ORIGINAL PAPER

Differential diameter-size effects of forest management on tree species richness and community structure: implications for conservation

Gabriel Gutiérrez-Granados · Diego R. Pérez-Salicrup · Rodolfo Dirzo

Abstract In this paper we tested the hypothesis that logging effects in the adult tree community reverberate upon the regeneration contingent. We examined the differences on the tree community between forest reserves and 10 year-old logged areas in the Yucatan Peninsula. We used a paired design in three independent sites to estimate the effects of logging on tree species richness, diversity, composition and structure. Analyses were conducted differentiating individuals of four diameter-size classes: 1–5, 5–10, 10–25, and >25 cm DBH. We found out that there were differential effects by size. Species richness in the smaller and larger diameter-size classes was significantly lower in logged areas. Floristic composition was also different between logged and unlogged areas, with a trend towards more secondary forest associated species and less primary forest associated species in logged areas, and a higher density of species represented by a single individual in unlogged reserves. In terms of structure, trees DBH <10 cm, lianas, and re-sprouting stumps were more abundant in logged areas. Our findings suggest that 10 years after logging, harvested areas show alterations in structure, and potentially a reduction in species richness. We suggest that to make timber extraction and forest conservation compatible at this site, it is necessary to gain a better understanding of the ecology and regeneration requirements of the less abundant species, and to assess whether current logging practices might hinder their permanence in the study area.

G. Gutiérrez-Granados (✉)
Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México.
Circuito Exterior, Edificio Nuevo, Módulo C. Apdo. Postal 70-153, C.P. 04510 Coyoacán,
Mexico, DF, Mexico
e-mail: ggranados@ecologia.unam.mx

D. R. Pérez-Salicrup
Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México,
Antigua Carretera a Pátzcuaro No. 8701 Col. Ex-Hacienda de San José de La Huerta,
C.P. 58190 Morelia, Michoacán, México

R. Dirzo
Department of Biology, Stanford University, 371 Serra Mall, Stanford, CA 94305, USA

Introduction

Forest management for timber extraction often results in a series of negative changes in forest diversity and structure (Verissimo et al. 1992; Panfil and Gullison 1998; ter Steege et al. 2002). For example, it was observed that felling of 4–8 target trees/ha resulted in the killing of about 30 percent of remaining trees in the state of Pará, Brazil, which in turn resulted in canopy damage of up to 80% (Uhl and Vieira 1989; Cannon et al. 1994; Johns et al. 1996). Such damages usually cause changes in the light regime and forest micro-climate, and could promote erosion, soil compaction and disruption of nutrient cycling (Pereira et al. 2002; Villela et al. 2006).

Even those practices recognized as reduced impact logging (RIL) generate damages in tropical forests. For example, ca. 10% of remaining living trees were killed by the logging of 1–2 target trees/ha, with an associated canopy damage of 10% in southern Amazonia (Feldpausch et al. 2005). These minor changes associated with RIL may have a variety of consequences on forest composition via direct effects on harvested trees species and by affecting tree regeneration (Dickinson et al. 2000; Costa and Magnusson 2003; Makana and Thomas 2005; Toledo-Aceves et al. 2009), which in turn could result in changes on community composition and structure. Hence, logging practices would potentially affect the whole contingent of plant species, and not only those which are directly harvested, as has been typically reported (Panfil and Gullison 1998; ter Steege et al. 2002).

Among timber exploitation programs documented worldwide, the community-based forest management of the Mayan zone in the Yucatan Peninsula, Mexico, has been considered as a prominent example of sustainable ecosystem management in terms of social participation and ecological sustainability (Bray et al. 2003). These promising indigenous people-runned programs reduce the damage of logging operations by planning the direction of the trees to be felled, by designing of a low impact road network, and by eliminating branches from fallen trees before skidding. Timber extraction in this participatory program has been considered as of low to moderate impact, with an average of 600 m^3 of *Swietenia macrophylla* (mahogany) and 1500 m^3 of other species harvested per year in stands that range in size between 100 and 500 ha, and which are harvested every 25 years. In addition, these indigenous communities have set aside forest patches to function as reserves for biodiversity conservation (Galletti 1999; Bray et al. 2003).

