# Logging impacts on forest structure and seedling dynamics in a *Prioria copaifera* (Fabaceae) dominated tropical rain forest (Talamanca, Costa Rica)

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**Abstract:** The factors that determine the existence of tropical forests dominated by a single species (monodominated forests) have been the subject of debate for a long time. It has been hypothesized that the low frequency of disturbances in monodominated forests and the tolerance to shade of the monodominant species are two important factors explaining the prolonged dominance of a single species. We determined the role of these two factors by examining the effects of logging activities on the floristic composition and seedling dynamics in a *Prioria copaifera* dominated forest in Southeastern Costa Rica. We determined the floristic composition for trees ≥2.5cm DBH and the associated recruitment, survival and mortality of tree canopy seedlings in two sites logged two (L-02) and 12 years (L-12) prior to sampling and an unlogged forest (ULF). Our results showed that L-02 stands had lower species richness (25 species) than the L-12 and ULF stands (49 and 46 species, respectively). As expected, we found significant logging effects on the canopy structure of the altered forests, particularly when comparing the L-02 and the ULF stands. Seedling density was higher in ULF (0.96 seedlings/m$^2$) than in the L-02and L-12 stands (0.322 and 0.466 seedlings/m$^2$, respectively). However, seedling mortality was higher in the ULF stands (54%) than in the L-02 (26%) and L-12 (15%) stands. *P. macroloba* in L-02 was the only species with abundant regeneration under *P. copaifera* in L-02 stand, where it accounted for 35% of the seedlings. Despite the reduction in seedling abundance observed after logging, *P. copaifera* seems to maintain large seedling populations in these forests, suggesting that this species maintains its dominance after logging disturbances. Our findings challenge the hypothesis that the regeneration of monodominant species is not likely to occur under heavily disturbed canopy conditions. Rev. Biol. Trop. 62 (1): 347-357. Epub 2014 March 01.

**Key words:** *Carapa guianensis*, floristic composition, forest structure, logging impact, tropical monodominance, tree regeneration, *Pentaclethra macroloba*, *Prioria copaifera*.

Monodominant forests (stands where more than 60% of the basal area is dominated by a single species) are widespread throughout the tropics. Monodominant forests are scattered across much of the Congo basin in Africa as well as in the lowlands of Central and South America (Whitmore, 1998) and Southeastern Asia (Richards, 1996; Yasuda, Matsumoto, & Osada, 1999). For all Neotropical and Paleotropical African forests, member of Caesalpinioideae subfamily (Fabaceae) are the dominant tree (Connell & Lowman, 1989; Nascimento, Proctor, & Villela, 1997), whereas in South East Asian forests are dominated forms by members of Dipterocarpaceae (Whitmore, 1998). Often these forests thrive next to significantly more diverse communities without a clear reason for their existence (Connell & Lowman, 1989), although several hypotheses had been proposed (Janos, 1985; Torti & Coley, 1999; Villela & Proctor, 2002).

Hart, Hart, & Murphy (1989) proposed that the main mechanism explaining this phenomenon is the conjunction of high seed production, poor seed dispersal systems, low light conditions and seedling adaptation to low luminosity. Following studies show that most monodominant tropical legumes (Caesalpinioideae subfamily) in South America (Forget, 1989; Nascimento, & Proctor, 1997; Henkel, Mayor, & Woolley, 2005) and Africa (Hart, 1995; Torti, Coley, & Kursar, 2001) as well as Dipterocarpaceae in South Asia (Herrera, Jordano, Guitián, & Traveset, 1998;Yasuda et al., 1999) follow a mast fruiting pattern, supporting the idea that high episodes of seed outputs are a key factor in maintaining the stable dominance. Moreover, most of these species, especially those adapted to flood conditions, have large self-dispersed seeds that tend to create large seedling banks, thus promoting monodominance (Lopez, 2001; Ter Steege, 1994; Ter Steege, & Hammond, 2001).

