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The recovery of logged forests proves that a viable management is possible in the Venezuelan Guayana Shield

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Abstract

Aim of study: To compare the diversity and biomass of logged forests, with different ages after harvesting and the risk of their degradation to liana forests.

Area of study: We studied 18 plots at the central zone of the Imataca Forest Reserve (Guayana shield), Venezuela.

Material and methods: We used 1-ha plots, to measure individuals with dbh > 10 cm in control plots (0 years) and in logged plots with 3, 9, 12, 15 and 18 years after logging. The main variables evaluated were enlarge importance index (EII), richness (R), Shannon-Weaner index (H´), Alpha Fischer (α), basal area for commercial species (BA_comm), above-ground carbon (C) and lianas abundance at the understory (Lianas_%Au).

Main results: Diversity variables (R: 62-77 spp ha^{-1}, *p*: 0.117-0.838; H´: 2.8-3.4, *p*: 0.181-0.677; α: 18.6-25.4, *p*: 0.293-0.922) and biomass (89.6-180.2 MgC ha^{-1}, *p*: 0.171-0.895) did not have significant differences between control and most of the logged plots. Only the 18 years-old forests had statistically higher values of diversity (R: 81-94 spp ha^{-1}, *p*: 0.000; H´: 3.8-3.9, *p*: 0.000; α: 26.8-31.7, *p*: 0.000), perhaps due to a high impact skidding operation. Commercial species were not recovering after logging.

Research highlights: Forest management can be viable in this area, but it requires reduced impact logging techniques and better silvicultural systems to guarantee future harvest of high value commercial timber.

Additional key words: Imataca; Venezuelan Amazon; tropical silviculture; logging; ecological restoration; above-ground carbon stock.

Abbreviations used: α (Alpha Fischer index); BA (basal area); BA_comm (basal area of commercial species); C (above-ground carbon); dbh (diameter at breast high); EII (Enlarged Importance Index); FSC (Forest Stewardship Council); H´(Shannon-Wiener index); IFR (Imataca Forest Reserve); Lianas_%Au (abundance of lianas in the understory); PEFC (Program for the Endorsement of Forest Certification); R (species richness); SCF (structural conversion factor).

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Supplementary material (Table S1) accompanies the paper on *Forest System*´s website

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Introduction

Timber harvesting in tropical forests evidently has impacts on the remaining stand. Some pioneering works demonstrated the occurrence of damage and loss of biodiversity triggered by logging (Nicholson, 1958; Uhl & Guimaraes, 1989; Johnson & Cabarle, 1995). Although, many of these studies were short-term and did not evaluate the mechanisms of plant succession, which recover forests in the medium and long-term. Ignoring the forest ecosystems resilience is one of the most marked trends in evaluating the effects of forest harvesting. But, more recent documents show examples of recovery of floristic diversity, biomass and carbon stock in several logged tropical forests (Van Andel, 2001; Berry *et al.*, 2008; Gourlet-Fleury *et al.*, 2013; Decocq *et al.*, 2014; Rutten *et al.*; 2015). In the alluvial plains of western Venezuela, an acceptable recovery of diversity and biomass was also reported in a period of 25 years after harvesting (Lozada *et al.*, 2016a, 2020).

The recovery of the ecosystem is fundamental for the conceptual treatment of conservation. Initially, forest degradation was considered as an instantaneous event where a negative alteration of the structure or functioning of a stand occurred, and consequently the supply of goods or services decreased (FAO, 2001). Later, it was indicated that degradation is considered when this reduction occurs in the long-term and it affects the carbon stock, wood supply, biodiversity, other goods and services (FAO, 2003). Degradation is not considered to be the reduction of canopy cover, which is later recovered within the normal cycle of forest management operations (ITTO, 2005). Therefore, the concept of degradation must have a resilience-based approach; it occurs when recovery capacity is reduced, lost or stopped and/or when human intervention is needed to initiate a restoration process (Ghazoul & Chazdon, 2017).

Notable authors are (recently) giving high value to the forests that have experimented a selective timber harvesting. These forests would be a type of "intermediate situation" between total protection and deforestation, which deserves more attention for conservation management, because it maintains a large part of the original diversity (flora and fauna), the carbon stock, the hydrological functions, and other ecosystem services (Putz *et al.*, 2012; Edwards *et al.*, 2014; Laurance & Edwards, 2014; Cerullo & Edwards, 2019). All of these benefits are orders of magnitude higher than agricultural lands that frequently threaten logged forests (Bousfield *et al.*, 2020).

The resilience of forests indicates that forest management can be feasible. Different sustainability certification systems are being implemented in forestry operations; the most important are the Forest Stewardship Council (FSC, started in 1995) and the Program for the Endorsement of Forest Certification (PEFC, started in 2000). Linking both schemes, there are currently 557 million certified hectares in the world, which includes natural forests and forest plantations; the most used criteria to endorse sustainable forest management are (FSC, 2015; PEFC, 2021): to protect biodiversity and high-value ecosystems, to protect the ecosystem services of forests, to reduce deforestation and degradation of forest ecosystems, to keep the rights of indigenous peoples and other local communities, to promote the economic development of rural communities, rights and job security for forest workers, mitigation of climate change, permanent monitoring, environmental impact as-