Although the Mayan logging program implements some RIL strategies, logging per se might impact the whole tree community, and consequently future timber yields. An evaluation of the effects of current logging practices is key to incorporate new strategies that might mitigate the negative impacts of past practices (Christensen et al. 1996). In this study, we tested the hypothesis that logging effects on adult tree community have effects on the regeneration contingent which would compromise future management in the area. We posit that plant diversity analyses pooling all the individuals disregarding their size could bias management and conservation decisions, thus we analyzed the tree community parameters in four different size-categories. Our analysis was based upon the theoretical issue that species accumulate as a function of the number of individuals counted, and because there are more juvenile individuals than adults, then species richness may vary by the size category analyzed (Condit et al. 1996). Therefore, we evaluated whether 10 years

after logging operations logged areas differ from nearby forests set aside for conservation in terms of species richness, diversity and composition.

Materials and methods

Study site

Field work was carried out in the Municipality of Carrillo Puerto (88°00′–88°20′W, and 19°00′–20°00′N), State of Quintana Roo, Mexico, within what is known as the Mayan zone. The predominant substrate is karstic material with limestone-derived thin soils (5–10 cm depth). Climate is characterized as hot and humid, with a mean monthly temperature of 25°C and a mean annual precipitation of 1200 mm, most of which is received during the May–October wet season (100–200 mm per month). During the dry season (November–April), only 30–60 mm of rain are received per month. The predominant vegetation is tropical moist forest (sensu Holdridge 1967), with intermingled patches of savanna and flooded forest, depending on microtopographic and substrate variations (Pérez-Salicrup 2004). Olmsted and Durán (1990) report *Brosimum alicastrum*, *Manilkara zapota*, and *Talisia olivaeformis* as the dominant evergreen species and *Vitex gaumeri*, *Bursera simaruba*, and *Caesalpinia gaumeri* as deciduous co-dominants. Height of the dominant arboreal trees ranges from 15 to 25 m.

Logging has been practiced in the study area since ancient Mayan periods (Snook 1999). Forest management during the late nineteenth century and for most of the twentieth century was largely unregulated, and targeted in a few valuable timber species (*Swietenia macrophylla* and *Cedrela odorata*), on a few hard wooded species used for railway ties (e.g. *Metopium brownei, Manilkara zapota*), and in the latex of *Manilkara zapota* which is still the most important non timber forest product harvested from this region (Snook 1999; Negreros-Castillo et al. 2003). In the 1980s the management program currently practiced by most *ejidos* (communally-owned and managed lands) were implemented. In 1997, some *ejidos* commenced the harvesting of small diameter individuals to be used for railway ties (Negreros-Castillo and Mize 2008). Today, the region and the communities within are well known for their efforts at conducting low impact, socially fair, community based forestry management programs (Galletti 1999; Bray et al. 2003). Timber extraction is performed using harvesting stands with a cutting cycle of 25 years. Harvesting is still centered on mahogany, although management programs include the integral management of the forest and the extraction of as many as 90 tree species which are cut at a diameter breast high (DBH) ≥35 cm.

Sampling design

We used a paired design, sampling areas logged in 1996, 10 years before field work for this study was conducted, and nearby areas set aside as reserves by the local inhabitants in each of three different *ejidos*. Hereafter, we will refer to these areas as logged and unlogged, respectively. Paired plots were established on three independent *ejidos*, Naranjal, Petcacab and Señor. On each *ejido* we established two pairs of plots for a total of six replicated pairs (each pair: logged and unlogged condition). These three *ejidos* were selected given that they contribute with a high proportion (collectively ca. 40%) of the timber extracted in the entire region (Gutiérrez-Granados 2009). All the study areas are part of a continuous tropical forest known as Permanent Forest Zone of Quintana Roo, thus we expected that

floristic composition differences found in logged and unlogged areas would result from forest management.

