

ORIGINAL RESEARCH ARTICLE

Forest dynamics in different scenarios: Selective logging in the middle Magdalena (Colombia)

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ABSTRACT

Selective logging is a frequently used forest use activity that has been shown to have less impact on biodiversity than clear-cutting. However, both the magnitude and direction of ecological change after logging depend on its intensity and subsequent forest dynamics. Therefore, it is important to conduct studies to understand the functioning of different ecosystems after selective logging. This study analyzed forest dynamics in the El Paujil reserve (Middle Magdalena, Colombia) in terms of demography, regeneration, clear-cutting dynamics, biomass accumulation and floristic composition by comparing two one-hectare plots in a fragment of the little disturbed (primary) forest and two one-hectare plots in a fragment of the forest that was selectively logged in the past. As expected, forest structure and biomass accumulation are altered by selective logging, but it did not have a significant impact on the other aspects mentioned, since it seems that the steep slopes of the area cause high mortality and promote the formation of clearings in both logged and lightly disturbed forests.

Keywords: Aerial Biomass; Primary Forest; Floristic Composition; Demography; Serranía de las Quinchas

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1. Introduction

Selective logging in tropical forests is a growing activity that has been shown to produce less soil and canopy damage than generalized deforestation. It is also the forest use activity with the least impact on diversity, as selectively logged forests have high mature forest species richness^[1,2]. However, both the magnitude and direction of ecological change after logging depend strongly on its intensity and the subsequent spatial and temporal dynamics of the affected forest^[3].

Among the most important consequences of selective logging in forests is the loss of biomass, not only during the logging period, but also in the time after the activity. In studies conducted in the Brazilian Amazon, Figueira *et al.*^[4] found that during the four years following logging activities the forest lost biomass. Mortality was higher than predicted for this forest type, possibly due to the effects of mechanical damage, given the increased wind exposure of trees adjacent to logging sites^[4]. However, long-term studies such as that of Gourlet-Fleury *et al.*^[5] have found that selective logging favors increases in biomass, growth and survival of trees in all diameter classes below 70 cm, as well as recruitment of fast-growing tree species (pioneers), which increases rates of aboveground biomass gain in the forest. Another important effect of selective logging on forests is the formation of clearings, which allow more light to enter the understory, benefiting lianas

and pioneer species, as these are plants that mostly grow rapidly when there is high light availability^[6]. Subsequent dynamics are variable, pioneer trees can reach canopy height and become established or die from lack of light when the canopy forms above them again^[6]. Lianas, if they manage to grow into the canopy and establish on mature forest trees, may even topple them with their weight, encouraging the formation of new clearings^[7]. Thus, Schnitzer & Bongers^[7] show that there is a negative relationship between the density of lianas and the density of mature forest trees, while the density of lianas is positively related to the density of pioneer species.

In neotropical countries such as Colombia, with its diverse climate and relief, it is even more difficult to predict the direction of recovery of selectively logged forests. Despite having 52.6% (60 million hectares) of the national territory occupied by forests^[8], Colombia presents high deforestation rates, with losses of 5.4 million hectares of forest in the last 20 years^[9]. The Magdalena basin is the most deforested in South America and the tenth most deforested in the world^[9], but it presents regions such as the Serranía de las Quinchas, in the middle Magdalena, where some areas of continuous forest are preserved. For example, the El Paujil bird reserve includes 3419 hectares protected as a private civil society reserve^[10] and has at least four forest types identified by Aldana *et al.*^[11]: forest with a moderate level of selective logging (logged forest), floodplain forest, young secondary forest (secondary forest) and forest with subsistence logging (primary forest).

The objective of this study is to analyze the effect of selective logging on the dynamics of the tree community in the forest of the El Paujil reserve in the middle Magdalena region of Colombia. These dynamics are evaluated in terms of biomass accumulation capacity, clear-cutting dynamics, regeneration, demography and floristic composition. Given the effects of increased light availability and exposure to wind after logging, it is expected that logged forests will have a higher recruitment and mortality rate, a negative rate of population change and a lower capacity to accumulate biomass. Likewise, due to the direct effects of logging, it is expected to

find a lower density of large individuals and a lower canopy cover, which will also allow for a higher density of seedlings and juveniles in the logged forest. In addition, given that selective logging has not been considered to have a great impact on forest diversity, we expect to find similarities in plant species composition and turnover between the two forest types, but a greater abundance of pioneer plants in the logged forest.

2. Materials and methods

2.1 Study area

This study was conducted in the El Paujil bird reserve, in the departments of Santander and Boyacá (74°11'W, 5°56'N) with a geographic altitude ranging from 150 m to 1,200 m and an average annual temperature of 27.8 °C^[11]. There are two rainy periods during the year, the first one between April and May and the last one between September and November. Relative humidity ranges between 85% and 89%^[11,12].