Several authors also point out that understory light conditions in tropical monodominant forests are shadier than that of adjacent mixed-forests (Richards, 1996; Whitmore, 1998). In fact, Torti et al. (2001) found that sunlight levels in the understory were on average lower and more homogeneous in a *Gilbertiodendron dewevrei* dominated stand than in adjacent mixed-forests. These data are consistent with the deep crowns and canopies characteristic of species forming monodominant stands (Richards, 1996). Poor luminosity is considered an important ecological filter maintaining monodominance, as the regeneration of the dominant species benefits from the environmental conditions created by the canopy trees (Frelich, Calcote, Davis, & Pastor, 1993). Therefore, it has been proposed that intense disturbances could reverse monodominance as regeneration of light demanding tree species would proliferate under the new light conditions (Hart, 1995; Peh, Lewis, & Lloyd, 2011). However, this hypothesis has not been formally tested.

*Prioria copaifera* is one of the Neotropical caesalpinoids trees species known to form monodominant stands. It accounts for 60-90% of the basal area in the lowlands forest subjected to periodic flooding distributed from Nicaragua to Colombia and Jamaica (Gonzáles, Gómez, & Arteaga, 1991; Kursar, & Grauel, 2002). Commercially available stands have been extensively described (Linares, 1987; Condit, Hubell, & Foster, 1993) and heavily exploited for wood during the last century (Lamb, 1953; Kursar, & Grauel, 2002). However, there is still a lack of reliable information about the effects of logging activities on the structure and diversity of these forests (Grauel, 2004; Webb, 1997, 1999). The aim of this study was to understand how traditional logging practices affect forest structure, diversity and seedling regeneration in *P. copaifera*-dominated forests.

Studies in undisturbed forests show that monodominant species maintain a high seedling representation in the understory, which has been interpreted as a requirement for continuous dominance through time (Hart, 1995, Peh et al., 2011). Therefore, if logging activities are able to disrupt the *P. copaifera* stand dominance we would expect: 1) an increase in other tree species regeneration under *P. copaifera* canopy with respect to undisturbed conditions, 2) an increase in *P. copaifera* seedling mortality at logged stands in comparison with the unaltered areas (Guariguata, 2000) and 3) a decrease in seedling recruitments in logged forests.

## MATERIALS AND METHODS

**Study area:** This study was conducted in a 63ha forest near the Gandoca-Manzanillo Wildlife Refuge, Talamanca, Costa Rica (9º37’83” N - 82º38’52” W). The area is classified as a tropical humid forest with 2 500-3 100mm of precipitation annually and temperature ranging from 25 to 27ºC (Herrera, 1985). The forest thrives on lowland alluvial flood plain soils identified as Hydric Psamments (Vázquez, 1979). The dominant floristic component for this type of forest is *Prioria copaifera* Griseb (Fabaceae-Caesalpinioidae) that represent as much as 60% of the basal area of the stand. The canopy is also interspersed by *Carapa guianensis* Aubl. (Meliaceae) and *Pentaclethra macroloba* (Willd.) Kuntze (Fabaceae-Mimosoidae). Simira maxonii (Standl.) Steyerm. (Rubiaceae) is the dominant understory tree.

The study site received two episodes of timber extraction, one in 1988 and the other in 1997. Approximately 60% of all trees ≥60cm in DBH were harvested in each stand. Official records for the logging episode conducted in 1997 reported an average of 7 trees/ha, for a total of 109 trees in the 15ha logged. There were no official records available for the logging operation conducted in 1988, but the wood extraction intensity was likely to be similar to that of 1997 considering the homogeneity of the forest and that extractions were made following the same legislation (Quirós & Finegan, 1994). The stands were designated as logged-02 (L-02) and logged-12 (L-12), according to the time from the extraction operation to the beginning of this study. An additional 33ha unlogged forest stand was also used in this study and it was designated as ULF. This unlogged stand is adjacent to the logged areas and is owned by a non-governmental organization dedicated to the preservation of this lowland tropical flood plain forest.

**Floristic structure, composition and seedling bank analysis:** In order to compare floristic composition between the three stands, we established two 0.05ha (10x50m) plots in each site during November 2000. All saplings and trees were identified and their DBH was measured. The floristic structure of each plot was determined on basis of all individuals ≥2.5cm DBH. For individuals with multiple stems, especially fallen trunks of *P. macroloba*, each stem was counted separately and measured but the tree, as a whole, was considered as a single individual.