Floristic diversity, composition and structure were recorded using a modification of the method devised by Gentry (1982) for the study of alpha-diversity in tropical forests. Our protocol consisted in establishing ten randomly-located 50 × 2 m transects, for a total of 0.1 ha per plot (60 transects per forest condition). Transects were set perpendicularly to the main road of the logging areas, and from the main access road in the reserves. We began each transect about 10 m inside the vegetation in order to minimize the edge effects caused by the road. Each transect was placed on either side of the road defined randomly by a toss of a coin. Distances between transects range 100–850 m. All trees with a diameter at 1.3 m (DBH) $\geq$1 cm, were identified at species level and their diameter recorded. Voucher specimens were collected and taken to National Herbarium (MEXU) for further corroboration or accurate identification, with the assistance of curator Esteban Martinez. Sampling protocol like the one adopted here (1000 m^2 per site), has been successfully used to analyze and compare sites across the tropics (e.g. Phillips and Miller 2002) in a very different subtypes of tropical forests (Clinebell et al. 1995; Trejo and Dirzo 2002; ter Steege et al. 2003), and has been considered useful to provide a good indication of species richness and floristic composition in tropical forests (Gentry 1982; Condit et al. 1996).

Data analyses

Analysis of the effects of logging on tree species richness, diversity and composition were conducted using a diameter-size classes approach. Four diameter-size classes were defined: 1–5, 5–10, 10–25, and >25 cm. We used rarefaction curves (100 randomizations) for comparisons of the number of observed species in both management conditions and used two non-parametric estimators of species richness CHAO-2 and ICE (see Colwell and Coddington 1994). We used these estimators because they match each other in precision and accuracy when estimating species richness using relatively small samples (i.e., small sampling effort; ICE), and small grain size (i.e., community level; CHAO-2), as previously reported by Chazdon et al. (1998), Brose et al. (2003), and Hortal et al. (2006). Floristic similarities were assessed using the Sorensen-Chao similarity index, which takes into account both species abundance and unseen species (Chao et al. 2005). All estimations were made with EstimateS ver. 7.5 (Colwell 2005). Changes in abundance of less abundant tree species were assessed using species represented by one individual (singletons).

Since our data met the requisites of normality and variance homoscedasticity, we used parametric analyses for the comparison of tree species richness, Shannon's Diversity Index, the non-parametric estimators of tree species richness, and abundance of species represented by a single individual. We used analyses of variance (ANOVA) for completely randomized block designs to maintain our paired design. In our design we used *ejidos* as blocks with two replicates within each *ejido* and management condition (logged versus unlogged) as factors (Sokal and Rohlf 1995). In the case of the comparison of the general similarities between floristic compositions we pooled similarity values by both logged and unlogged and used a parametric *t*-test.

Changes in floristic composition were further analyzed using the Importance Value (IV), calculated for each of the tree species (see Cottam 1949). Importance values were calculated from the relative values of species density (D = no. individuals of the ith species by area), frequency (F = no. of sites occupied by the ith species/total number of sites) and dominance (Do = sum of the basal area of all plants of the ith species/total basal area), as IV = RD + RF + RDo. To further describe vegetation, we classified tree species

into two guilds as either pioneer, light-demanding species, and mature-forest, shade-tolerant species, according to Durán et al. (1998).

In addition, we performed a multidimensional scaling analysis (MDS) using a Sorensen-Chao floristic similarity matrix in order to define an ordination of the sites according to management type. To confirm MDS's tendencies we performed a multi-response permutation procedure (MRPP) by diameter size-class to statistically compare both management types according to their floristic composition.

Finally, we performed a principal component analysis (PCA) to evaluate whether sites with and without logging could be separated based on their structural characteristics. We evaluated five structural variables: (1) liana (>1 cm at stem base and rooted within the transect) abundance, (2) density of adult trees (DBH >10 cm), (3) number of stumps with no sign of re-sprouting, (4) number of re-sprouting stumps, and (5) basal area. We displayed the results of PCA on a biplot (Jongman et al. 1987). Unless otherwise indicated, all data are shown as means (±SD). In all cases results are considered statistically significant when $P < 0.05$. Analyses were conducted with Statistica v.8 (Stat Soft, Inc), while in particular MRPP was done with PC-Ord v.6 (MjM Software design).

Results

Logging effects on tree richness and diversity

In total we sampled 6443 trees, of which 3668 (56.9%) were present in logged sites and 2775 (43.1%) in unlogged sites. These individuals represent 287 species in total. Of these 191 ± 52 were present in logged and 212 ± 56 were in unlogged sites. Despite this disparity in species richness, we found no significant differences in the number of species between logged and unlogged sites when the entire tree species pool was analyzed ($F = 2.1$, df $= 1,2$; $P < 0.05$), giving similar results for diversity ($F = 1.4$, df $= 1,2$; $P < 0.05$).