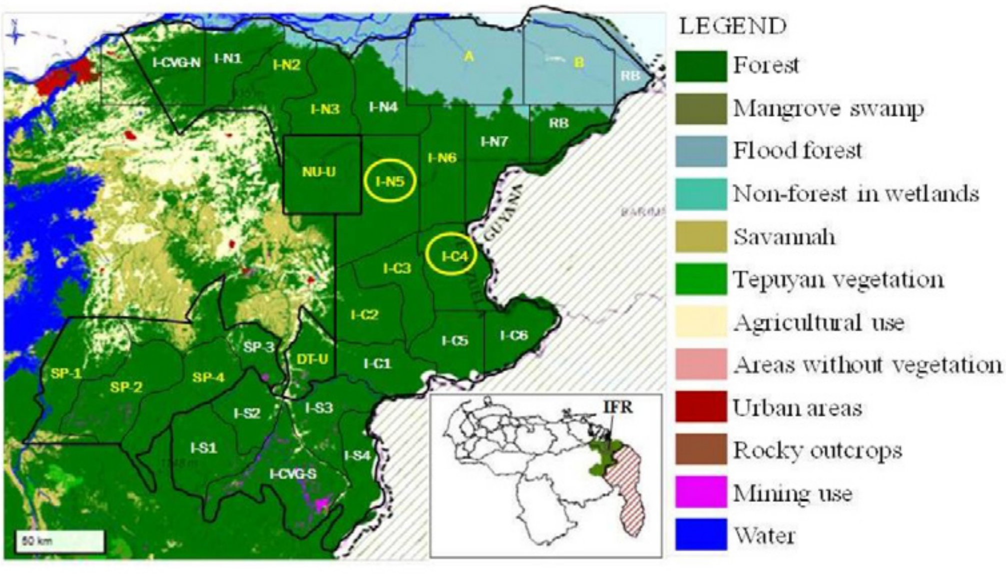

Figure 1. Land use map in the northeast sector of Venezuelan Guayana for the year 2020. Yellow letters indicate forest management units that (fully or partially) had selective timber harvesting in the period 1983-2010. Circles indicate the study sites of this research. Adapted from Provita (2021).

sessment, management to restores the forest mass by natural or artificial regeneration. Therefore, sustainable forest management is a very broad concept and for that reason our analysis remains in the context of a management that could be "viable".

There is a sequence of maps on changes in land use, in the period 2000-2020, in the Venezuelan Amazon (Provita, 2021). It is shown that areas where there was timber harvesting, since 1983, today have high forest coverage (Fig. 1). Logically, these forests must be efficiently fulfilling the functions of habitat for fauna, regulation of the water regime, erosion control, and maintenance of genetic resources, mitigation of climate change and other ecosystem services. These maps show that the most serious threat to forest ecosystems is deforestation due to agricultural land increase; these activities are invading and destroying areas legally declared for the permanent production of wood and other forest goods and services.

According to previous reports in tropical forests, we hypothesize that a successful resilience process also occurs in the harvested forests of Imataca. Therefore, the aim of this research was to determine the efficiency of the recovery after selective logging, in a sector of Venezuelan Guayana, through floristic and structural quantitative characteristics, such as richness, diversity, carbon stock, presence of species with commercial value and presence of lianas. We also intend to provide evidence that can reorient land use planning schemes and the design of forest management plans.

Material and methods

Study area

The Imataca Forest Reserve (IFR) covers an area of 3,822,000 ha (MARN-UCV, 2003) and is located in western of Venezuela, between coordinates 006°00' N 59°50' W and 008°30' N 62°10' W. The research sites belong to hills in the Units I-C4 and I-N5, located in the central sector of the reserve (Fig. 1). Annual precipitation is between 1,400 and 1,700 mm and the average annual temperature is 26°C (MARN-UCV, 2003).

The geology is dominated by metamorphosed granitic, volcanic and turbid rocks from the Precambrian. The physiography is soft or moderately undulating peneplain with valleys in the lower areas. The soils are acidic, highly leached, with a very low cation exchange capacity, low base saturation and aluminum is at toxic levels (Lozada *et al.*, 2014). According to the Holdridge System, the study area belongs to tropical humid forest (Ewel *et al.*, 1976) and, from the physiognomic and structural point of view they are tall evergreen forests (Huber, 1995). The most frequent species, in the central zone of the IFR, are *Pentaclethra macroloba* (Willd.) Kuntze and *Carapa guianensis* Aubl. In the hills dominate *Alexa imperatricis* (R.H. Schomb.) Baill., *Protium tenuifolium* (Engl.) Engl., *P. decandrum* (Aubl.) Marchand, *Eschweilera decolorans* Sandwith and *E. parviflora* (Aubl.) Miers. There is a wide valley type, with permanent flooding, where *Catostemma commune* Sandwith and *Pterocarpus officinalis* Jacq dominate. There are other narrow valleys and foothills, with temporary flooding during the rainy season, where *Mora excelsa* Benth dominates forming forests with high homogeneity (Lozada *et al.*, 2011).

According to Venezuelan laws, Forest Reserves are areas intended for the continuous supply of wood and other goods and ecosystem services, without deterioration of the forest. Selective logging in the IFR began in 1983 and continued until 2010. The forests were harvested according to traditional methods: felling with a chainsaw, skidding with CAT-518 and CAT-528 rubber wheel machines (or similar) from the felling site to log landing yards located on secondary roads; the average skidding distance was 400 m. Reduced impact logging techniques were not applied; the trees were not located using coordinates and the operators located the trees through field walks. In particular, most of the 18 years-old forest had a disorderly logging and the stems were skidded directly to the roads without using the log landing yards (personal observation).

Experimental design and data processing

The research was carried out through a design with 6 treatments, according to age after logging (3, 9, 12, 15 and 18 years), and 3 replications in each (except the control plots, which had 6 replications). The control plots correspond to old-growth forests (not logged, 0 years).