Seedling dynamics were evaluated by measuring all tree regeneration between 50 and 150cm in height within 10 randomly selected 5x5m quadrats in each sampling plot. The initial measurement was conducted in November 2000 and seedling survival, recruitment and mortality were surveyed during May 2001 and December 2001. All live seedlings were considered as survivors, even if they were physically damaged. Seedlings dead or missing were recorded as mortalities; new seedlings were recorded as recruits and seedlings whose growth exceeded 150cm were considered as saplings.

Differences in stand structure were analyzed using the relative abundance of the most common species that were shared among stands (*P. copaifera, P. macroloba, C. guianensis, S. maxonii* and *Musa textilis*; Table 1). For the two most common species in all stands (*P. copaifera* and *P. macroloba*), we compared the proportion of individuals in each in diametric classes for each stand. To capture different aspects of species diversity among stands, five indicators of diversity were calculated as recommended by Chazdon, Colwell, Denslow, & Guariguata (1998): 1) species richness, 2) Simpson's diversity index (D), 3) Shannon Diversity index (H'), 4) the proportion of species with only one individual (singletons) and 5) the incidence coverage estimator (ICE). Differences in species richness among stands were examined comparing the 95% confidence intervals of the rarefaction curve based on ICE estimations (Magurran, 1988; Colwell et al., 2012). Additionally, we used Sorensen and Chao-Jaccard similarity indexes to determine the similarity in species composition and abundance among stands. Index estimations were performed using the EstimateS 9.1.0 software (Colwell, 2013).

Differences in the initial and final seedling bank densities were estimated using one-way analyses of variance (ANOVA) after probing that all responses fulfilled the assumptions of homoscedasticity and normal distribution of residues. Seedling species composition, annual recruitment and mortality among stands were compared using logistic regression to compare the abundance of the most abundant seedlings (*P. copaifera, P. macroloba* and *C. guianensis*) among stands and across species. The six remaining most abundant species were pooled together and treated as a single group for these analyses. All statistical analyses were performed using JMP Data Analysis software (version 5.1.2, SAS Institute, NC, USA).

TABLE 1
Number of trees (N), basal area, relative abundance (AR), relative dominance (DR) and Importance Value Index (IVI) for the five top species (≥2.5 cm DBH) for a two-year (L-02) and twelve-year (L-12) old logged stand and an unlogged stand of *Prioria copaifera* forest in the Caribbean lowlands of Costa Rica. Species ranked for IVI.
Numbers in parenthesis indicate standard errors

| | Stems/ha | Basal area ($m^2$/ha) | AR (%) | DR (%) | IVI (%) |
|---|---|---|---|---|---|
| L-02 | | | | | |
| Pentaclethra macroloba | 340 (9) | 15.10 (0.74) | 21.25 | 43.79 | 32.52 |
| Musa textilis | 570 (12) | 4.10 (0.05) | 35.63 | 11.85 | 23.74 |
| Prioria copaifera | 150 (5) | 10.80 (1.72) | 9.38 | 31.37 | 20.37 |
| Simira maxonii | 120 (5) | 0.55 (0.05) | 7.50 | 1.39 | 4.45 |
| Quararibea bracteolosa | 40 (4) | 1.70 (0.74) | 2.50 | 4.98 | 3.74 |
| Total | 1620 (18) | 34.50 (0.60) | - | - | - |
| L-12 | | | | | |
| Prioria copaifera | 240 (8) | 35.60 (2.92) | 15.48 | 70.17 | 42.83 |
| Pentaclethra macroloba | 190 (7) | 7.50 (0.63) | 12.26 | 14.78 | 13.52 |
| Musa textilis | 120 (6) | 1.80 (0.08) | 7.74 | 3.57 | 5.66 |
| Simira maxonii | 100 (4) | 0.30 (0.02) | 6.45 | 0.67 | 3.56 |
| Carapa guianensis | 70 (4) | 0.50 (0.06) | 4.52 | 0.91 | 2.71 |
| Total | 1670 (21) | 50.78 (1.26) | - | - | - |
| ULF | | | | | |
| Prioria copaifera | 150 (6) | 32.50 (3.89) | 10.00 | 62.39 | 36.19 |
| Pentaclethra macroloba | 260 (10) | 8.20 (0.60) | 17.33 | 15.62 | 16.48 |
| Simira maxonii | 80 (5) | 3.90 (0.87) | 5.33 | 7.39 | 6.36 |
| Carapa guianensis | 120 (6) | 1.50 (0.17) | 8.00 | 2.85 | 5.43 |
| Rinorea dasydeana | 110 (5) | 0.30 (0.02) | 7.33 | 0.57 | 3.95 |
| Total | 2500 (21) | 52.10 (1.38) | - | - | - |

