RESEARCH ARTICLE

Recovery after 25 years of the tree and palms species diversity on a selectively logged forest in a Venezuelan lowland ecosystem

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Abstract

Aim of the study: We evaluate palm and tree species diversity in a floodplain forest and the changes affecting the plots subjected to different intensities of selective logging.

Area of study: The western alluvial plains of Venezuela.

Materials and Methods: A randomized complete blocks design was established 25 years ago with three felling treatments (trees with diameter greater than 20 cm, 40 cm and 60 cm). Each treatment had three replications, using 1 ha permanent plots. We have measured all trees and palms bigger than over 10 cm in diameter. The data set was used to calculate the Importance Value Index of each species, the Shannon-Wiener index, the Hill Numbers and the Chao-Sørensen index.

Main results: Disturbance increases the importance value index of pioneer species like *Cecropia peltata*, *Ochroma pyramidale* and *Triplaris americana*. All treatments produce changes on the floristic diversity but most of them are not significant. Only the high impact treatment causes a decrease in the species richness, but after 5 year of recovery this parameter is close to its previous levels (N0= 43.5). In logged forests, species loss (9.2%) is lower than in the control plots (11.7%) and is also lower than the rate of occurrence of species input (14.6%).

Research highlights: In these logged forests restoration of diversity is acceptable because is higher than 91% (Chao-Sørensen index). Selective logging, with low and medium intensity, is a disturbance that works in a similar way to natural disturbances. All the diversity indexes recovered the pre-harvest level values.

Keywords: Caparo - Venezuela; ecological restoration; forest dynamics; forest management; forest succession; Intermediate Disturbance Hypothesis; permanent plots.

Introduction

Tropical forests harbor at least two-thirds of the floristic diversity of the planet (Kier *et al.*, 2005). This is a vital natural resource as it provides ecosystem services such as food, fresh water, timber, fuel, climate and flood regulation, cultural values, spiritual, educational and recreational resources (Butler *et al.*, 2005).

Much of old-growth tropical forests have been declared as forest concessions; these are areas of perma-

nent timber production. The management in forest concessions is not clear-felling, but is a selective extraction that preserves much of the forest cover after cutting. This fact creates some opportunities for biodiversity conservation because many forest concessions, which were formerly designed for timber production, are now the main restricted-use areas to give shelter to plant and animal species whose habitat, outside concessions, has been destroyed (Roche, 1997; Arets, 2005). The selectively logged forest is a kind of "intermediate situation" between total protection and deforestation,

which deserves more attention to conservation management because it preserves much of the original diversity and its associated ecosystem services (Putz *et al.*, 2012; Edwards *et al.*, 2014).

Selective harvesting of timber generates impacts that may lead to an alteration or reduction of floristic composition and diversity (Hamilton, 1988). Johnson & Cabarle (1995) indicate that high harvest rates have generated threat levels in species such as *Dalbergia nigra, Pericopsis elata, Swietenia mahogani* and *Guaiacum officinale*. Similarly, ter Steege *et al.* (2002) point out that (after 75 years) logging of *Chlorocardium rodiei* in Guyana decreased 63 percent in its abundance and it reduces the financial feasibility of its current yield. However, Gourlet-Fleury *et al.* (2013) suggest that many of the reports, which describe a negative effect of harvesting on diversity, come from a high variety of situations (frequency and intensity of the felling, the initial state of the forest, interaction with other types of disturbances) that could hide a possible increase in species richness.

The process of plant succession that takes place after a disturbance is closely related to the theory of gaps (Hartshorn, 1980). In the early stages of succession (before 30 years) conditions are propitious for pioneer species that develop throughout their life cycle in a full light incidence (Felton *et al.*, 2006). That circumstance could decrease diversity initially, but in a few years, the nomadic species will arrive and finally the tolerant species, typical of mature forest, will do the same (Kariuki *et al.*, 2006).