Each replication was evaluated using a 1-ha plot, where all trees, palms and lianas larger than 10 cm dbh (diameter at breast high) were measured. An Enlarged Importance Index (EII) was calculated for each species and plots according to Eq. (1) of Lozada *et al.* (2011):

$$EII = As\% + Fs\% + Ds\% + Au\% + Fu\% \quad [1]$$

where, As% is the structural relative abundance *, Fs% is the structural relative frequency *, Ds% is the structural relative dominance *, Au% is the understory relative abundance **, and Fu% is the understory relative frequency **[1].

In each 1-ha plot, 4 sub-plots of understory (100 m^2 each) were evaluated where all forms of life (spermatophytes) were surveyed. Because each variable is a relative value, the sum of the EII has a value of 500 in each plot with all species.

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[1] * Individuals larger than 10 cm dbh, as established by Curtis & McIntosh (1951). ** Individuals smaller than 10 cm dbh, as established by Lozada *et al.* (2011).

Voucher specimens were located at Herbarium MER (Universidad de Los Andes, Mérida, Venezuela). Floristic diversity was evaluated through Richness (R), Shannon-Wiener Index (H’) and Fisher’s Alpha (α) according the equations of Magurran (1988). Similarity between plots was calculated using the Chao-Sørensen Index (Chao *et al.*, 2005).

The development of the forest biomass was assessed by means of basal area (BA; m^2 ha^{-1}) and above-ground biomass (AGB, kg); the last is according Eq. (2) of Chave *et al.* (2014) applied to each individual tree:

$$AGB = e^{\left[-1.803-(0.976*E)+0.976\ln(WSG)+2.673\ln(dbh)-0.0299\ln(dbh)^2\right]} \quad [2]$$

where, E is the bioclimatic stress factor (dimensionless), WSG is the density of the wood, (g/cm^3), and dbh (cm) is the diameter at breast height. WSG was taken from Zanne *et al.* (2009). It was assumed that above-ground carbon (C; MgC ha^{-1}) corresponds to 50% of the biomass (Brown & Lugo, 1982; Houghton *et al.*, 1997).

The structural conversion factor (SCF) was calculated to determine “the mean amount of biomass supported per unit of forest basal area” (Mg m^{-2}) as proposed by Malhi *et al.* (2006), and that has been more recently used by other authors (Targhetta, 2015).

Cluster analysis was developed to identify (with a graphic method) the floristic similarities and differences between the plots or groups of plots evaluated; for this purpose, we used the MVSP v3.13I © software (Kovach Computer Services, 2004), by means of Ward’s method, which builds the clusters by decreasing the internal variability in each one of them. This method only works with the Quadratic Euclidean Distance and takes into account, not only the presence-absence of the species, but also their quantitative values; for that aim the EII was used.

Table 1. Botany families and species richness in logged native forests from Venezuelan Guayana.

Family	Species
Fabaceae	48
Bignoniaceae	12
Apocynaceae	11
Arecaceae	10
Chrysobalanaceae	7
Lecythidaceae	7
Rubiaceae	7
Sapotaceae	7
Burseraceae	6
Euphorbiaceae	6
Others (56)	128

SPSS v15.0.1 software was used to perform a one-way ANOVA for the age of harvest and each variable separately (R, H´, α, BA, C). In each case, a comparison was made between the harvested plots (3, 9, 12, 15 and 18 years) and the old-growth forests (year 0). Data normality tests were performed. In the cases in which this condition was not fulfilled, we continued with the ANOVA because this analysis was robust to the violation of this assumption, that is, it did not alter the Type I Error (Montgomery, 1991; García-Berthou *et al.*, 2009). Homoscedasticity was also assessed using the Levene test; if this condition was met, the *post hoc* analysis was completed with the least significant difference (LSD) test; otherwise, a transformation of the data was made and, if the lack of homoscedasticity persisted, the interpretation was made using the Games-Howell test (SPSS, 2006).

Table 2. Average of the enlarged importance index (EII), for the most important species, in each evaluated forest.

Species	LP[a]	Years from logging					
		0	3	9	12	15	18
Alexa imperatricis (R.H. Schomb.) Baill.	Sup	45.3	55.0	40.5	41.4	55.4	0.2
Pentaclethra macroloba (Willd.) Kuntze	Sup	40.4	20.3	45.3	51.8	52.0	9.0
Eschweilera decolorans Sandwith	Sup	34.4	40.4	44.1	37.7	44.7	8.5
Eschweilera parviflora (Aubl.) Miers	Sup	21.8	30.1	22.2	17.0	26.8	26.1
Inga alba (Sw.) Willd.	Sup	5.6	6.5	1.2	7.4	3.3	14.6
Cecropia angulata I.W. Bailey	Sup	0.0	0.3	0.4	1.5	1.4	6.2
Rinorea riana Kuntze	Und	6.5	3.5	6.2	8.6	8.9	5.1
Bactris maraja Mart.	Und	4.5	2.6	4.4	3.5	3.9	3.4
Calathea sp.	Und	0.6	14.4	0.0	4.5	0.5	0.7
Cheiloclinium hippocrateoides (Peyr.) A.C.Sm.	Cli	5.9	4.6	5.7	4.9	4.7	5.4
Bauhinia scala-simiae Sandwith	Cli	3.4	7.6	5.6	5.9	3.1	4.4
Machaerium macrophyllum Benth.	Cli	3.6	3.9	3.2	3.7	2.8	2.2

[a] LP: layer position. Sup: superior layer, big trees and palms. Und: exclusive for understory. Cli: climbers.