## RESULTS

**Canopy structure:** Two years after logging activities, the L-02 stand was dominated by *P. macroloba* (IVI=32.52), where it accounted for most of the basal area and number of stems per ha (Table 1). *Prioria copaifera* had lower basal area in the L-02 stand; in fact, this was the only stand were *P. copaifera* was not the dominant species. In contrast, *P. macroloba* only accounts for a smaller fraction of the basal area in the unlogged stand (ULF). The diametric distribution of individuals in the L-02 stand showed a continuous presence of *P. macroloba* in all the diametric categories, indicating both dominance in the canopy and abundant regeneration of this species. On the other hand, *P. copaifera* had most of the individuals grouped in the lower categories with only a few individuals in the adult range in the L-02 stand (Fig. 1).

The L-12 and ULF stands were similar in their species composition and abundance. *Pentachletra macroloba* was also an abundant species in these two stands, but its abundance was four to five times lower than that of *P. copaifera* in the unlogged stand (Table 1). *Prioria copaifera* and *P. macroloba* showed an almost continuous presence throughout the diametric distribution in both stands, but *P. copaifera* had a higher number of individuals in the bigger DBH categories, evidencing the canopy dominance of this species. Furthermore, for *P. macroloba*, most of the individuals were included in the 10 and 30cm DBH categories, suggesting a suppressed condition beneath *P. copaifera* canopy (Fig. 1).

**Stand diversity:** Analysis of plant diversity in all stands showed that the L-02 stand had a sharp decrease in species richness, whereas

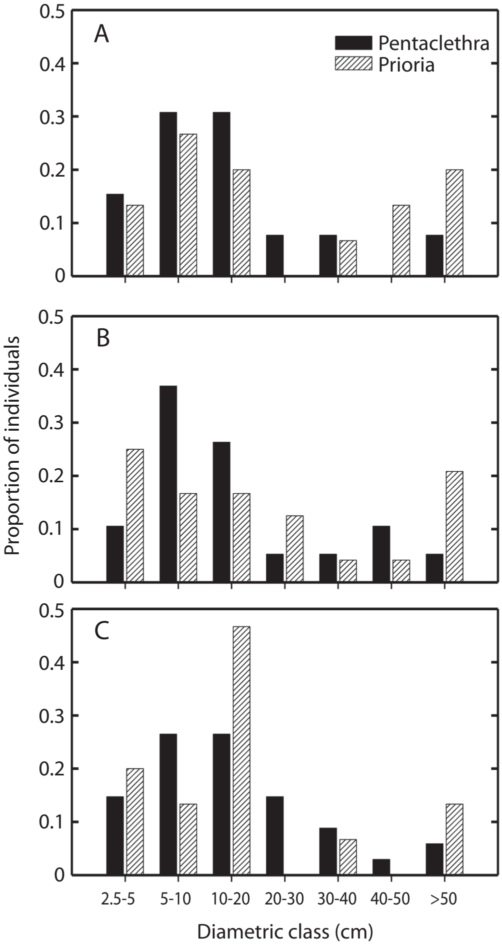

Fig. 1. Distribution of *Prioria copaifera* and *Pentaclethra macroloba* trees with ≥2.5cm DBH according arbitrarily established DBH categories in the *Prioria copaifera* dominated lowland rain forests of Southwestern Costa Rica. Graphs show DBH distribution in three different forest stands: (A) unlogged stand, (B) stand logged twelve prior to our sampling, and (C) stand logged two years prior to our sampling.

the L-12 stand had similar diversity than the unlogged stand (ULF) (Table 2, Fig. 2). The number of species in 0.1 ha in the L-02 stand was nearly half of that of the other two stands. The species accumulation curve for the L-12 and ULF stands were also similar (Fig. 2). *Musa textilis* was abundant at L-02 stand (IVI=23.74, Table 2) and also present in lower abundance at L-12 stand (IVI=5.66). *Carapa guianensis* showed higher abundance in the unlogged stand compared to the logged stands.