However, rarefaction curves by diameter-size classes showed that there were more species in unlogged sites for individuals 1–5 cm ($F = 3.6$, df $= 1,5$; $P < 0.05$) and >25 cm ($F = 2.3$, df $= 1,5$; $P < 0.05$) DBH. In the latter case, the number of individuals recorded in unlogged sites was higher and consequently more species were registered. The other two diameter-size classes showed no differences in number of species observed between both conditions (Fig. 1a–d).

Species diversity, as defined by Shannon–Weiner's index, was statically significant just for the first diameter-size class (Table 1). However, expected richness, calculated by both non-parametric estimator CHAO-2 and ICE showed significant differences between both management conditions in 1–5, 5–10, and 10–25 cm classes, although there were no differences in the number of species expected in the >25 class (Table 1).

The total number of singletons accounted for $3.4 \pm 1.2\%$ of all sampled individuals. In absolute terms, all three *ejidos* had a lower number of species represented by a single individual in the logged sites ($F = 13.64$, df $= 1,5$; $P < 0.001$, Fig. 2), but the contrast was higher in *ejido* Señor.

Species similarity was high in general terms, with an overall value of 0.75. Among logged sites similarity was comparatively higher than among unlogged sites, with 0.88 ± 0.09 and 0.74 ± 0.12, respectively ($t = 3.8$, df $= 28$; $P < 0.001$), suggesting greater floristic homogeneity among the former. The MDS analyses based on the Sorensen-Chao similarity index for each diameter-size class showed statistical differences between
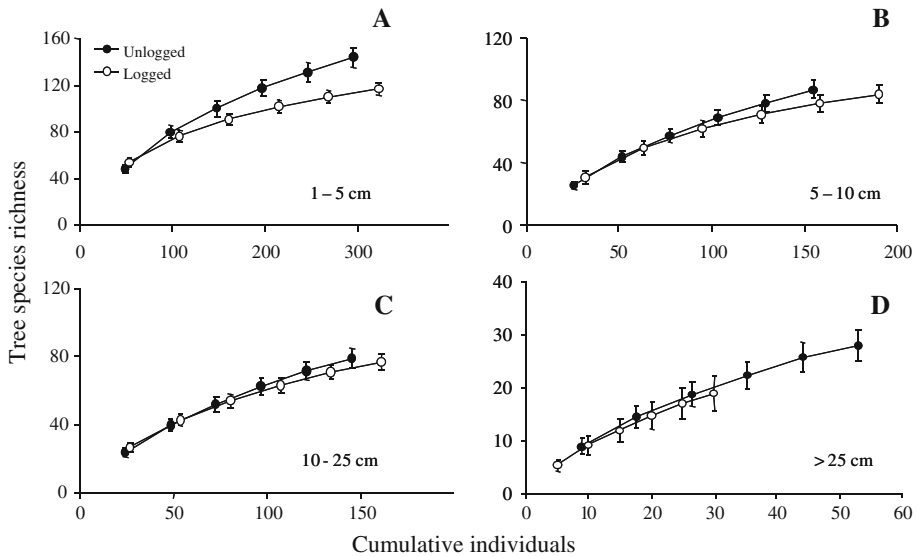
Fig. 1 Tree species accumulation curves (mean ± SD) considering the four diameter-size classes analyzed and the two management conditions in the Mayan zone, Mexico

Table 1 Diversity differences by diameter-size class for Shannon–Weiner's species diversity index (±SD) and number of species (±SD) estimated by the two non-parametric estimators in the two management conditions studied at the Mayan zone, Mexico