Assessment of the commercial value of the species

This is a point relatively subjective, since it depends on the color, density, texture and, mainly, on the timber market. Nor is it a permanent value; a species may have marginal value at one moment and, years later, it may be low or medium. A commercial forestry species has wood anatomical characteristics that allow its use as a technological or industrial material and is demanded in the market. Depending on the price it reaches, it is considered high, medium and low commercial value. Species that can be worked, but are not in demand in the market, are classified as "potential"; those that cannot be worked are considered as "marginal". Table S1 [suppl] shows the main harvested species and the valuation established in three Forest Management Plans (Intecmaca, 1989; Aserradero Hermanos Hernández, 1992; Comafor, 1995), in the central area of the Imataca Forest Reserve; an average value was obtained and the following classes were assigned, according to Lozada (2008):

- Class I (high value). Species with very good technological characteristics and high market demand.
- Class II (medium value). Suitable technological species and medium to low sale price when large volumes are available.
- Class III (low value). Suitable technological species and low market demand.
- "Potential" and "marginal" are all others, and do not appear in Table S1.

The recovery of species with commercial value is something important for sustainability. In this research it was considered by means of the BA of all the commercial species (BA_comm; m^2 ha^{-1}); this variable was also analyzed using an ANOVA and *post hoc* procedure as indicated above.

Assessment of the presence of lianas

To consider this component, a comparison was made with data from not logged liana forests (lf_1, lf_2, lf_3), previously described by Lozada *et al.* (2016b). The analysis was made with the relative abundance of lianas in the understory (Lianas_%Au). This variable did not meet the homoscedasticity criterion (Levene's value = 0.045); therefore, a transformation using the square root (SqRt_Lianas_%Au) was carried out. In addition, a possible relationship between the presence of lianas and the intensity of logging was evaluated, which is expressed by the number of cut stumps found in each plot.

Results

Floristic composition and diversity

In the evaluated plots, a total of 249 species were found, of which 171 were trees and palms that reach the upper strata (they had more than 10 cm dbh), 45 were climbers and 33 were exclusive to understory. These species belong to 66 families and the three most important are Fabaceae, Bignoniaceae and Apocynaceae (Table 1). If the 12 most important species are considered, the analyzed forests have quite similar floristic composition (Table 2), and are dominated by

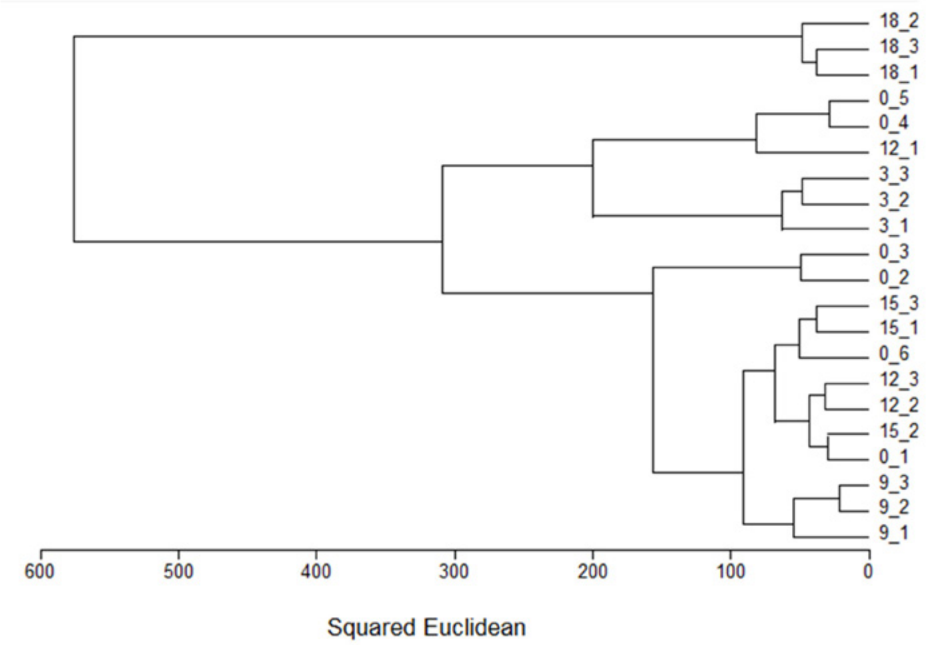

Figure 2. Cluster analysis using the EII of all recorded species for this study in Venezuelan Guayana forest plots, logged from 3, 9, 12, 15 and 18 years ago and control forests (0).

P. macroloba, A. imperatricis, E. decolorans and *E. parviflora*. *Inga alba* and *Cecropia angulata* are pioneers, which are occasionally present due to the occurrence of gaps.

Logged forests had high levels of floristic similarity (Chao-Sørensen index) with respect to control forests (Table 3); the general average was 82%. However, the lowest similarity was observed among the 18-year-old harvested forests and the other types of forests, with an average value of 69%.

In the cluster analysis using the importance value (EII) of all species, the control plots are clustered together the 3, 9, 12 and 15 years logged plots, whereas the 18-year-old plots (18_1, 18_2 and 18_3) constitute a separate cluster (Fig. 2).

The average richness (R) in control plots was 72 species and in most of the logged plots it reached similar values: 69 spp for 3 years, 76 spp for 9 years, 72 spp for 12 and 15 years. In 18-year-old plots the R increased to 90 species. The assessment by H' and α confirmed the same trend (Fig. 3). The analysis of variance and *post hoc* analysis of the three variables indicates that there were no significant differences between the control and most logged plots; but these differences only occurred with the 18-year-old plots (Table 4).