Simpson diversity (D) and Shannon diversity (H’) indexes were not different among stands (Table 2). The number of singletons was the lowest in the L-02 stand, suggesting that the reduction in diversity in this stand was mainly due to the loss of rare species. Indicators of similarity in species composition and abundance among stands show similar values for all pairwise comparisons (Table 2), suggesting that the similarity among stands is due to the high dominance of the same species.

**Seedling dynamics:** Initial seedling density was higher in the ULF stand, where 345 seedlings were recorded in twenty 50m$^2$ plots (0.91±0.08 S.E. seedlings m$^{-2}$), than in the L-12 (0.47±0.04m$^{-2}$) or the L-02 stands (0.32±0.05m$^{-2}$) ($F_{5,54}$=4.9; p=0.01). Multiple contingency table analysis indicates that mortality rates varies among stands (likelihood ratio test, $\chi^2$=12.57, df=2, p-value 0.0019) and among species ($\chi^2$=13.54, df=3, p-value 0.0049). The highest number of seedlings of *P. copaifera* in the ULF stand was coupled with the highest mortality (176 out of 345 seedlings, 51%, Table 3). In contrast, the L-02 stand had the smallest number of seedlings for all species (161) but associated with a lower mortality rate (42 individuals, 26.1%). *Prioria copaifera* was the species with the largest numbers of seedlings in the ULF and the L-12 stands, accounting for more than75% of the total tree seedling population in these two plots. In contrast, the L-02 stand showed a similar abundance of *P. copaifera* and *P. macroloba* seedlings. *Pentaclethra macroloba* had a lower presence in the L-12 stand, representing only 21% of the seedlings present in the plots, whereas in the ULF it showed the lowest abundance corresponding to less than 8 percent of the seedlings (Table 3).

Seedling recruitment was also different among species ($\chi^2$=13.56, df=3, p-value 0.0036) but not among stands ($\chi^2$=0.61, df=2, p-value 0.73, Table 3). *Pentaclethra macroloba* registered the highest recruitment rates in the L-02 stand (35 individuals), even higher than that of

TABLE 2
Species diversity and similarity indexes estimated for trees (≥2.5cm dbh) and seedling banks among logged and undisturbed stands in a *Prioria copaifera* dominated forests in the Caribbean lowlands of Costa Rica (Standard deviation in paranthesis)

| Diversity indexes | Trees | | | Seedlings | | |
|---|---|---|---|---|---|---|
| | L-02 | L-12 | ULF | L-02 | L-12 | ULF |
| Number of individuals sampled | 165 | 160 | 155 | 161 | 233 | 453 |
| Number of species (0.1 ha) | 25 | 49 | 46 | 6 | 8 | 9 |
| Simpson index (D) | 13.96 (5.7) | 12.51 (4.64) | 13.03 (3.72) | 1.79 (0.26) | 1.77 (0.09) | 1.77 (0.01) |
| Shannon index (H') | 2.96 (0.5) | 3.03 (0.41) | 3.15 (0.27) | 0.8 (0.13) | 0.84 (0.07) | 0.89 (0.01) |
| Sigletons | 8.9 (2.16) | 18.43 (2.7) | 17.01 (2.48) | 1.32 (0.47) | 1.62 (0.49) | 1.0 (0.42) |
| Similarity indexes | L-02/L-12 | L-02/ULF | L-12/ULF | L-02/L-12 | L-02/ULF | L-12/ULF |
| Species shared | 17 | 16 | 23 | 4 | 4 | 4 |
| Sørensen | 0.459 | 0.451 | 0.484 | 0.8 | 0.615 | 0.615 |
| Chao-Jaccard | 0.681 | 0.422 | 0.556 | 0.951 | 0.951 | 0.951 |

Acronyms of the stands as referred in Table 1.