The reserve was created in November 2003 to conserve the blue-billed curassow (*Crax alberti*)^[10] and its tropical rainforest habitat. Prior to the establishment of the reserve, the reforestation company Bosques del Futuro practiced selective logging for timber for five years in part of the forest. Silva-Herrera^[13] reported that the reforestation company planned to harvest 50 m³ of standing timber from the forest per hectare per year, distributed as follows: 15 m³ of fine woods and 35 m³ of ordinary woods. Accordingly, the reforestation company harvested approximately five trees per hectare, which could be verified by the researchers at the time of establishing the plots in 2006. This forest is located in the department of Boyacá, in the village of Puerto Pinzón in the municipality of Puerto Boyacá. The primary forest was exploited by the owners of the property for subsistence, which corresponds to at least one tree per hectare per year, as could be evidenced by the researchers during the establishment of the plots. This forest is located in the department of Santander, in the municipality of Bolivar. The distance between the two forest types (the sampling sites) is approximately 8 km. The forests sampled present a topography with slopes of

up to 40°, and a geographic altitude from 194 masl to 471 masl.

2.2 Data collection

For each forest type, two one-hectare plots were sampled, established in 2006 by Aldana *et al.*^[11] They measured diameter at breast height (DAP) for all individuals with DAP greater than 5 cm and identified them to species (or morphospecies if this was not possible). Decision to include individuals from 5 cm DAP but not from 10 cm as it is usually done, it is due to the presence of a large number of tree species that do not reach this size (**Annex 1**). Therefore would be left out of the sampling, which would lead to an underestimation of the diversity and accumulated biomass of the site^[14]. In 2013, they were censused again, measuring DAP for individuals sampled in 2006, reporting dead or missing individuals and noting the causes of mortality where possible, following the protocol of Phillips *et al.*^[15]. All individuals that entered the size category greater than 5 cm DAP were included as new recruits. Wood samples were collected to determine their density, using a borer and taking samples of at least five individuals of the most abundant species of the two forest types.

For regeneration estimates, the number of seedlings and juveniles present in the two forest types was compared by taking data from 100 plots of 2 × 2 m for seedlings and 100 plots of 5 × 5 m for juveniles^[16]. This sampling was carried out systematically, within the 1 ha plots. To quantify the entry of light into the forest understory, 50 subplots of 20 × 20 m per forest type, located within the 1 ha plots, were used. Two photos of the canopy were taken at the central point of each of the subplots with the camera parallel to the ground at 1 m height. A fisheye lens was used and the camera was programmed to take the photos in black and white, with a constant 22 cm aperture and variable speed.

2.3 Data analysis

The information obtained in 2006 was compared with that of 2013 to establish the annual rates of growth, mortality and recruitment of the tree community for each plot using the formulas presented by Sherman *et al.*^[17]. Then, in order to statis-

tically compare these behaviors and make them comparable with the information obtained on clear-cutting and regeneration dynamics, comparisons were made at a scale of 20 × 20 m, with 50 subplots for each forest type. Using the statistical program R version 3.0.1^[18] one-tailed *t*-tests were performed for two samples, with Welch's approximation when variances were not similar.

For the analysis of clearings, photos taken at the center point of each of the 20 × 20 m subplots were used, choosing one per subplot to determine the gray value per pixel (where 0 means black and 255 means white) with the Image J program^[19]. This value represents the light intensity in the understory and is compared with a one-tailed *t*-test for two samples between the two forest types using the statistical program R version 3.0.1, Vegan library^[18]. Additionally, as indicators of the regeneration process of the forests after the disturbance, the number of seedlings and juveniles present in the two forest types were compared with one-tailed two-sample *t*-tests with Welch's approximation when variances were not similar in the statistical program R version 3.0.1^[18].

The density of wood samples obtained in the field was determined as the specific gravity (dry weight/green volume) following the wood density protocol of Chavé^[20]. For species for which no wood sample was taken, the wood density data of Casas *et al.* (unpublished data) and Zanne *et al.*^[21] were used. Subsequently, the height of each tree was estimated using the allometric equation derived from the Weibull function adapted for South America presented by Feldpausch *et al.*^[22]. The cumulative biomass of each tree was calculated using equation I.3 of Alvarez *et al.*^[23] for tropical rainforest in Colombia, which takes into account that diameter at breast height, tree height and wood density. According to Alvarez *et al.*^[23], it is the best equation for estimating carbon in Colombia, given the low uncertainty and variability with respect to the other equations generated by them. With the initial and final biomass values, the annual biomass change in Mg ha⁻¹ year⁻¹ was determined.