The theory of "climax" indicates that the process of plant succession means a restoration that appropriately recovers the original or pristine condition (Odum, 1972). The results of some studies in tropical forests seem to support this assumption (Faber-Lagendoen, 1992; Magnusson *et al.*, 1999; Guariguata & Ostertag, 2001). "Climax" is one of those terms that has generated more controversy in ecology, but is still used by eminent authors like Dajoz (2002), Strasburger *et al.* (2004), Molles (2006), Odum & Warret (2006), Smith & Smith (2007). The dispute comes from the idea of the climax like a stable state. However, along the succession, there is a recovery of structure, floristic composition and ecosystem services that arrive at a situation very similar to the original one. Along this work we use the "consensus" term **old-growth forest** instead climax forest.

According to Connell (1978), the "Intermediate Disturbance Hypothesis" (IDH) implies an increase of ecosystem diversity after small and frequent disturbances that generate greater habitat heterogeneity. This hypothesis has also been the subject of intense debate, has acquired support from the results of Burslem &

Whitmore (1999), Sagar *et al.* (2003) and the compilation made by Kershaw & Mallik (2013). Obviously, there is no consensus and the controversy continues. For example, Fox (2013) pointed out that the IDH must be abandoned. Sheil & Burslem (2013) replied that, although there could be misunderstandings, the IDH still was valid and useful.

Anyway, some studies show a satisfactory recovery of richness, of floristic diversity, or even an increase in these parameters after selective logging. Situations like these have been reported in Uganda (Plumptre, 1996), Guyana (Van Andel, 2001), Borneo (Verburg & van Eijk-Bos, 2003; Berry *et al.*, 2008), Central Africa (Gourlet-Fleury *et al.*, 2013; Decocq *et al.*, 2014) and Tanzania (Rutten *et al.*, 2015).

Considering the above arguments, we hypothesize that after several years of a selective logging perturbation, some tropical forest plots recovers most of its diversity, and the secondary forest is quite similar to the original. Our aims are to evaluate the changes that occur in the tree and palm diversity throughout the secondary plant succession taking place in a forest, after a selective timber harvest with different levels of intensity. Our results could be also useful in order to improve the conservation strategies that different countries must implement in tropical forest concessions.

Materials and Methods

Study area

The Caparo Forest Reserve is located in the western plains of Venezuela covering an area of 174,000 ha. The Experimental Station is located at the west of the reserve (70°50' W, 07°25' N) and has approximately 7,000 ha (Jurgenson, 1994). Currently, the Experimental Station is a relict forest from the former original ecosystems; while most of the surrounding areas were deforested for agricultural purposes (Pacheco *et al.*, 2011).

The area is in a floodplain located about 50 km from Los Andes mountains. The average altitude is 140 m, with maximum slopes of 2 m in 10 km and a slight inclination to the east (Jurgenson, 1994).

The average annual temperature is 24.8°C and total annual precipitation is 1,753 mm. Rainfall is markedly seasonal and goes from March to December; the most humid month is July (Franco, 1982). According to the Rivas-Martínez system (2004), bioclimatic classification of this area is Tropical Pluviseasonal, Upper Infratropical, Upper Subhumid.

Soils constitute a continuum between two extreme geomorphologic units (Franco, 1982; Schargel, 2005).

The "levee" occurs in relatively high positions, with a sandy textured soils, moderate to well drained, with fluctuations in the water table and absence of flooding. The "depression" soils are located in lower positions, exposed to floods, with clay texture, slow permeability and strong mottling of iron and manganese oxides due to high fluctuations in the water table. The high clay content of "depression" soils gives rise to cracking, caused by contraction and expansion of soil components; this process, in conjunction with a reticular erosion and earthworm activity, generates "micro-mound" formation. Due to recent material, the soils of the floodplain are rich in nutrients, when compared with other Neotropical ecosystems (Kammesheidt *et al.*, 2001a).

The specific study site is located in "depression" type soils. The forest canopy is 25 m high, with a coverage of 70% and usually stratified in three or four vegetation layers. These forests belong to a phytosociological unit dominated by the palm *Attalea butyracea* (Mutis ex L. f.) Wess. Boer. Other important species in these old-growth forests are *Pouteria reticulata* (Engl.) Eyma, *Spondias mombin* L., *Trichantera gigantea* (HBK) Ness, *Terminalia oblonga* (Ruiz & Pav.) Steud., *Sapium stylare* Müll.Arg., *Syagrus sancona* H. Karst., *Pachira quinata* (Jacq.) WS Alverson, *Brosimum alicastrum* Sw. and *Luehea seemannii* Triana & Planch. (Lozada *et al.*, 2009).