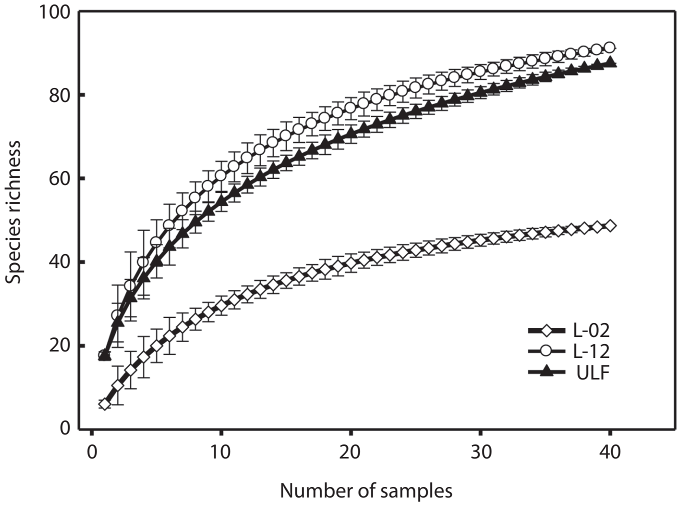

Fig. 2. Estimated number of species as a function of the cumulative number of individuals sampled across 40 25-m$^2$ quadrats in three different stands of *Prioria copaifera* dominated forest of the Caribbean lowlands of Costa Rica. Species richness was estimated using the Incidence Coverage Estimator (ICE) option of EstimateS 9.1.0 (Colwell 2013). Stands were logged two (L-02) and twelve (L-12) years prior the study and compared to an un-logged stand (ULF). Bars indicate 95% confidence intervals.

*P. copaifera,* but both species experienced high mortality (Table 3). *Prioria copaifera* showed a large recruitment in the L-12 stand (91 individuals) due to a large seed crop during the study period. *Carapa guianensis* was the third most abundant species in the seedling and saplings banks, but it was mainly restricted to the ULF stand (53 out of 61 individuals). In fact, *C. guianensis* seedlings encompassed 11 percent of the total seedling population in the ULF at the beginning of the study, much higher than the number observed for *P. macroloba*. However, high mortality rates reduced the population by 77% after one year (41 out 51 seedlings).

TABLE 3

Seedling dynamics for canopy tree regeneration in a *Prioria copaifera* dominated forests in the Caribbean lowlands of Costa Rica, showing the initial number of seedling for the most common tree species found in each stand at the beginning of the study, the number of seedlings that die, the number of seedling recruited and the number of seedling growing to saplings (more than 1.5m in height) during the duration of the study

| Species | Initial number* | | | Mortality** | | | Recruits* | | | Seedlings to saplings* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | L-02 | L-12 | ULF | L-02 | L-12 | ULF | L-02 | L-12 | ULF | L-02 | L-12 | ULF |
| *Carapa guianensis* | 8<br>(0.02) | - | 53<br>(0.11) | 3<br>(37%) | - | 41<br>(77%) | 10<br>(0.02) | - | - | 7<br>(0.14) | - | - |
| *Pentaclethra macroloba* | 57<br>(0.11) | 48<br>(0.10) | 31<br>(0.06) | 19<br>(33%) | 13<br>(27%) | 23<br>(74%) | 35<br>(0.07) | 12<br>(0.24) | 12<br>(0.24) | 2<br>(0.004) | 4<br>(0.008) | 1<br>(0.002) |
| *Prioria copaifera* | 93<br>(0.19) | 179<br>(0.36) | 345<br>(0.69) | 19<br>(20%) | 19<br>(11%) | 176<br>(51%) | 8<br>(0.16) | 91<br>(0.18) | 21<br>(0.04) | 1 | - | - |
| Other six tree species | 3<br>(0.006) | 7<br>(0.01) | 24<br>(0.48) | 1<br>(33.3%) | 4<br>(57%) | 5<br>(21%) | - | - | - | - | - | 1<br>(0.002) |
| Total (all species) | 161 | 233 | 453 | 42 | 36 | 245 | 53 | 103 | 33 | 10 | 4 | 2 |

* Numbers in parentheses indicate number of seedlings per meter square.

** Numbers in parentheses indicate percent mortality from the initial census.

Acronyms of the stands as referred in Table 1.

Moreover, some *C. guianensis* seedlings grew to samplings in the L-02 stand during in the study period (Table 3). No *C. guianensis* seedling was found in the L-12 stand.

Seedling diversity was similar among stands (Table 2). *Prioria copaifera*, *P. macroloba* and *Symphonia globulifera* (Clusiaceae) were recorded in all the stands, whereas the rest of the species were present only in one or two sites. *Otoba novogranatensis, Virola koschnyi* (Myristicaceae) and *Sterculia recordiana* (Malvaceae) were only found in the ULF, whereas *Rollinia pittieri* (Annonaceae)*,* an indicative of large disturbances in the canopy (Guariguata, 1997), was present only in the logged stands.