Basal area and carbon stock

All the logged forests showed lower values of BA than the control plots (Fig. 4); the BA and C values met the homoscedasticity criterion, and the different logged plots did not have statistically significant differences with old-growth forests (Table 4).

There was a high variability in the presence of commercial value species (Fig. 4), and the variable used did not meet the homoscedasticity criteria. In all the logged plots there were fewer commercial species; but the significant differences only occurred with the 9- and 18-year-old plots (Table 4), which had the lowest values of commercial species BA.

Presence of lianas

All harvested forests contained different amounts of lianas in their structure. But the 18-year-old forests had higher abundance than the other plots and according to the post hoc analysis were similar to liana forests (Table 4).

There was not relationship between the presence of lianas and the intensity of logging (F(1,22)=0.084; *P*=0.755; R^2=0.004). Lianas were very abundant both in unlogged and logged forests. This was evident when the liana forests and the control plots were compared with the other forests evaluated; *e.g.,* the control plots had an average of 11.6% liana presence in the understory and the 15-year-old forests had 9%, the latter having an average of 2.7 cut stumps per hectare (Table 5).

It seems obvious that the strong impact, where trunks were directly skidded onto the roads (without using

Table 3. Floristic similarity (Chao-Sørensen index) between all the plots.

	0_2	**0_3**	**0_4**	**0_5**	**0_6**	**3_1**	**3_2**	**3_3**	**9_1**	**9_2**	**9_3**	**12_1**	**12_2**	**12_3**	**15_1**	**15_2**	**15_3**	**18_1**	**18_2**	**18_3**	**Ave**	**SD**
0_1	0.89	0.87	0.83	0.85	0.84	0.83	0.86	0.83	0.85	0.91	0.91	0.81	0.89	0.91	0.87	0.90	0.87	0.54	0.64	0.62	0.83	0.10
0_2		0.91	0.80	0.82	0.83	0.78	0.76	0.78	0.79	0.86	0.85	0.76	0.83	0.87	0.84	0.86	0.82	0.63	0.67	0.64	0.79	0.08
0_3			0.67	0.70	0.78	0.71	0.70	0.68	0.78	0.84	0.81	0.75	0.81	0.84	0.82	0.85	0.79	0.49	0.58	0.52	0.73	0.11
0_4			.	0.92	0.91	0.79	0.76	0.83	0.76	0.83	0.86	0.85	0.83	0.87	0.81	0.84	0.86	0.71	0.74	0.67	0.81	0.07
0_5					0.93	0.86	0.75	0.83	0.78	0.81	0.82	0.87	0.79	0.87	0.81	0.82	0.84	0.60	0.69	0.67	0.80	0.08
0_6						0.85	0.80	0.86	0.84	0.84	0.86	0.86	0.84	0.87	0.83	0.84	0.85	0.64	0.71	0.67	0.81	0.08
3_1							0.81	0.89	0.82	0.81	0.84	0.87	0.84	0.88	0.84	0.79	0.83	0.53	0.67	0.63	0.79	0.11
3_2								0.89	0.89	0.91	0.87	0.78	0.86	0.87	0.88	0.82	0.87	0.58	0.66	0.63	0.81	0.11
3_3									0.85	0.88	0.85	0.91	0.84	0.91	0.89	0.80	0.87	0.67	0.76	0.72	0.83	0.08
9_1										0.90	0.87	0.79	0.84	0.89	0.90	0.89	0.89	0.70	0.71	0.72	0.83	0.08
9_2											0.93	0.80	0.90	0.91	0.91	0.91	0.90	0.70	0.75	0.74	0.85	0.09
9_3												0.83	0.90	0.91	0.91	0.93	0.93	0.71	0.80	0.79	0.86	0.08
12_1													0.80	0.92	0.81	0.84	0.83	0.59	0.76	0.72	0.78	0.10
12_2														0.92	0.87	0.90	0.91	0.59	0.71	0.68	0.80	0.13
12_3															0.92	0.92	0.93	0.61	0.74	0.72	0.81	0.14
15_1																0.92	0.92	0.66	0.78	0.75	0.81	0.11
15_2																	0.94	0.62	0.76	0.77	0.77	0.13
15_3																		0.62	0.77	0.77	0.72	0.09
18_1																			0.88	0.89	0.89	0.01
18_2																				0.94	0.94	-
Ave	0.89	0.89	0.76	0.82	0.86	0.80	0.78	0.82	0.82	0.86	0.86	0.82	0.84	0.89	0.86	0.86	0.87	0.62	0.72	0.71	0.71	-
SD	-	0.03	0.08	0.09	0.06	0.06	0.05	0.07	0.04	0.04	0.04	0.05	0.03	0.02	0.04	0.05	0.04	0.06	0.07	0.09	-	-

Table 4. Analysis of biodiversity indices, basal area, carbon stock, basal area of commercial species and presence of lianas, in logged forests from Venezuelan Guayana shield. Significant differences are indicated in bold.

Variables	Homoscedasticity (Levene's test)	Test	3	9	12	15	18	
		Post hoc analysis (*p*) respect to control plots						
Species richness (R)	0.323	LSD	0.542	0.117	0.684	0.838	**0.000**	
Shannon-Wiener index (H´)	0.449	LSD	0.396	0.181	0.677	0.383	**0.000**	
Fisher's alpha (α)	0.670	LSD	0.840	0.551	0.922	0.293	**0.000**	
Basal area (BA)	1.542	LSD	0.129	0.336	0.451	0.998	0.093	
Carbon stock (C)	1.466	LSD	0.171	0.868	0.663	0.895	0.634	
Commercial species basal area (BA_comm)	0.036	Games-Howell	0.104	**0.035**	0.925	0.156	**0.029**	
		Post hoc analysis (*p*) respect to liana forests						
Square root of liana relative abundance (SqRt_Lianas_%Au)	0.282	LSD	**0.000**	**0.000**	**0.001**	**0.000**	**0.000**	0.728

log-landing yards), broke the lower strata, removed the soil cover (Fig. 5) and favored the establishment of lianas.