Finally, the four most important species in each plot were identified with the importance value index determined by the density, frequency and rel-

ative basal area of each species. We looked for whether these species are exploited for their timber and timber quality^[24] to relate any possible changes in the dominant species with logging. The conservation status of these species in Colombia was also sought^[25] to investigate the vulnerability of the timber trees present in this forest. Additionally, a comparison of the species present and their abundance in the plots was made with a cluster represented in a dendrogram. Since pioneer species play an important role as indicators of disturbances (logging or tree fall), the individuals sampled were categorized into three groups depending on their wood density, as this is one of the most important functional traits in the determination of primary forest species and pioneer species^[6]. Tree species with low wood density were considered those with values between 0.10 g/cm³ and 0.39 g/cm³, medium with wood between 0.40 g/cm³ and 0.59 g/cm³ and high those with wood between 0.70 g/cm³ and 0.90 g/cm³. Subsequently, the proportion of trees in each category was compared between forest types with a G-test in R version 3.0.1^[18].

3. Results

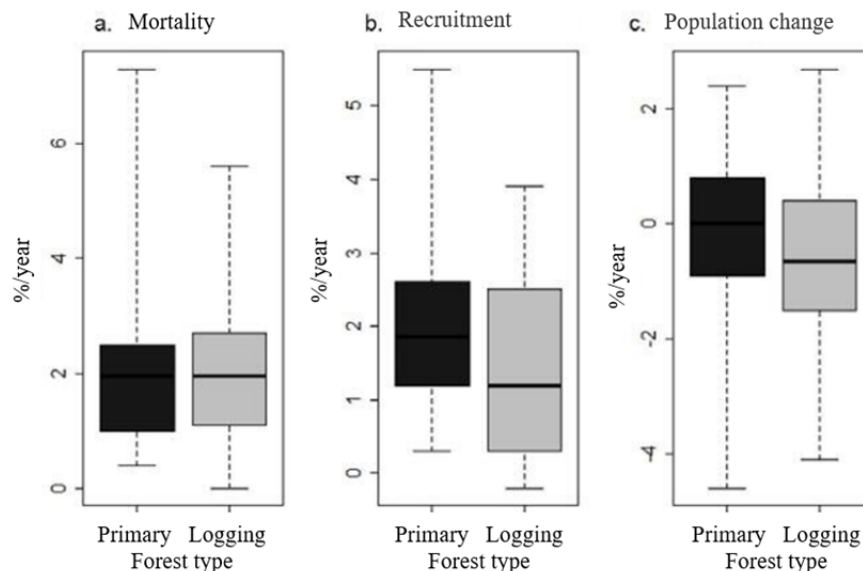


Figure 1. Comparison of annual demographic rates in 50 subplots of 20 × 20 m for primary forest and 50 subplots of 20 × 20 m for logged forest in the forests of the Paujil reserve (Colombia). (a) mortality, (b) recruitment and (c) population change. Mortality showed no significant differences, recruitment was higher for primary forest $*(t = 2.91, gl = 98, p < 0.01)$ and population change was zero for primary forest and negative for logged forest, with significant differences bn $*(t = 2.16, gl = 98, p = 0.02)$.

3.2 Analysis of clearings and regeneration.

The amount of light reaching the understory in

3.1 Demographics

The logged and primary forests in the El Paujil reserve did not show significant differences in the annual mortality rate ($t = 0.13, gl = 98, p = 0.45$; **Figure 1a**), despite the variation found when analyzing by 20 × 20 m subplots. It can be seen that when comparing between 1 ha plots, the average is equal for the two types of forest, with an average annual mortality rate equal to 2% (**Table 1**). Recruitment was higher for the primary forest ($t = 2.91, gl = 98, p < 0.01$; **Figure 1b**), and, as in the case of mortality at the 1 ha scale, the result is corroborated (**Table 1**). The population change was zero for primary forest and negative for clear-cutting. At the 20 × 20 m scale, significant differences were found between forest types ($t = 2.16, gl = 98, p = 0.02$; **Figure 1c**).

Table 1. Annual mortality rate (m), recruitment (r) and population change (λ) in 2 one-hectare plots established in primary forests (P3 and P4) and 2 one-hectare plots in logged forests (P1 and P5) in the El Paujil reserve (Colombia)

Forest type	Plot	m	r	λ
Primary	P3	2.0	1.8	-0.2
	P4	2.0	2.2	0.2
	P1	1.7	0.6	-1.1
Logging	P5	2.3	2.2	-0.1

the forests of the El Paujil reserve is similar in both forest types ($t = 0.32, gl = 98, p = 0.63$; **Figure 2a**). Likewise, both the amount of seedlings and juve-

niles do not show significant differences between forest types (Welch's $t = -2.18$, $gl = 197$, $p = 0.98$;

welch's $t = -4.09$, $gl = 155$, $p = 1$, respectively; **Figures 2b and 2c**).