## DISCUSSION

The results of this study show that the basal area found in the L-02 forest is approximately 35% of that found in the unlogged stand (ULF). This finding is consistent with similar studies in monodominant forests harvested at similar intensities (Table 1, Johns, Barreto & Uhl, 1996; Nicholson, 1998). The similarities in basal areas and tree composition between the L-12 and ULF forest suggest a rapid recovery of *Prioria copaifera* stands after tree harvest. Linares (1996) and Grauel (2004) also indicate a fast biomass recovery in *P. copaifera* stands at low and moderate extraction rates, but not at high intensities (Grauel & Putz, 2004), supporting a rapid response of *P. copaifera* regeneration after moderate canopy disruptions.

Other timber species found in these forests, such as *Carapa guianesis*, with wider acceptance and higher value in the local markets, probably suffered a more extensive extraction (Jiménez-Madrigal, Rojas-Rodríguez, Rojas, & Rodríguez, 2002). Overexploitation may explain the lack of adult *C. guianensis* trees in the logged stands, as suggested by the high harvest of *C. guianensis* reported for the L-02 stand, where this species accounted for 40% of the total wood harvested. Such preference for *C. guianensis* wood may explain why the abundance found in the ULF stand did not match the abundance of this species in logged stands. These observations support the notion that *C. guianensis*, a supra-annual dioecious species, is more susceptible to logging than *P. macroloba* or *P. copaifera*, two hermaphroditic trees with annual seed production (Flores, 1994; Jiménez-Madrigal et al., 2002).Therefore, *C. guianensis* should be excluded from commercial logging in these swamp forests. It is important to indicate that these observations were made without measurements of forest structure previous to the logging impacts, limiting the inferences we can make about the real impact of timber extraction on the forest structure. Future logging studies will be important to quantify more accurately the recovery capacity of *P. copaifera* stands to logging impacts.

We found that seedling survival varied among species and among forests stands. In general, seedling survival was higher in logged forests with higher light intensities than in the unlogged forest. These findings suggest that disturbances are crucial for the recruitment and future composition of the tree composition of these forests. Seedling density also seems to be an important factor determining future composition of logged stands, suggesting that reproductive ecology plays a key role determining the impact of logging (Gauriguata, 2000).

Seedling density in this *Prioria copaifera* dominated forest was lower than that of 1 to 7 seedlings m$^{-2}$ reported for other monodominant forests in the Neotropics (Henkel et al., 2005), but similar to inter-masting seedling density of *Gilbertiodendron* stands in the Congo basin (Hart, 1995). Similarities among *P. copaifera* and *P. macroloba* seeds in terms of mass and flooding tolerance may explain their prevalence in the seedling bank (Lopez, 2001; Lopez & Kursar, 2003, 2007). Nonetheless, they showed different recruitment and survival patterns. Consistent with our expectations, *P. copaifera* seedlings showed higher survival rate than *P. macroloba* and *C. guianensis* under shaded conditions. However, these two species also had similar low mortality rates in the logged stands, suggesting that they can survive well under more open canopy conditions. The low recruitment of *P. copaifera* seedlings observed in the L-02 is probably related to the lower abundance of fruiting trees with respect to the unlogged stand and the low dispersal range associated with their large seeds (Foster, 1986; Forget, 1989; Dalling, Harms, & Aizprúa, 1997). Our findings suggest that, despite the reduction in survival rate observed in *P. copaifera* seedlings in logged stands, this species has some ability to respond to abrupt light environment changes. This ability to respond to changes in the light conditions may be crucial for the maintenance of the dominance of *P. copaifera* in lowland tropical swamp forests.