Discussion

The results of this work are important for the definition of environmental viability options in logging operations, in what refers to the maintenance of the floristic composition, biodiversity, carbon reserves and avoiding the infestation of lianas. This is very relevant because in South America there are 100 million hectares committed to forestry production (FAO, 2021).

It was found that the most important family was Fabaceae; it has been reported as the taxonomic group with the

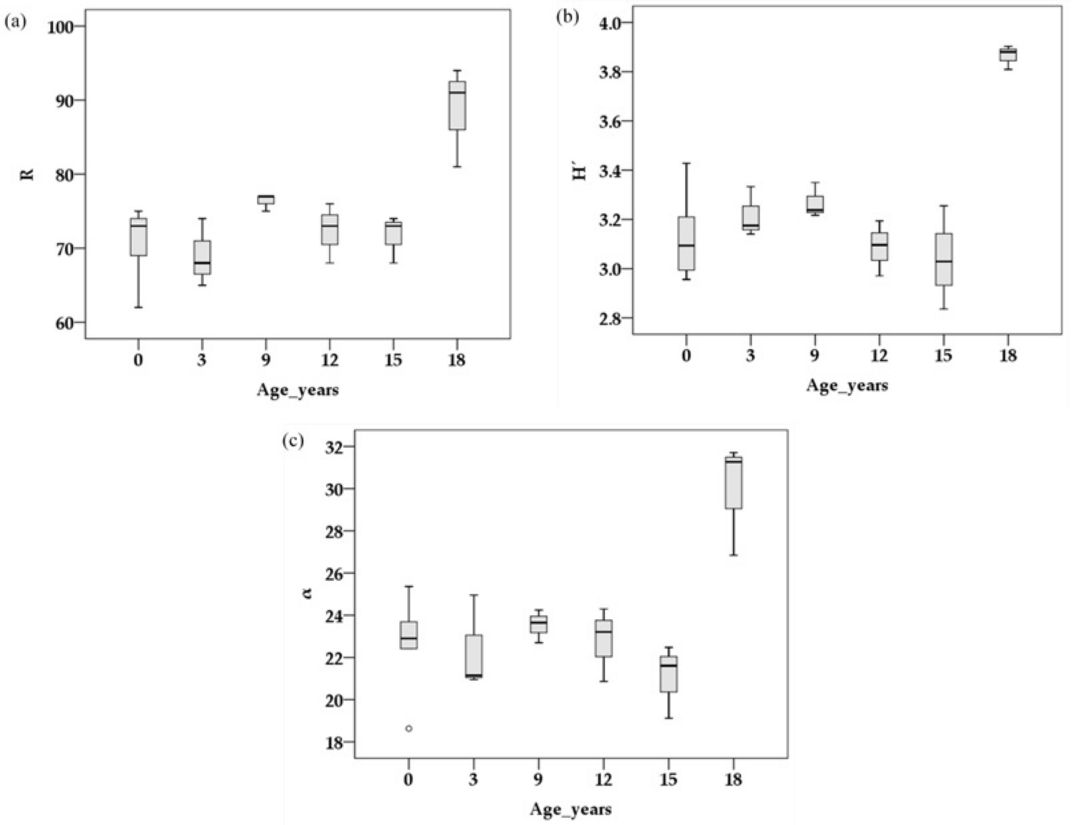

Figure 3. Values of floristic diversity in forests with different temporal distance since logging, in Imataca Reserve, from Venezuelan Guayana: a) species richness R, b) Shannon-Weaner index H', and c) Fisher's α.

largest number of species in the world (Mabberley, 1997) and particularly in the neotropics (Gentry, 1992). Guevara (2001) points out that they have competitive advantages, due to their ability to sprout and association with mycorrhizae; this means that they are very well adapted to develop in oligotrophic soils such as those of the IFR (Lozada *et al.*, 2014).

Results of the floristic composition showed that logged forests in Venezuelan Guayana were very similar to old-growth forests; selective timber harvesting has not meant a considerable loss of floristic diversity. *P. macroloba* is the most important species in the entire central sector of Imataca; *A. imperatricis, E. decolorans* and *E. parviflora* are dominant in the top and hillside forests of that region (Lozada *et al.*, 2011). Therefore, most of recently logged sites (3-15 years-old) did not show notable changes for the presence of species considered to be late successional; 18-year-old forests had a slightly different behavior that is discussed later. These results are similar to those found by Ter Steege *et al.* (2002) in Guyana, where the low rate of logging had not generated a remarkable modification in the floristic composition, and there was no significant ingress of pioneer species.

In the 18-year-old plots there was a high importance of pioneer species such as *Inga alba* (EII: 14.6) and *Cecropia angulata* (EEI: 6.2), which is considered a symptom of a more intense disturbance (de Avila *et al.*, 2015; Rivett *et al.*, 2016). These plots had the lowest similarity concerning to the others and formed a separate cluster. The rest of the clusters respond more to ecological patterns of distribution of the species, than to the effect of logging. These plots also showed the highest diversity, which is possibly linked to the Intermediate Disturbance Hypothesis (Connell, 1978; Sheil & Burslem, 2013), which proposes an increase in diversity when certain levels of intervention occur. It was pointed out in the previous paragraphs that, in general, logging in Imataca is considered to be of low intensity and does not generate a significant change in the floristic composition. However, in the 18-year-old forest, disorderly logging or more intense intervention could allow larger gaps and greater entry of pioneers which compete with the development of commercial species.