Experimental design

In 1987, a research was performed to evaluate the response of the ecosystem facing different interference types. One kind of analyzed perturbation was selective logging that was assessed by means of a randomized complete blocks design: three selective logging treatments with three replications each, and two control plots. The size of each plot was 100 × 100 m; all the trees and palms with dbh ≥ 10 cm were measured. Treatments were applied according to the following cutting limits in dbh (diameter at breast height, approximately 1.3 m in height):

Treatment 9 (T9): trees with dbh > 20 cm (three plots: 9.1, 9.2, 9.3).

Treatment 10 (T10): trees with dbh > 40 cm (three plots: 10.1, 10.2, 10.3).

Treatment 11 (T11): trees with dbh > 60 cm (three plots: 11.1, 11.2, 11.3).

Treatment 0 (T0): control plots (two plots: 0.1, 0.2).

Treatments were applied only once (in 1987). After this selective logging, measurements were done in different occasions and the plots naturally recovered through the mechanisms of forest succession. All plots were sampled before treatment and at 2, 5, 10, 15, 20 and 25 years since treatment (except the control plots, which were measured until 20 years).

Different treatments generated different disturbance levels (Table 1) which lead to two control plots, three low disturbance plots, two medium disturbance plots and four high disturbance plots. Such levels of impact were taken into account for the interpretation of our results.

The Importance Value Index (IVI) of each species in each plot was calculated (Curtis & McIntosh, 1951). The Shannon-Wiener index (H′) and the Hill Numbers from 0 to 2 (N0 equivalent to species richness, N1 equivalent to exponential of Shannon-Wiener index and N2 equivalent to inverse of Simpson dominance) were calculated according to Magurran (1988). Chao-Sørensen index (Chao *et al.*, 2005) was used to make comparisons of floristic similarity be-

Table 1. Disturbance levels as loss of basal area (adapted from Lozada, 2008 and Lozada *et al.*, 2012)

Disturbance Levels	Plots	Original values		Basal area loss after logging
		tree ha^{-1}	m^2 ha^{-1}	%
Control	0.1	365	25.95	5*
	0.2	430	22.39	3*
Low	9.3	214	16.45	−3
	11.1	251	16.20	−12
	11.3	248	16.57	−13
Medium	10.2	334	22.59	−34
	11.2	323	23.62	−39
High	10.1	309	21.81	−63
	10.3	192	17.32	−65
	9.1	273	21.89	−76
	9.2	256	17.93	−79

*: no treatments were applied

tween each pair of inventories. These calculations were carried out with MVSP 3.13I © (Kovach Computing Services, 2004) and EstimateS 9.1.0 (Colwell, 2013).

The software SPSS v 15.0.1 was used to perform a One-Way ANOVA for each level of impact and each diversity parameter separately. In each case, a comparison between the years assessed (2, 5, 10, 15, 20 and 25) and the year 0 was made. Tests of normality of the data were made. When normality was not satisfied we continued with the ANOVA because this analysis is robust to the violation of this assumption, that is to say that it does not upset the Error Type I (Hays, 1988; Montgomery, 1991; García-Berthou *et al.*, 2009). The homoscedasticity was also evaluated by means of the Levene test; if this condition was satisfied the "post hoc" analysis was completed with the test Bonferroni; otherwise, a transformation of the data was made and if the lack of homoscedasticity still persisted the interpretation was made by the Games-Howell test (SPSS, 2006).

Results

Changes in floristic composition

The dominant palm *A. butyracea* has not been affected by any impact level (Table 2). As should be expected, the floristic composition in the control plots is maintained with very slight changes in the IVI values of each species.