In contrast, *P. macroloba* shows high recruitment and survival levels only in the L-02 stand, which is consistent with previous responses of this species to logging activities (Linares, 1996; Delgado, Finegan, Zamora, & Meier, 1997; Finegan, Camacho, & Zamora, 1999; Grauel, 2004), suggesting that closed canopy conditions are detrimental for *P. macroloba* regeneration. Lopez (2001) analyzed seed and seedling traits for several common tree species in Central America freshwater swamps and classified *P. copaifera* seed and seedlings as better adapted to prevalent conditions in seasonal flooded forests than *P. macroloba*. Lopez and Kursar (2003) pointed out that *P. copaifera* seeds are larger and able to endure flooded conditions for long periods of time. Large seed size is also related with longer growth and expansion of the hypocotyl after germination, allowing the expansion of leaves away from the soil and thus avoiding the submersion of their leaves (Foster, 1986). Furthermore, larger seeds also have higher carbohydrate reserves which allow seedlings to survive under prolonged shade conditions, intense physical damage (Dalling et al., 1997) or prolonged droughts (Lopez & Kursar, 2007). Thus, even when conditions in the recently logged stands may favor *P. macroloba* survival (Palomaki, Chazdon, Arroyo, & Letcher, 2006), our findings suggest that *P. copaifera* eventually regains its dominance as canopy cover recovers.

In summary, we found that the removal of a large number of canopy trees in *Prioria copaifera* dominated forests changes the distribution of the remaining trees across all stem diameter categories and facilitates the proliferation of *Pentachletra macroloba* seedlings and saplings in the understory. Moreover, our study also suggests that the overexploitation of canopy species that are typically found in low abundance in these forests (i.e., *C. guianensis*) may not recover after intense logging episodes, threatening their continuity in this community. Finally, logging also impacts seedling composition and abundance, affecting both recruitment and mortality rates rather than seedling density. Although long term studies are important to corroborate trends in seedling composition, current evidence suggest that *P. copaifera* seedlings are well adapted to environmental conditions in this frequently flooded swamp forests and are able to maintain their dominance after severe disturbance.

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## RESUMEN

**Impactos de la extracción en la estructura y la dinámica de plántulas en un bosque tropical dominado por** *Prioria copaifera* **(Fabaceae), (Talamanca, Costa Rica).** La determinación de los factores responsables de la existencia de bosques tropicales dominados por una sola especie (bosques monodominados) ha sido motivo de debate por largo tiempo. Se ha propuesto que la baja frecuencia de alteraciones en esos bosques y la tolerancia a la sombra de las plántulas de la especie monodominante son dos de los factores que contribuyen a explicar la prolongada dominancia de una sola especie en estos bosques. Se estudió el rol de estos dos factores evaluando el efecto de la extracción de madera sobre la composición florística y la supervivencia y crecimiento de plántulas en un bosque dominado por *Prioria copaifera* en la región sureste de Costa Rica. Para ello se determinó la composición florística de los árboles con un diámetro a la altura de pecho (DAP) ≥2.5cm y el reclutamiento, supervivencia y mortalidad de las plántulas de especies arbóreas en sitios donde se extrajo madera dos (L-02) y doce años (L-12) antes de este estudio y un sitio del que nunca se ha extraído madera (ULF). Nuestros resultados muestran que los bosques L-02 tienen una riqueza de especies menor (25 especies) que los bosques L-12 y ULF (49 y 46 especies, respectivamente). Como era de esperar, la extracción de madera tuvo efectos significativos en la estructura del dosel del bosque, particularmente al comparar los bosques L-02 y ULF. La densidad de plántulas fue mayor en bosques ULF (0.96 plántulas/m$^2$) que en L-02 y L-12 (0.322 and 0.466 plántulas/m$^2$, respectivamente). Sin embargo, la mortalidad de plántulas fue mayor en ULF (54%) que en L-02 (26%) y L-12 (15%). *Pentachletra macroloba* fue la única especie que mostró abundante regeneración bajo *P. copaifera* en parcelas L-02, representando el 35% las plántulas encontradas. A pesar de la reducción de la abundancia de plántulas observada después de la extracción de madera, *P. copaifera* parece capaz de mantener grandes poblaciones de plántulas en estos bosques. Estos resultados sugieren que *P. copaifera* puede mantener su dominancia después de las alteraciones causadas por la extracción de madera. Nuestros resultados no apoyan la hipótesis de que la regeneración de las especies monodominates es menos probable cuando el dosel del bosque sufre fuertes alteraciones.

**Palabras clave**: *Carapa guianensis,* composición florística, estructura del boque, impacto de la extracción de madera, monodominancia en bosques tropicales, regeneración del bosque, *Pentaclethra macroloba, Prioria copaifera,* alteración del bosque.

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