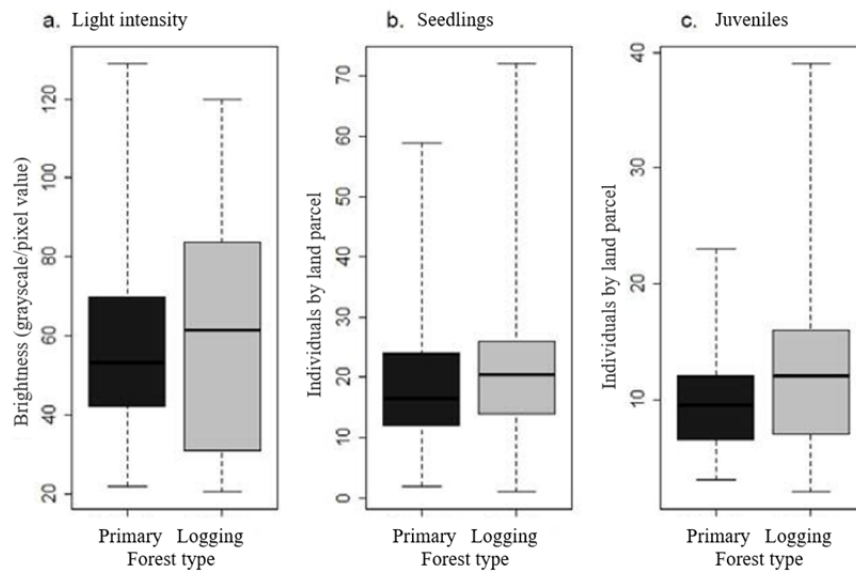


Figure 2. Analysis of the amount of light in the understory and plant density regenerating 50 subplots of 20×20 m for primary forests and 50 subplots of 20×20 m for logged forests in the El Paujil reserve (Colombia). **(a)** Light intensity. **(b)** Seedlings. **(c)** Juveniles.

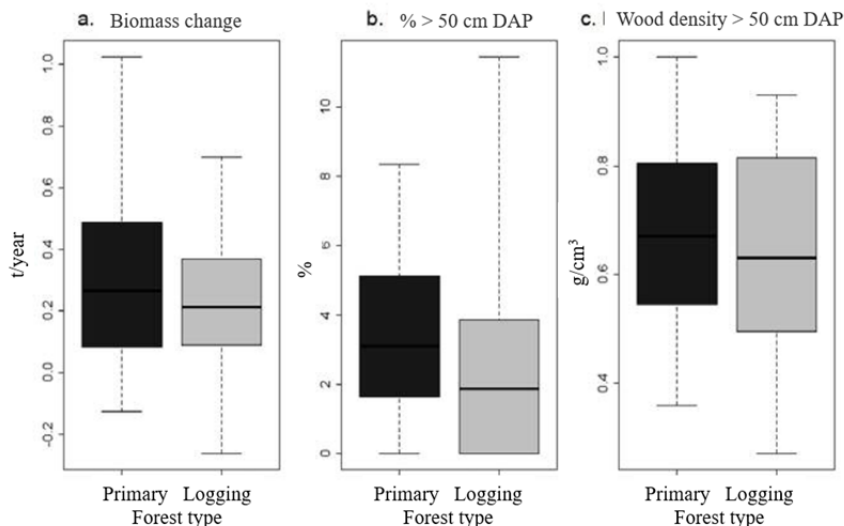


Figure 3. Comparison of structural aspects between 50 subplots of 20×20 m for primary forest and 50 subplots of 20×20 m for logged forest in the El Paujil reserve (Colombia). **(a)** Percentage of large trees (DAP > 50 cm), where the primary has a higher value $(t = 1.40$, $gl = 98$, $p = 0.04)$. **(b)** Wood density of large trees for primary and logged forest, where the primary has a higher value $(t = 2.17$, $gl = 107$, $p = 0.016)$.

3.3 Biomass change

The primary forest gained on average $4 \text{ Mg biomass ha}^{-1} \text{ year}^{-1}$, going from having on average 459.5 Mg ha^{-1} in 2006 to having 487.6 Mg ha^{-1} in 2013, while the logged forest gained less biomass, with an average of $0.9 \text{ Mg ha}^{-1} \text{ year}^{-1}$, going from having 440.6 Mg ha^{-1} in 2006 to having 447.1 Mg ha^{-1} in 2013. We found that there are fewer trees with a DAP greater than 50 cm in the logged forest ($t = 1.40$, $gl = 98$, $p = 0.04$; **Figure**

3a), and, that the wood density of these trees (<50 cm DAP) is lower than in the primary forest ($t = 2.17$, $gl = 107$, $p = 0.016$; **Figure 3b**).