Diameter-size class (cm)	Unlogged	Logged	F	P
Shannon-Weiner's index				
1–5	3.4 ± 0.6	2.6 ± 0.6	3.7	0.01
5–10	2.7 ± 0.8	2.3 ± 0.5	0.9	n.s.
10–25	2.6 ± 0.9	2.4 ± 0.2	0.8	n.s.
>25	2.3 ± 0.4	2.1 ± 0.6	0.8	n.s.
ICE				
1–5	267.8 ± 26.8	161.48 ± 9.28	4.7	0.001
5–10	178.6 ± 22.9	117.63 ± 14.04	3.2	0.033
10–25	158.6 ± 7.6	126.24 ± 15.59	2.8	0.029
>25	50.2 ± 9.7	47.51 ± 11.69	0.7	n.s.
CHAO 2				
1–5	269.4 ± 30.5	158.2 ± 14.0	4.3	0.002
5–10	135.3 ± 15.3	110.1 ± 10.3	2.8	0.037
10–25	132.9 ± 17.7	107.8 ± 11.6	2.5	0.023
>25	38.9 ± 6.7	35.2 ± 10.4	1.2	n.s.

n.s. not significant

unlogged and logged areas in three of the four size classes analyzed (Fig. 3). The difference in the 1–5 and 5–10 cm DBH classes was significant (MRPP $T = -2.25$; $P = 0.02$, and $T = -1.85$; $P = 0.04$ respectively). The 10–25 DBH class showed no statistical differences in floristic composition (MRPP $T = -0.22$; $P = 0.39$), while the >25 cm DBH

Fig. 2 Density of species represented by a single individual (singletons) in logged and unlogged areas per *ejido* in the Mayan zone, Mexico. The cumulative area for 20 samples is 0.2 ha. *L* logged, *UL* unlogged
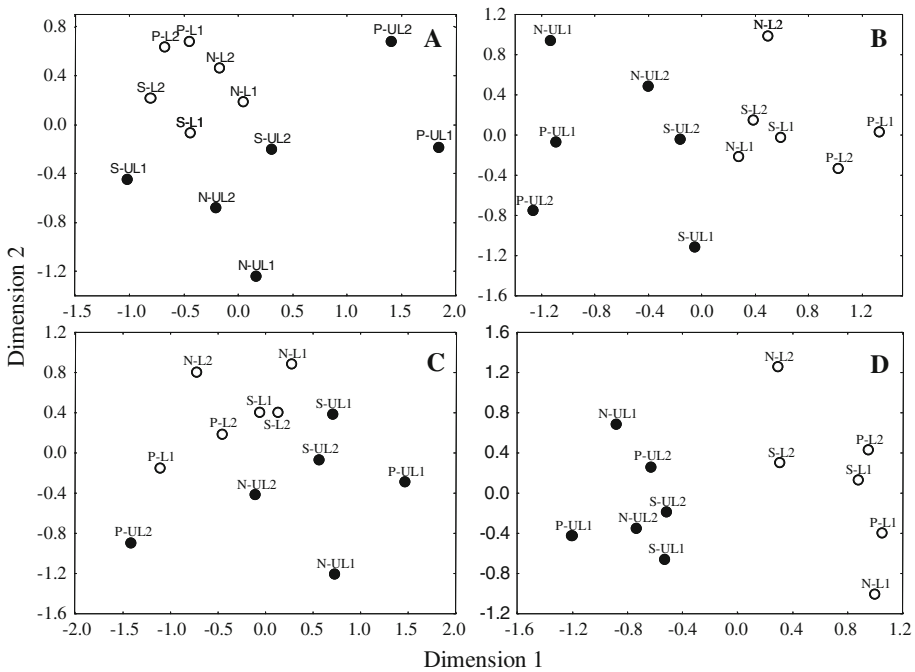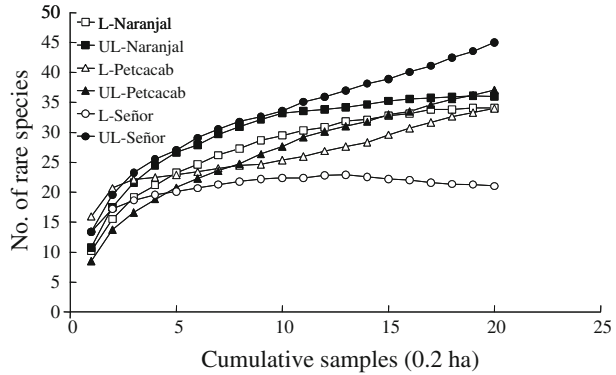
Fig. 3 Multidimentional scaling analysis showing site ordination according to their species composition in four DBH classes: 1–5 cm (A), 5–10 cm (B), 10–25 cm (C), >25 cm (D) in the Mayan zone, Mexico. *Black dots* represent unlogged sites (UL); *white dots* represent logged (L) sites, in the three analized *ejidos*, Señor (S), Petcacab (P) and Naranjal (N)

class, which includes individuals targeted for logging, has significantly different compositions between unlogged areas and logged ones ($T = -3.05$; $P < 0.05$; Fig. 3).