With low disturbance level we observe that *T. gigantea* and *S. mombin* are almost always among the five most important species. In year 10 the entrance of the pioneer *Cecropia peltata* with an IVI of 14 is observed; by year 15 this species drops to 13.1 in IVI and it does not longer appears among the five most important species.

In the medium impact level, the input of pioneers is more evident. *Guazuma ulmifolia* is very important in years 5 and 10. *C. peltata* is among the most important species in years 10, 15, 20 and 25; this species reaches a maximum value of IVI in year 15 (IVI = 29.3) and

Table 2. IVI average value, for the most important species, in each treatment and each age evaluated. Own data generated by our 7 inventories

Year 0		Year 2		Year 5		Year 10		Year 15		Year 20		Year 25	
Treatment: Control													
Atbu	44.8	Atbu	44.5	Atbu	44.2	Atbu	42.4	Atbu	45.3	Atbu	49.0		
Pore	29.4	Pore	30.1	Pore	30.0	Pore	26.8	Pore	28.1	Pore	25.8		
Trgi	24.9	Trgi	24.9	Trgi	23.9	Trgi	24.6	Trgi	24.2	Trgi	23.1		
Sast	14.5	Sast	14.3	Spmo	14.7	Spmo	16.4	Spmo	17.4	Spmo	18.2		
Spmo	13.9	Spmo	14.2	Sast	14.3	Sast	13.3	Sast	12.9	Coth	13.1		
Treatment: Low Impact													
Atbu	50.6	Atbu	54.5	Atbu	47.9	Atbu	46.6	Atbu	43.7	Atbu	48.2	Atbu	54.4
Trgi	23.0	Trgi	21.7	Trgi	26.6	Trgi	24.4	Trgi	25.2	Trgi	25.4	Trgi	28.5
Pore	15.4	Pore	15.3	Spmo	12.9	Cepe	14.0	Luse	13.8	Spmo	14.2	Spmo	14.8
Sast	15.4	Spmo	14.6	Teob	12.8	Spmo	12.9	Teob	13.3	Luse	13.8	Teob	13.3
Spmo	14.3	Sast	13.9	Lopi	10.9	Teob	12.5	Cepe	13.1	Teob	12.9	Bana	12.1
Treatment: Medium Impact													
Atbu	67.0	Atbu	78.5	Atbu	75.5	Atbu	61.7	Atbu	55.8	Atbu	54.1	Atbu	55.5
Paqu	19.9	Teob	15.9	Teob	15.5	Cepe	26.3	Cepe	29.3	Cepe	21.8	Tram	18.0
Spmo	17.3	Pore	14.2	Pore	12.9	Ing1	14.5	Tram	17.1	Tram	18.8	Cepe	17.8
Pore	16.8	Slte	12.5	Slte	11.3	Guul	14.3	Ing1	15.0	Spmo	15.6	Spmo	16.1
Teob	13.0	Trgi	11.9	Guul	11.0	Teob	14.2	Teob	14.3	Teob	15.1	Sast	14.0
Treatment: High Impact													
Atbu	46.0	Atbu	88.2	Atbu	58.2	Atbu	41.2	Atbu	37.2	Atbu	43.4	Atbu	47.8
Pore	17.7	Trgi	23.8	Cepe	25.2	Cepe	35.6	Cepe	34.7	Tram	25.6	Trgi	20.0
Paqu	15.5	Sysa	15.7	Ocpy	17.7	Ing1	29.2	Ocpy	31.4	Cepe	23.4	Tram	19.4
Trgi	12.7	Ing2	14.3	Ing1	16.5	Ocpy	19.9	Tram	24.6	Trgi	19.2	Sast	18.0
Ing2	12.7	Oco1	11.3	Trgi	16.1	Tram	16.6	Trgi	17.1	Sast	15.6	Guul	16.1