4. Composition

The most important species in the primary forest plots differ from those in the logged forest, and they are mostly trees with good quality timber^[24], the target of the reforesters (**Table 2**). The component that most influenced the determination

of the importance index was the relative basal area (**Annex 2**). The conservation status of these species has mostly not been assessed, however *Clathrotropis brunnea* is known to be endangered, *Hymenaea courbaril* is of least concern and *Grias haughtii* is vulnerable (**Table 2**).

A high floristic affinity was found in the primary forest plots, while the logged forest is more heterogeneous, with one plot more similar to the primary forest group than that of the same forest type (**Figure 4**).

Table 2. Most important species for each one-hectare plot (two per forest type) established in the El Paujil reserve, with their importance index value, wood use, wood quality and conservation status in Colombia

Forest type	Plot	Species	Importance index	Use of wood	Wood quality	State of conservation
Primary	P3	<i>Eschweilera andina</i>	11.87	x	good	NE
		<i>Andira chigorodensis</i>	7.62	x	very good	NE
		<i>Garcinia madruno</i>	7.11		bad	NE
		<i>Clathrotropis brunnea</i>	6.21	x	bad	EP
	P4	<i>Clathrotropis brunnea</i>	14.66	x	bad	EP
		<i>Pseudolmedia rigida</i>	7.95	x	bad	NE
		<i>Hymenaea courbaril</i>	6.58	x	half	CA
		<i>Eschweilera andina</i>	6.2	x	good	NE
Logging	P1	<i>Cavanillesia platanifolia</i>	13.86		bad	NE
		<i>Simira rubescens</i>	7.95	x	half	NE
		<i>Grias haughtii</i>	7.02	x	half	PM
		<i>Ephedranthus colombianus</i>	6.79		bad	NE
	P5	<i>Pourouma melinonii</i>	13.53		N/A	NE
		<i>Laetia procera</i>	8.15	x	N/A	NE
		<i>Chrysophyllum lucentifolium</i>	7.63	x	good	NE
		<i>Trichospermum galeottii</i>	7.11		bad	NE

Conventions: NE = Not Evaluated, EP = Endangered, CA = Near Threatened, N/A = Information Not Found, PM = Least Concern.



Figure 4. Dendrogram comparing the floristic composition of 2 one-hectare plots established in primary forests (P3 and P4) and 2 one-hectare plots in logged forests (P1 and P5), in the Quinchas mountain range (Colombia).

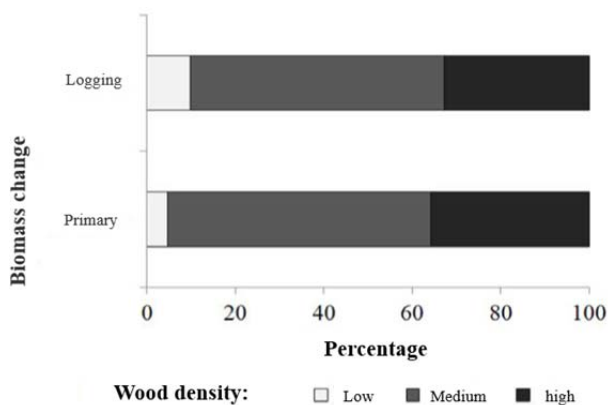


Figure 5. Proportion of individuals sampled in 2 plots of 1 ha for primary forest and 2 plots of 1 ha for logged forest in the El Paujil reserve (Colombia) grouped into three categories of wood density, corresponding to: low between 0.10 g/cm³ and 0.39 g/cm³, medium between 0.40 g/cm³ and 0.69 g/cm³ and high between 0.70 g/cm³ and 0.90 g/cm³.

As a result of the classification by wood den-

sity, it was found that the proportion of trees in each wood density category depended on forest type ($g = 44.266$, $gl = 2$, $p < 0.01$), finding a higher proportion of species with low wood density in logged forest (**Figure 5**).

5. Discussion

5.1 Demographics

The demographic components analyzed for the forests of the El Paujil reserve did not behave as expected. Mortality was the same for both forest types (**Table 1** and **Figure 1a**), although it was expected to be higher in the logged forest due to mechanical damage because of greater exposure to wind from trees adjacent to logged areas^[4]. Recruitment, which was expected to be higher in logged forest due to the greater amount of light available as a consequence of logging, was higher in primary forest (**Table 1** and **Figure 1b**) and in fact there were no differences in the amount of light entering the understory in the two forest types (**Figure 2a**). The population of primary forest did not change, while that of logged forest decreased (**Table 1** and **Figure 1c**), showing significant differences between the two forest types.