Logging effects on tree community structure

Basal area by diameter-size classes was similar in the first two size classes between logged and unlogged areas, but the number of individuals was higher in the logged area for the first diameter-size class. These combined results suggest a change in the diameter

Fig. 4 Basal area (A) and
number of individuals (B) in the
four diameter-size classes
analyzed in the two management
conditions studied in the Mayan
zone, Mexico
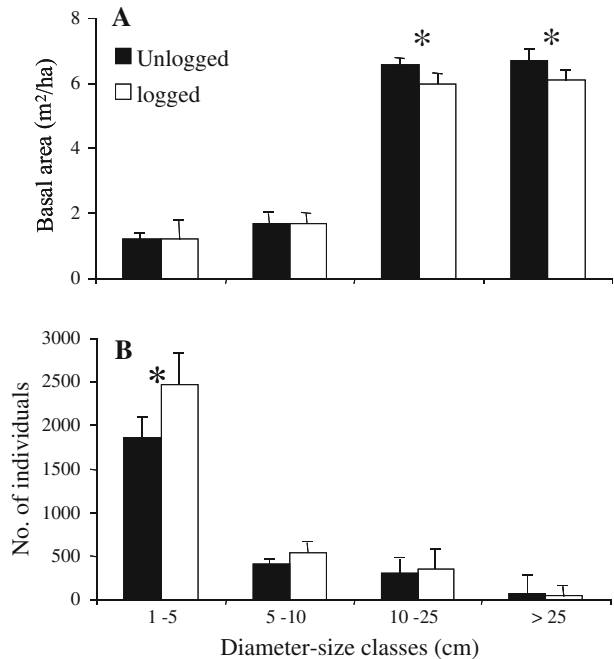
distribution of individuals, and hence in the structure of vegetation. In the first diameter-size class, logged areas had more trees, but with smaller diameters than in the unlogged area. In the second diameter-size class, there was no difference for either number of individuals or basal area. For the last two classes, a similar number of individuals in both areas resulted in higher basal areas in unlogged areas than in the logged ones, because the former areas have trees with larger DBH (>60 cm; Fig. 4a, b).

The IV provided insights regarding the changes in both composition and structure. To illustrate this, we show the 20 species with the highest IV in the two conditions of management (Fig. 5). Only 10 species were the same in both forest types, but they occupied different rank positions. Furthermore, 16 of the 20 most important species in unlogged sites are mature-forest species and the other four occupied positions 6th, 7th, 18th, and 20th. In contrast, in logged sites, 6 out of the 20 most important species were pioneer species, two of which occupied positions 1st and 4th (Fig. 5).