Acronyms. **Atbu:** *Attalea butyracea* (Mutis ex L. f.) Wess. Boer; **Bana:** *Banara* sp.; **Cepe:** *Cecropia peltata* L.; **Coth:** *Cordia thaisiana* G. Agostini; **Guul:** *Guazuma ulmifolia* Lam.; **Ing1:** *Inga* sp.1; **Ing2:** *Inga* sp.2; **Lopi:** *Lonchocarpus pictus* Pittier; **Luse:** *Luehea seemannii* Triana & Planch.; **Ocpy:** *Ochroma pyramidale* Sw.; **Oco1:** *Ocotea* sp.1; **Paqu:** *Pachira quinata* (Jacq.) W.S. Alverson; **Pore:** *Pouteria reticulata* (Engl.) Eyma; **Sast**: *Sapium stylare* Müll.Arg.; **Slte:** *Sloanea terniflora* (Sessé & Moc. ex DC.) Standl.; **Spmo:** *Spondias mombim* L.; **Sysa:** *Syagrus sancona* H. Karst.; **Teob:** *Terminalia oblonga* (Ruiz & Pav.) Steud.; **Trgi:** *Trichanthera gigantea* (HBK) Ness; **Tram:** *Triplaris americana* L.

then decline very gradually. *Triplaris americana* is very important in year 15 and still in year 25 is progressively rising its IVI value.

On plots with high impact level we find an interesting abrupt rise in the IVI of *A. butyracea* in year 2; this is because this palm was not felled down during the experimental set up. *C. peltata* takes a prominent role in early and medium years after treatment: by year 15 it achieves a very high IVI value (34.7) almost equal to *A. butyracea*, and then declines very slowly. In this treatment, we should also highlight the high IVI values of other pioneers like *Ochroma pyramidale*, *Inga* sp.1 and *T. americana*.

The list of all the species found in this study is shown in Table S1 [supplementary]. In this table, we also assess the variation in species presence by means of the comparison of the records at the beginning versus the end of the evaluated period. It is important to note that even without human intervention there is

a dynamism that in the control plots generates the disappearance of 8 species (11.7%) and the occurrence of 3 species input (4.4%). In harvested areas, changes seem more intense; but on average, the species input (12; 14.6%) is greater than the species lost (7; 9.2%).

Variation in the palm and tree species diversity

The assessment of the palm and tree diversity in control plots shows that there is no permanent stability, but rather small variations in the analysed parameters (Fig. 1).

In plots with low and medium impact, a small decrease of species richness (N0) and Shannon exponential (N1) in year 2 is observed (immediately after logging). However, these parameters recover quickly and
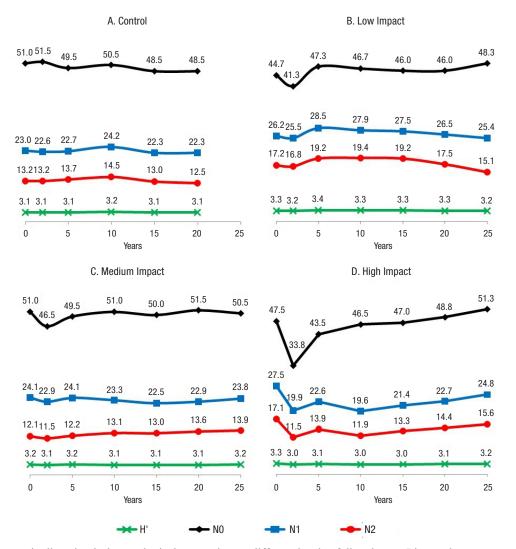

Figure 1. Changes in diversity during ecological succession, at different levels of disturbance. Lines values represent the average of the plots belonging to each level. Diversity indicators: Shannon-Wiener index (H'), Hill Numbers (N0, N1, N2).

for the end of the measurement period (year 25) the previous level is recovered or even exceeded.

On plots with high impact logging there is a severe reduction in species richness (N0); by year 2 there are 14 species less than at the beginning, but at the end of the assessment period (25 years), there are 4 more species than in the former inventory. Shannon exponential (N1) and the reciprocal of Simpson's dominance (N2) have a different behavior, dropping gradually until year 10 and then showing a slow recovery; by year 25 they have not yet reached the previous values, but the upward trend is very clear and it seems that in a few more years they would reach the initial level.

Results from the "post hoc" test (Table 3) show that selective logging does not affect the palm and tree species diversity, according to the different indexes evaluated. Only the species richness (N0) decrease significantly (p= 0.02, Bonferroni test) in the high impact level at year 2 and recovers at year 5.