As mentioned above, the forest sites sampled have a geographic altitude ranging from 194 m to 471 m, in areas with slopes up to 40°. It has been shown that soil slope is a primary ecological factor, which controls the mortality rate by tree fall and, therefore, induces a strong light gradient in the understory that favors the growth and recruitment of pioneer species^[26]. In the forest of the El Paujil reserve, where high mortality is almost equal in areas with selective logging and primary forest, it can be said that the effect of slope on tree mortality can mask the effect of logging as suggested by Ferry^[26].

On the other hand, a high abundance of lianas in the primary forest would contribute to the formation of clearings, since it negatively affects mature forest trees^[7]. To evaluate this explanation, the relative abundance of lianas in both forest types was determined and compared, which corroborated the prediction, as it was higher in the primary forest (Welch's $t = 2.09$, $gl = 85$, $p = 0.02$). However, it could be seen that the percentage of lianas in the primary forest of the El Paujil reserve has a high value (2.98% on average) compared with other plots of the same extension established by researchers of the Laboratory of Ecology of Tropical Forests and Primatology (LEBTYP) in Colombia, but not significantly higher compared to the other plots of dry land (1.46% on average $N = 20$) (Welch's $t = 2.92$, $gl = 2$ $p = 0.93$). Therefore, there is still uncertainty about the effect of liana abundance on the dynamics of these forests.

5.2 Clearance analysis and regeneration

The magnitude of the clearings in the forests of the El Paujil reserve, is similar in both forest types (**Figure 3**) as well as the previous results. It leads us to think that the dynamics are mainly shaped by the effect of the slope of the terrain, causing a high mortality by falling trees similar to or greater in magnitude than that caused by the effect of disturbance (wind) after logging activities. Winds have been identified as a key factor in mortality and post-disturbance dynamics mainly in relatively flat areas, as for example in the Amazon, where the influence of wind can be greater^[27,28].

Although there is a similar proportion of clearings and quantity of seedlings and juveniles in

the two forest types, the higher recruitment observed in the primary forest could be the result of the effect of mechanical damage caused to seedlings and juveniles in the logged forest by the constant movement of people (e.g. tourists and researchers). That is due to its easy access has a much higher influx than in the primary forest.

5.3 Biomass change

Estimates of biomass reserves per hectare for the two forest types are relatively high when compared to estimates made for these forests in Colombia^[29], however, this is explained by the fact that in this study trees from 5 cm DAP were included. This is not a common practice in biomass estimation studies. However, it is important to include smaller individuals, given that it not only increases the estimates of biomass reserves per ha^[14], due to the effect of the increase in the number of individuals counted, which can be almost double, but also the estimates of species diversity (**Annex 1**).

As expected, the primary forest had a higher net biomass gain per hectare than the logged forest. This is in agreement with what has been reported in studies of biomass dynamics in tropical primary forests, where annual increases in biomass per hectare have been reported in the order of 3 to 20 tons^[30]. However, it is notable that the lower values, reported in the present study for logged forest, resemble values reported by other studies of biomass dynamics in fragmented forests^[31]. Additionally, the greater number of large trees observed in the primary forest (**Figure 2b**), added to the fact that these have trees with higher density timber (**Figure 2c**), shows an effect of selective logging that cannot be easily compared with intrinsic factors of forest dynamics and that takes long periods of time to return to normal. The decline in the populations of certain tree species, which are subject to logging for the quality of their timber, is clear. It is important to highlight that, if fragmentation and selective logging continue in this region, the effects on carbon dynamics could be extremely negative to the point that these forests may cease to be carbon reservoirs and become sources of CO₂ emissions, as has been predicted for fragmented forests in the Amazon^[32].

5.4 Composition

Assuming that the forests had a similar composition before logging, the differences in comparing composition and dominance between forest types (**Table 2** and **Figure 4**) can be related to this activity. For example, large tree species (larger basal area) and high wood density (considered an important quality factor) are less important in the logged forest (**Table 2**, **Figure 5**). Again, it is evident that the strongest effect of selective logging on the forest was to generate changes in species composition by decreasing the populations of timber tree species. This factor should be considered in timber industry management plans, as some of these species are in a state of vulnerability (**Table 2**) or their current conservation status is unknown^[25]. Additionally, it may have implications in the trophic interactions of the ecosystem, where critically endangered and declining populations of critically important dispersers such as the spider monkey (*Ateles hybridus hybridus*) inhabit^[11].

Other studies have reported changes in the species composition of forests in the region, as a response to changes in climate^[33], which added to the effects of selective logging that we evidenced in this study, could cause strong declines in the populations of plant species in these forests.