In other old-growth forests of the Guiana Shield it has been reported that the frequency of large gaps is very low, pioneers have dispersal limitations and soil seed banks are scarce (ter Steege *et al.*, 2002). A low forest harvest is supposed to mimic the functioning of the ecosystem; *e.g.*, reduced impact harvesting in Guyana has resulted in a very low or null regeneration of *Cecropia* spp. since successful regeneration of this genus requires large gaps, greater than 100 m^2 (Rivett *et al.*, 2016). In forests of Caparo (Venezuela), it was also found that with low and medium logging levels there were no significant differences in diversity,

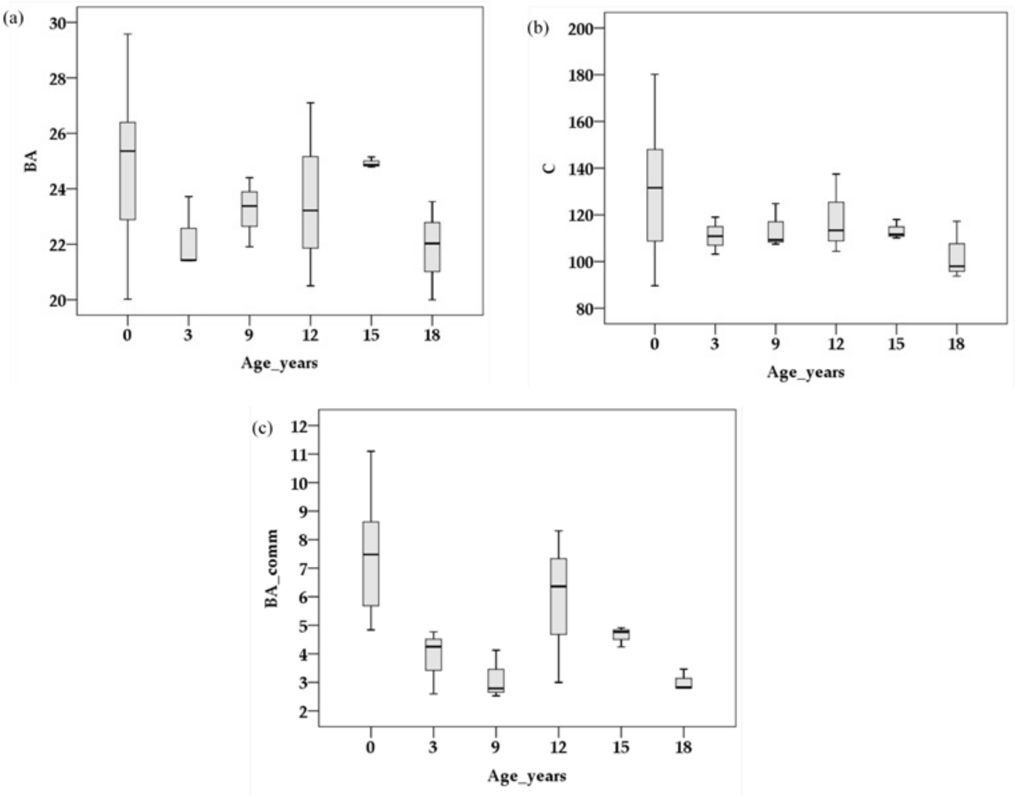

Figure 4. Biomass values in forests with different temporal distance since logging, in Imataca Reserve: a) basal area (m^2 ha^{-1}), b) above-ground carbon (Mg C ha^{-1}), and c) basal area of all commercial species (m^2 ha^{-1}).

Table 5. Analysis of lianas presence and logging intensity, in the evaluated forests of the Venezuelan Guayana shield.

Years from logging	Relative abundance of lianas in the understory (Lianas_%Au)		Number of cut sumps	
	Average	SD	Average	SD
Liana forests	21.9	7.1	0.0	0.0
0	11.6	5.2	0.0	0.0
3	12.7	4.6	3.3	1.3
9	12.7	3.3	2.7	1.8
12	12.9	7.4	2.3	0.5
15	9.0	5.2	2.7	0.5
18	20.9	6.7	5.3	1.0

whereas with high impact logging there was a significant loss in species richness at 2 years, but at 5 years the forest was recovered (Lozada *et al.*, 2016a). Other studies also showed a suitable restoration of floristic richness and diversity at levels similar to the pre-harvest condition in different tropical forests. Situations like these have been reported in Guyana (Van Andel, 2001), Central Africa (Gourlet-Fleury *et al.*, 2013), Congo Basin (Decocq *et al.*, 2014), Tanzania (Rutten *et al.*, 2015), China (Ding *et al.*, 2017), Mexico (Tadeo-Noble *et al.*, 2019) and Borneo (Berry *et al.*, 2008; Mahayani *et al.*, 2020).

The average values of old-growth forests were 24.9 m^2 ha^{-1} for the BA and 10.4 Mg m^{-2} for the SCF. According to Malhi *et al.* (2006), this SFC value is within the range of 9-12 Mg m^{-2} described for the Amazonian forests, where the presence of species with high wood density is frequent, but BA was under the reported levels of 30-31 m^2 ha^{-1}. This reduced BA could be attributed to the negative effect that toxic levels of aluminum have on plants, as was indicated for other sites of the Guayana Shield (Fölster & Dezzeo, 1994), in the Amazon forests (Quesada *et al.*, 2012) and the Imataca Forest Reserve (Lozada *et al.*, 2014). The lower values of BA observed in logged forests concerning control plots could be related to the extraction of higher stems and the ecosystem must take a few years to recover the initial biomass.