Local heterogeneity and recovery of the palm and tree composition

All plots are located in the same forest type and in the same type of soils, but an obvious pre-treatment spatial heterogeneity was found. Thus, the Chao-Sørensen index fluctuates from 0.67 to 0.93, the general average is 0.84 and standard deviation is 0.06 (Table 4). Post-treatment spatial similarity is slightly greater than pre-treatment condition, the Chao-Sørensen index

fluctuates from 0.70 to 0.96, the general average is 0.88 and standard deviation is 0.06 (year 20). Comparison of the two data sets shows that homoscedasticity condition is satisfied (p= 0.61, Levene test) and the increase of similarity is significant (p= 0.00).

The similarity analysis for control plots shows that palm and trees keep their composition over time since a Chao-Sørensen index variation in the range 0.98-1.00 is observed (Table 5).

In the plots with low and medium impact, similarity over time slightly decreases and remains in the range 0.94 to 0.99. In the plots with more intensive use, the similarity falls down to 0.82 in year 5, but a recovery is detected and it reaches 0.91 by year 25.

Discussion

The high dominance of the palm *A. butyracea* has already been reported in the western plains of Venezuela by Kammesheidt (1998) and Guevara (2001). Similarly, the pioneer temperament of genus *Cecropia*, *Guazuma*, *Inga*, *Triplaris* and *Ochroma* has been mentioned in reports of Kammesheidt (2000) and Castro-Luna *et al.* (2011).

Changes in species composition are supported not only by the increased importance of pioneer species but also by the decrease of nomadic species (such as *P. quinata*, *P. reticulata*, according to the definition of Vásquez-Yanes & Guevara, 1985) especially in the treatments of medium and high impact. These results are consistent with the abundant literature on the dy-

Table 3. Significance values, for the "post hoc" analysis, for each parameter evaluated compared with year 0. A significant difference occurs when Significance ≤ 0.05

Impact Level	Parameter	Statistical Test	Years					
			2	5	10	15	20	25
Control	H´	Bonferroni	1.00	1.00	1.00	1.00	1.00	
	N0	Games-Howell	1.00	1.00	1.00	0.93	0.99	
	N1	Games-Howell	0.99	1.00	0.64	0.99	0.99	
	N2	Bonferroni	1.00	1.00	1.00	1.00	1.00	
Low Impact	H´	Bonferroni	1.00	1.00	1.00	1.00	1.00	1.00
	N0	Bonferroni	1.00	1.00	1.00	1.00	1.00	1.00
	N1	Bonferroni	1.00	1.00	1.00	1.00	1.00	1.00
	N2	Bonferroni	1.00	1.00	1.00	1.00	1.00	1.00
Medium Impact	H´	Bonferroni	1.00	1.00	1.00	1.00	1.00	1.00
	N0	Games-Howell	0.70	0.95	1.00	0.98	1.00	1.00
	N1	Bonferroni	1.00	1.00	1.00	1.00	1.00	1.00
	N2	Games-Howell	1.00	1.00	0.99	1.00	0.97	0.92
High Impact	H´	Bonferroni	0.81	1.00	0.53	1.00	1.00	1.00
	N0	Bonferroni	**0.02**	1.00	1.00	1.00	1.00	1.00
	N1	Bonferroni	0.59	1.00	0.50	1.00	1.00	1.00
	N2	Bonferroni	1.00	1.00	1.00	1.00	1.00	1.00