6. Conclusions

The dynamics of the forest in El Paujil Reserve do not show great differentiation due to selective logging in the past. It is important to highlight the effect of topography on forest dynamics and studies on the effect of vines and human traffic are recommended. The structure of the forest changes and biomass reserves decrease due to selective logging, as there is a significant decrease in the populations of large trees of species with good quality wood in the logged forest, which can affect the trophic interactions of the forest and its capacity to be carbon sinks. This type of species must be managed to avoid irreversible declines in their populations.

Conflict of interest

The authors declare that they have no conflict

of interest.

References

1. Gibson L, Lee TM, Koh LP, *et al.* Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 2011; 478(7369): 378–381.
2. Norden N, Chazdon RL, Chao A, *et al.* Resilience of tropical rain forests: Tree community reassembly in secondary forests. *Ecology Letters* 2009; 12(5): 385–394.
3. Asner GP, Keller M, Silva JNM. Spatial and temporal dynamics of forest canopy gaps following selective logging in the eastern Amazon. *Global Change Biology* 2004; 10(5): 765–783.
4. Figueira AMMES, Miller SD, de Sousa AD, *et al.* Effects of selective logging on tropical forest tree growth. *Journal of Geophysical Research* 2008; 113(G00B05): 1–11.
5. Gourlet-Fleury S, Mortier F, Fayolle A, *et al.* Tropical forest recovery from logging: A 24 year silvicultural experiment from Central Africa. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 2013; 368(1625): 20120302.
6. Philipson CDD, Dent DH, O'Brien MJ, *et al.* A trait-based trade-off between growth and mortality: Evidence from 15 tropical tree species using size-specific relative growth rates. *Ecology and Evolution* 2014; 4(18): 3675–3688.
7. Schnitzer SA, Bongers F. The ecology of lianas and their role in forests. *Trends in Ecology and Evolution* 2002; 17(5): 223–230.
8. IDEAM (Instituto de Hidrología, Meteorología y Estudios Ambientales), Subdirección de Ecosistemas e Información Ambiental, Grupo de Bosques. Proyecto Sistema de Monitoreo de Bosques y Carbono (Spanish) [Forest and carbon monitoring system project] [Internet]. Bogotá D.C., Colombia: El futuro es de todos; 2014. Available from: <http://smbyc.ideam.gov.co/MonitoreoBC-WEB/reg/indexLogOn.jsp>
9. García Romero HG. Deforestación en Colombia: Retos y perspectivas (Spanish) [Deforestation in Colombia: Challenges and perspectives]. In: Dane F (editor). *El Desafío del Desarrollo Sustentable en América Latina*. Hong Kong: Konrad Adenauer Stiftung; 2013; 123–142.
10. ProAves. Reserva ProAves El Paujil (Spanish) [El Paujil bird reserve] [Internet]; 2010 [accessed 2010 Aug 8]. Available from: <http://www.proaves.org/rna-el-paujil/>.
11. Aldana AM, Beltrán M, Torres-Neira J, *et al.* Habitat characterization and population density of brown spider monkeys (*Ateles hybridus*) in Magdalena Valley, Colombia. *Neotropical Primates* 2008; 15: 46–50.
12. Balcazar MP, Rangel JO, Linares EL. Floristic diversity of the Las Quinchas mountain range, middle Magdalena (Colombia). *Caldasia* 2000; 22(2): 191–