Fourteen species are regularly used in logging operations, five of which are ranked among the most abundant species in the study zone (Fig. 5). The representation of these species was not consistently higher in the unlogged forests. Instead, there was considerable variation across species (Table 2). For instance, *Pseudobombax ellipticum* and *Lysiloma latisiliquum* had the same IV in both types of forest management conditions, but this was due to the fact that in the logged sites the number of plants, but not their basal area, was greater which could suggest the existence of regeneration for these species. On the other hand, *Swietenia macrophylla* had a higher IV in unlogged sites. We registered 13 individual of this species in logged areas, reaching a basal area of 2.04 m²/ha, whereas in unlogged areas we estimated a basal area of 4 m²/ha, with just eight mahogany trees. The extreme case of loss of representation occurred with *Caesalpinia mollis* and *Vitex gaumeri*, which were not present in the logged sites. Regeneration of this managed species showed
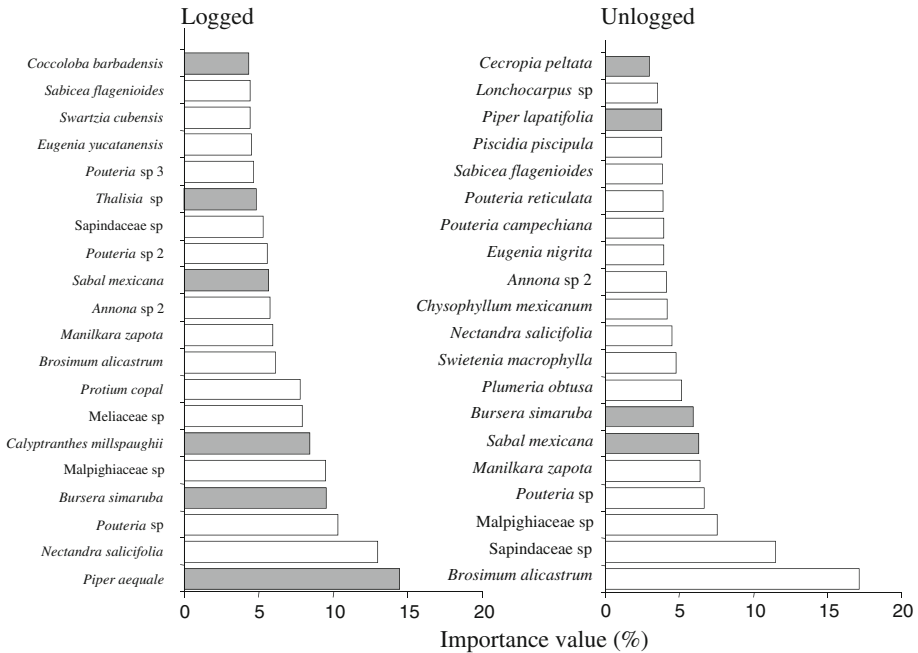
Fig. 5 Tree species arranged by Importance Value in logged and unlogged areas in the Mayan zone, Mexico. *Grey bars* represent pioneer species, and *white bars* represent mature forest species, according to Durán et al. (1998)

also a variation depending on the species (Table 2). Is remarkable to point out that, *Cordia dodecandra*, *C. mollis*, *S. macrophylla* and *V. gaumeri*, had no individuals within the smaller diameter category in logged sites.

Figure 6 shows the results of the PCA based on structural variables. The first axis of the biplot explained 61% of the total variance, while the cumulative variance explained by axis 1 and 2 was 80%. The PCA displays the study sites along axis 1, clearly separating the logged from the unlogged ones. The biplot also makes evident that the arrangement of the sites is clearly related to structural changes associated to logging operations such as liana abundance, number of resprouting stumps, and number of stumps, which were more abundant in the logged sites and explained the highest contribution in factor 1; with 28, 23 and 20% respectively. This analysis also showed a positive correlation of logged sites and basal area, which contributed with about 51% of the variance in factor 2. The density of adult trees (DBH >10 cm) was highly associated to unlogged sites, and explained about 23% of variance in factor 2.

Discussion

Our analysis approach allowed us to detect changes at different diameter-classes, and this in turn could be used to suggest management recommendations (see below). The immediate consequences associated to logging are a reduction on tree density throughout harvesting of larger individuals (DBH >35 cm in the study area), and the random death of smaller- or equivalent-size individuals, usually of unmarketable trees species (Webb 1997;

Table 2 Importance value (IV) and regeneration potential of the main harvested species in the two management conditions studied at the Mayan zone, Mexico