Table 4. Similarity analysis (Chao-Sørensen index) for all the plots

	0.1	0.2	9.1	9.2	9.3	10.1	10.2	10.3	11.1	11.2	11.3	Ave	SD
					Pre-treatment (year 0)								
0.1		0.91	0.79	0.83	0.77	0.83	0.87	0.88	0.84	0.85	0.80	0.84	
0.2			0.79	0.84	0.75	0.89	0.86	0.90	0.87	0.92	0.77	0.84	
9.1				0.90	0.81	0.88	0.93	0.86	0.86	0.89	0.77	0.86	
9.2					0.82	0.82	0.92	0.84	0.79	0.89	0.79	0.84	
9.3						0.67	0.88	0.88	0.71	0.74	0.88	0.79	
10.1							0.86	0.90	0.89	0.92	0.72	0.86	
10.2								0.91	0.86	0.90	0.87	0.88	
10.3									0.88	0.87	0.88	0.88	
11.1										0.93	0.70	0.82	
11.2											0.75	0.75	
11.3													
Ave		0.91	0.79	0.86	0.79	0.82	0.89	0.88	0.84	0.88	0.79	0.84	
SD													0.06
					Post-treatment (year 20)								
0.1		0.92	0.90	0.87	0.78	0.91	0.91	0.90	0.91	0.95	0.83	0.89	
0.2			0.92	0.88	0.74	0.95	0.88	0.92	0.96	0.95	0.79	0.89	
9.1				0.92	0.82	0.95	0.95	0.91	0.91	0.92	0.89	0.91	
9.2					0.87	0.89	0.94	0.88	0.86	0.91	0.88	0.89	
9.3						0.70	0.91	0.85	0.74	0.78	0.93	0.82	
10.1							0.92	0.94	0.94	0.95	0.77	0.90	
10.2								0.91	0.88	0.93	0.92	0.91	
10.3									0.92	0.95	0.89	0.92	
11.1										0.95	0.79	0.87	
11.2											0.80	0.80	
11.3													
Ave		0.92	0.91	0.89	0.80	0.88	0.92	0.90	0.89	0.92	0.85	0.88	
SD													0.06

Acronyms. Ave: average. SD: standard deviation.

namics of tropical forests (Hartshorn, 1980; Moret *et al.*, 2008; Ruschel, 2008; Lohbeck, 2014). Nevertheless, the decline of *C. peltata* from year 15 is not co-incident with some reports that indicate that pioneers such as this species have a life cycle up to 50 years and that at year 20 still maintains a high proportion of the basal area community (de Oliveira, 2005).

In forest ecosystems there is no an absolute stability, but a kind of dynamic balance caused by growth, recruitment and mortality processes that leads to changes in the presence, density and species dominance, mainly those with low abundance (de Oliveira *et al.*, 2014). That is why when making long-term assessments in forests with no anthropogenic interventions, small changes in floristic composition are reflected in changes in the IVI of species (Table 2).

The IVI decline of nomadic species with high commercial value is worrisome. In conventional logging these species have the highest pressure; if extraction continues in subsequent cutting cycles, to the long term they could be threatened by a significant decrease in population or its genetic diversity (Zimmermann, 1992; Plonczak, 1993; Kammesheidt, 1994). Therefore, harvesting cycles should be extended to at least 60 years

in order to achieve sustainable yields (Kammesheidt *et al.*, 2001b).

Sapium stylare shows an interesting behavior. It is a high value nomadic species, but is not harmed by the logging intensity and appears with elevated IVI values after 25 years in plots with medium and high impact. A similar performance was reported by Kammesheidt (1998) who reported that this is due to some ecological characteristics of this species: clumped distribution, well adapted to poorly drained soil, use of light availability derived from logging, the presence of sufficient remaining mature trees that allow regeneration and increase of individuals in the lower diameter classes.

The plant species diversity values found in this study generally approach the lower limits of the scope reported for South American tropical forests. The values of species richness are less than 80 spp/ha, which correspond to low diversity places that are mainly on flooded sites (Knab-Vispo *et al.*, 1999). The values of the Shannon-Wiener index are intermediates in the range (2.1-3.6) reported by Campbell *et al.* (1992) and Damasceno-Junior *et al.* (2005). Furthermore, areas with prolonged drought periods are reported to show low diversity indexes (ter Steege *et al.*, 2003; Saatchi *et al.*,

2008). In Caparo a combination of the limiting factors mentioned above are present: alternating of drought and flooding. Consequently, small decreases in diversity which were detected in this study as the result of logging have a low significant ecological importance. In other words, none of the parameters assessed changed from a condition of high to medium or low diversity.

