliberate retention of mature individuals of species as seed bearers at the time of harvest and thinning may be required to maintain tree species composition in the long term. This silvicultural approach may help sustain tree species composition more similar to unmanaged forests (Palik and Engstrom, 1999). Consequently, the maintenance of important ecosystem functions, flora and fauna interactions and the provision of goods and services may be supported over time.

The recovery of species composition takes longer than the recovery of species diversity, as was also observed in a tropical rainforest following clear cut and selective logging up to 50 years in China (Xu et al., 2015). Thus, compositional similarity should be regarded as an indicator of forest recovery, when evaluating the ecological sustainability of forest management, since measures related to the number of species do not reflect shifts in species composition and may lead to wrong interpretations. However, shifts in species composition should not be interpreted as an indication of failure of the silvicultural system. After all, the interventions are applied with the intention to change forest structure and composition to favor commercial species. The main question would rather be what level of change can be acceptable so that biodiversity conservation may be compatible with timber production. Our results suggest that reduction in basal area greater than 6.6 m^2 ha^{-1} should be avoided to reduce the risk of substantial changes in tree species composition for forests of the studied region. However, even smaller reductions in basal area might cause considerable changes in species composition, if mostly smaller trees are affected, as through damage and thinning. Nonetheless, the monitoring of biodiversity in other trophic levels is necessary to understand how they are affected by management interventions.

Yet, the magnitude of vegetation changes following silvicultural interventions has direct implications for the diversity of wildlife

Table 6
Spearman's correlation coefficients for the relationship between tree turnover rate and species turnover rate, rarefied number of species and similarity index.

Treatment	Poles			Trees		
	Species turnover	Species per 89 individuals	Morisita–Horn Index	Species turnover	Species per 77 individuals	Morisita–Horn Index
C	0.65***	−0.13	0.09	0.79***	0.13	−0.42*
L	0.83***	−0.10	−0.14	0.79***	−0.12	0.18
LLTI	0.82***	−0.31*	0.25	0.81***	−0.12	0.36*
LMTI	0.85***	−0.28**	0.16	0.80***	−0.20	0.22*
LHTI	0.86***	−0.18	0.27	0.81***	−0.09	0.26

See Table 1 for treatment abbreviations.

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

(Meijaard et al., 2005), such as mammals and birds (Burivalova et al., 2014). This effect in turn will influence vital process for plants, such as pollination and dispersion (Sheil and van Heist, 2000). Given that high intervention intensity generally changes composition towards light-demanding and wind-dispersed tree species, damage should be kept to a minimal level and strong thinning interventions should be avoided. This may enhance ecosystem resilience and diversity maintenance at other trophic levels. A study carried out in Guyana showed that management using reduced impact logging did not impair communities of birds, bats and large mammals (Bicknell et al., 2015). Lastly, our results also indicated that managed forests still harbor a substantial amount of tree species diversity. Thus, while well-managed areas cannot replace the value of natural reserves for biodiversity conservation (Meijaard et al., 2005; Didham, 2011), they can complement these areas to enhance tropical biodiversity conservation at the landscape scale.

5. Conclusions

Our results demonstrate that the composition of tree species (DBH ≥ 10 cm) was substantially affected by high silvicultural intervention intensities (basal area reduction > 6.6 m^2 ha^{-1}) over a period of 30 years after initial selection harvest in a tropical rainforest. Beyond this limit in basal area reduction, changes in tree species composition are still ongoing without signs of recovery towards pre-logging conditions. Strong reductions in basal area through logging damage and follow-up thinning contributed substantially to these changes. This shift may affect biodiversity at other trophic levels and the provision of goods and services by these ecosystems. Nonetheless, species diversity was not impaired by silvicultural interventions, indicating a high remaining conservation value of these managed forests. Our study also indicates that 30 years are not enough to monitor the ecological consequences of silvicultural interventions in these ecosystems and that long-term monitoring is needed.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version http://dx.doi.org/10.1016/j.biocon.2015.08.004.

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