- 224.
13. Silva Herrera LJ. Feasibility and strategic plan of the reforestation company Bosques del Futuro S.A. located in Magdalena Medio. Bogotá: Universidad de La Salle; 1999. p. 1–130.
 14. Baraloto C, Molto Q, Rabaud S, *et al.* Rapid simultaneous estimation of aboveground biomass and tree diversity across Neotropical forests: A comparison of field inventory methods. *Biotropica* 2013; 45(3): 288–298.
 15. Phillips O, Baker T, Feldpausch T, *et al.* Field manual for remediation and plot establishment. 2nd ed. In: RAINFOR (editor). PAN-AMAZONIA Project; 2009.
 16. Stevenson PR. The abundance of large ateline monkeys is positively associated with the diversity of plants regenerating in neotropical forests. *Biotropica* 2011; 43(4): 512–519.
 17. Sherman RE, Fahey TJ, Martin PH, *et al.* Patterns of growth, recruitment, mortality and biomass across an altitudinal gradient in a neotropical montane forest, Dominican Republic. *Journal of Tropical Ecology* 2012; 28(05): 483–495.
 18. R Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2013.
 19. Image J, Rasband W. Image J: Image processing and analysis in Java. Bethesda, Maryland: US National Institutes of Health; 2007.
 20. Chave J. Measuring wood density for tropical forest trees. A field manual for the CTFS sites. *Wood Density Measurement Protocol–J Chave* 2005; 1–7.
 21. Zanne AE, Lopez-Gonzalez GDAC, Ilic J, *et al.* Global Wood Density Database. Dryad Digital Repository; 2009. Available from: <http://hdl.handle.net/10255/dryad.235>.
 22. Feldpausch TR, Lloyd J, Lewis SL, *et al.* Tree height integrated into pan-tropical forest biomass estimates. *Biogeosciences Discussions* 2012; 9(3): 2567–2622.
 23. Álvarez E, Duque A, Saldarriaga J, *et al.* Tree above-ground biomass allometries for carbon stocks estimation in the natural forests of Colombia. *Forest Ecology and Management* 2012; 267: 297–308.
 24. Fern K. Useful tropical plant database [Internet]. [accessed 2014]. Available from: <http://tropical.theferns.info/>.
 25. Bernal R, Robbert Grandstein S, Celis M. Catalog of plants and lichens of Colombia [Internet] [accessed 2014]. Available from: <http://catalogoplantasdecolombia.unal.edu.co/>.
 26. Ferry B, Morneau F, Bontemps JD, *et al.* Higher tree fall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. *Journal of Ecology* 2010; 98(1): 106–116.
 27. Etter A, Botero RJ. Effects of climatic and geomorphological processes on the dynamics of the tropical rainforest of the Colombian amazon. *Colombia Amazonica* 1990; 4(2): 7–21.
 28. Laurance W F, Curran TJ. Impacts of wind disturbance on fragmented tropical forests: A review and synthesis. *Austral Ecology* 2008; 33(4): 399–408.
 29. Phillips JF, Duque AJ, Yepes AP, *et al.* Estimation of potential carbon stocks stored in aboveground biomass in natural forests in Colombia. Final Report. Bogotá D.C., Colombia: Instituto de Hidrología, Meteorología, y Estudios Ambientales-IDEAM; 2011. p. 68.
 30. Meister K, Ashton MS, Craven D, *et al.* Managing forest carbon in a changing climate. New York: Springer; 2012. p. 51–75.
 31. Nascimento HEM, Laurance WF. Biomass dynamics in Amazonian forest. *Fragments* 2004; 14(4): s127–s138.
 32. Laurance WF, Camargo JLC, Luizão RCCC, *et al.* The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation* 2011; 144(1): 56–67.
 33. Duque A, Stevenson PR, Feeley KJ. Thermophilization of adult and juvenile tree communities in the northern tropical Andes. *Proceedings of the National Academy of Sciences of the United States of America* 2015; 112(34): 10744–10749.

Annexes

Annex 1. Number of individuals and species for each one hectare plot including trees over 5 cm DAP and over 10 cm DAP, taken from Aldana *et al.*^[11]

Forest type	Plot	DAP > 5 cm		DAP > 10 cm	
		No. Species	No. Individuals	No. Species	No. Individuals
Primary	P3	246	1,048		606
	P4	226	924		446
	P1	234	1,070		721
Logging	P5	201	1,000		545

Annex 2. Most important species for each one hectare plot (two per forest type) established in the El Paujil reserve with values of density, frequency, relative basal area and importance index

Forest type	Plot	Species	Relative density	Relative basal area	Relative frequency	Importance index
Primary	P3	Eschweilera andina	2.19	9.57	0.11	11.87
		Andira chigorodensis	1.90	3.81	1.90	7.62
		Garcinia madruno	3.24	1.97	1.90	7.11
	P4	Clathrotropis brunnea	1.81	3.17	1.23	6.21
		Clathrotropis brunnea	3.87	8.06	2.73	14.66
		Pseudolmedia rigida	4.62	1.03	2.30	7.95
		Hymenaea courbaril	1.00	4.72	0.86	6.58

Annex 2. (Continued).

		<i>Eschweilera andina</i>	1.87	4.33	0.04	6.24
	P1	<i>Cavanillesia sp01</i>	0.26	13.25	0.35	13.86
		<i>Simira rubescens</i>	3.55	2.88	1.52	7.95
Logging		<i>Grias haughtii</i>	3.29	1.73	1.99	7.02
		<i>Ephedranthus colombianus</i>	1.90	3.37	1.52	6.79
	P5	<i>Pourouma melinonii</i>	4.62	5.91	3.00	13.53
		<i>Laetia procera</i>	2.49	3.80	1.86	8.15
		<i>Chrysophyllum lucentifolium</i>	2.72	2.91	2.00	7.63
		<i>Trichospermum galeottii</i>	2.72	2.81	1.57	7.11