Diversity indexes show very slight oscillations in the control plots. In logged forests this fluctuation is more accentuated and it seems to increase with the impact level (Fig. 1). However, the changes are not, in general, statistically significant (Table 3), except in one case. This could mean that small losses of diversity that might occur immediately are recovered in few years. Only the species richness (N0) in the high impact level is lower in year 2, but recovers at year 5. Similar results were found by ter Steege *et al.* (2002) in Guyana; but, these authors also suggest that the diversity indices commonly used (Fisher´s Alpha and H ') are not sensitive to detect changes in an area with many individuals and species. Meanwhile, Bongers *et al.* (2009) found that the disturbance is less important to explain the patterns of diversity in humid ecosystems; in dry forests disturbance explain more variation of diversity.

Under strong disturbances, large gaps produce immediate microclimatic changes that promote regeneration, development and dominance of pioneer species, which could decrease the ecosystem diversity (Denslow, 1980; Cannon *et al.*, 1998). This argument could explain the decrease observed at the high impact level in species richness. However, Guariguata & Ostertag (2001) indicate that the process of plant succession retrieves microclimatic conditions which, together with nearby seed source, generates a restoration of diversity in a few decades. Our results show that restitution occurs after 5 years (Table 3) and seems to be favored by our experimental design since the treated plots (1 ha) are surrounded by strips of an undisturbed forest of at least 100 m wide.

Space heterogeneity is a conspicuous property of tropical forest. In Caparo this is mainly caused by a geomorphological dynamics that produce a textural variability in the soils and its consequent diversity of floristic composition (Lozada *et al.*, 2010). These changes are noticeable in the IVI values for year 0 (Table 2) and Chao-Sørensen pre-treatment indexes (Table 4). But it is remarkable to note that post-treatment similarities (year 20) are higher than pre-treatment ones. These values prove that, for the treatments and period assessed, spatial changes are more important than logging induced changes, as has been previously reported by Bongers *et al.* (2009).

With respect to the recovery of floristic composition, Ferreira & Prance (1999) determined that a secondary

Table 5. Average values for similarity (Chao-Sørensen index), compared with the baseline assessment (year 0) in each treatment

	Year					
	2	**5**	**10**	**15**	**20**	**25**
Control	1.00	0.99	0.99	0.99	0.98	–
Low Impact	0.99	0.95	0.95	0.95	0.95	0.96
Medium Impact	0.99	0.97	0.95	0.94	0.94	0.94
High Impact	0.92	0.82	0.86	0.86	0.90	0.91

40-year-old forest in the Amazon recovered 95 percent of the original biomass, but the floristic similarity only reached 12 percent (Jaccard Index). Guariguata & Ostertag (2001) note that in some cases, even after 80-100 years, floristic composition is not similar to mature forest. In Panama, DeWalt *et al.* (2003) found that at the age of 70 years secondary forests reach structural features similar to those of primary forests, but with only a 26 percent of similarity (Sørensen Index). Therefore, the minimum level of similarity that we found in forests, after 25 years of selective logging, is quite adequate (91%, Table 5). The divergence on the figures of similarity, between other studies and ours, are probably related with the object of measurements (trees, palms, vascular plants…), but also with the type of similarity index used. Jaccard and Sørensen indexes are the most commonly used, but they are likely to underestimate the similarity between plots because they use presence/absence data and are very sensitive to rare species, which include the so-called "singleton" and "doubleton", i.e., those that have an abundance of 1 and 2 individuals respectively. The Chao-Sørensen index (Chao *et al.*, 2005) calculated in our work takes into account not only presence but also abundance of species and in this sense reflects the IVI values better.

Long-term research on the recovery of the Neotropical forests after logging is scarce (Verburg & Van Eijk-Bos, 2003). However, it is broadly stated that forests, even without human intervention, perform slight changes in floristic composition and diversity. Thus, we can conclude that selective harvesting of timber, with low and medium intensity, is a disturbance that works in a similar way to natural disturbances of similar intensity. For all the diversity indexes assessed a recovery to the pre-harvest level was found, but not an increase in such parameters.

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