The above-ground carbon data obtained in this research were within the reported range (75-200 MgC ha^{-1}) in tropical old-growth forests of South America (Malhi *et al.*, 2006; Chave *et al.*, 2008; Otani *et al.*, 2018). Other reports also point to a carbon recovery in logged tropical forests. Blanc *et al.* (2009) indicated that, in French Guiana, it would take 45 years to recover the same amount of carbon as an old-growth forest. Peña *et al.* (2011) found in Colombia a turnover rate of the forest between 30 and 35 years according to the intensity of logging. In Papua New Guinea it was observed that after 15 years, forests with selective logging had recovered 45% of the carbon stored in the above-ground biomass; this means 62 MgC ha^{-1}, compared to 137 MgC ha^{-1} that existed in old-growth forests (Fox *et al.*, 2011). In central Amazonia, above-ground biomass retrieved 14 years after logging (Otani *et al.*, 2018).

On the other hand, in the Imataca Forest Reserve, Vilanova *et al.* (2010) estimated that it took 150 years for the forest to recover the original biomass. Some of their plots were probably located in sites where disorderly logging operations were carried out, generating heavily disturbed areas (50% loss of biomass) with very low biomass in that residual forest.

All logged forests did not have significant differences in terms of BA and carbon stock with respect to the old-growth forest (Table 4). We consider that these operations did not have an exceptionally high impact because the logging intensity was 3.3 trees ha^{-1}, according to cut stumps found in all logged plots (Table 5). It matches with harvesting ranges reported in the Amazon (Verissimo *et al.*, 1992; Jackson *et al.*, 2002), with the maximum

Figure 5. Disturbance in the lower strata as a result of skidding operations in logged forests from Venezuelan Guayana.

level of harvesting recommended by Sist *et al.* (2003) to apply reduced impact logging (8-10 trees ha^{-1}), and with the moderate intensities of the careful CELOS system developed in Suriname (Roopsind *et al.*, 2018; 8 trees ha^{-1}). In any case, the small losses that may occur can be recovered in the short-term through the mechanisms of forest succession.

Considering the presence of commercial species, the natural variability appears to be more important than the effect of logging and age of recovery since there was not a significant bias related to temporal distance to disturbance. These are not permanent plots and differences may occur due to species distribution. Despite the 9- and 18-year-old forests had less in the BA of commercial species (Table 4, Fig. 4), they already had a biomass of commercial species that must grow and guarantee a future harvest. For the other plots, it was estimated that during the first exploitation cycle, low biomass levels had been extracted without a substantial change in the floristic composition. Therefore, there was no evidence that indicates the recovery of the BA of commercial species, as the age after exploitation increases. We interpret that the commercial BA in the logged plots correspond to small individuals and seed-bearing trees. Commercial species are scarce but they are no considered to be at extinction levels, and the gaps created by logging activities could be utilized for enrichment with these species.

The studies by Serrano (2002) and Lozada *et al.* (2003) report a diameter growth between 0.55 and 0.35 cm year^{-1} for commercial species; this means that reaching a minimum cutting diameter of 50 cm, would require between 91 and 142 years. The management plans establish cycles close to 30 years and if this scheme is maintained, after two or three cycles, there will occur a decrease in commercial species and it will be necessary to take advantage of species that were not harvested in the first cycle (Zimmerman & Kornos, 2012; da Cunha Castro *et al.*, 2021). In any case, it will be important to continue measurements in logged plots to determine with better precision the growth rates and the dynamic of these forests.

On the other hand, liana forests have been reported in Imataca as evidence of high disturbance and degradation of the ecosystem (Hernández, 1997); it has been pointed out that these elements can stop the successional process for many years (Schnitzer & Carson, 2010). The possible origin of liana forests are hurricane winds; this ecosystem is characterized by a relative abundance greater than 20% of this form of life in the understory (Lozada *et al.*, 2016b), and 18-year-old forests showed similar to this condition. However, there were no records of hurricane winds in 18-year-old forests, and the harvesting of trees (5.3 trees ha^{-1}, Table 5) is within reasonable limits, as mentioned before. This shows that an unplanned forest logging could generate damages that can exceed the level of resilience of the ecosystem. Lianas can increase drought stress, tree mortality, and reduce the growth of the above-ground biomass of the ecosystem (di Porcia *et al.*, 2019; Meunier *et al.*, 2021).

Conclusions

Results of this work demonstrated that harvested forests from Venezuelan Guayana maintain a floristic composition, levels of diversity and above-ground carbon stock, similar to old-growth forests when moderate exploitation is applied. However, there is no evidence that commercial species are taking advantage of the spaces created by logging; they are not at extinction levels, but there is no certainty that these species exist in the same quantities in the second and subsequent cycles. Similarly, there is a high probability that more intensive or unplanned logging can lead to a process of degradation to a liana forest, and that condition can persist for many years.

Therefore, a sustainable management would be possible through intensive silvicultural systems that promote the best bioclimatic and edaphic conditions for high value commercial species and fast growth species. Cutting cycles should be extended and reduced impact logging techniques should be applied.

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Authors' contributions

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Formal analysis: J. R. Lozada, Y. A. Carrero, M. Durán.
Investigation: J. R. Lozada.
Methodology: J. R. Lozada.
Supervision: J. R. Lozada, P. Soriano.
Writing – original draft: J. R. Lozada, Y. A. Carrero, M. Durán.

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