| Species	Total IV		Regeneration potential	
	Unlogged	Logged	Unlogged (Ind)	Logged (Ind)
Brosimum alicastrum	23.17	6.13	34	37
Bursera simaruba	5.90	9.51	12	29
Caesalpinia mollis	1.22	0	29	0
Coccoloba spicata	1.60	3.19	8	9
Cordia dodecandra	0.53	0.64	6	0
Lysiloma latisiliquum	1.24	1.10	2	5
Manilkara zapota	6.42	5.91	67	118
Metopium brownei	1.49	2.52	6	20
Piscidia piscipula	3.81	2.23	35	8
Pseudobombax ellipticum	1.50	1.56	4	3
Simarouba glauca	0.26	0.79	4	10
Spondias mombin	0.55	0.32	4	0
Swietenia macrophylla	1.00	4.80	2	6
Vitex gaumeri	0.64	0	4	0
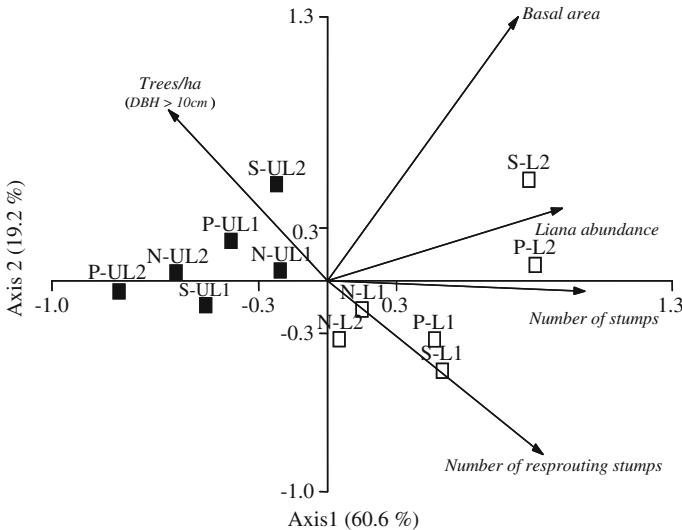
Fig. 6 Principal Component biplot showing the structural characteristics of the logged (L) and unlogeed (UL) sites in the Mayan zone, Mexico. Habitat characteristics are represented by *arrows*

Cannon et al. 1998). Because species population recovery can be positively or negatively affected by changes associated to logging operations (Dickinson et al. 2000; Toledo-Aceves et al. 2009), we would expect that the tree community in logged sites would differ from unlogged sites. This would be particularly true after a number of years in which seedlings of some tree species might have had time to grow beyond the seedling bank. In this work we documented that logged sites were associated with lower number of tree

species, lower number of tree species represented by a single individual, a higher dominance of pioneer species, and with more homogeneous (similar) tree species composition.

Logging effects on tree richness and diversity

In logged sites we documented a reduction in number of tree species in the smaller DBH class (1–5 cm), and in the larger DBH class (>25 cm). This first class represents the tree regeneration contingent, and the larger DBH class includes the individuals upon which logging is performed. Reductions in species richness of the regeneration pool and of the larger trees could have important and synergic consequences, such as local extinction of those intensively harvested species and on the future of the rainforest composition (Jackson et al. 2002; Lawes et al. 2007).

The effect of logging is directly related to the amount of extracted biomass and the precautions taken towards reducing damage to the surrounding vegetation which highly influence the potential negative effects of timber extraction on the remaining tree species after logging operations (Huth and Ditzer 2001; Parrota et al. 2002). In the Maya zone, the volume of timber extracted every year is low to moderate in comparison with other sites in the tropics (Toledo et al. 2011), and preventive measures to reduce the impact of felled trees on the remaining trees are currently taken. In the study sites, diversity loss can be related to the reduction in the number of species represented by just one individual in logged sites. In *ejido* Señor we documented the highest number of singletons. In this site we found the largest difference between logged and unlogged sites in terms of overall tree species diversity and number of singletons species. Generally, species with low abundances are fortuitously impacted when trees are felled, by skidding, and with road construction (Webb 1997; Cannon et al. 1998). Yet, a reduction in the number of species represented by a single individual can in turn decrease the number of tree species in logged sites considerably.

Data indicated a reduced regeneration potential of some marketable species, including mahogany. It has been documented that after logging the initial densities of seedlings are low (Jackson et al. 2002; Peña-Claros et al. 2008). However in the study site, a reduced density of seedlings was still detected 10 years after timber harvesting, in comparison to unlogged areas, suggesting a long term effect of harvesting upon seedling recruitment. Several mechanical damages are associated with logging, one of which is soil compaction, which in turn can affect the rooting capacity of seedlings (Whitman et al. 1997; Pinard et al. 2000). Nonetheless, other causes could be directly related to the absence of propagule contribution by logged adults, as documented in this study site, as well. However, a detailed analysis about the processes involved in the loss of diversity warrants further work.

Diversity loss in logged sites can also be explained by the overrepresentation of pioneer species recorded in logged areas. Thus, the increasing of the dominance of pioneer species, coupled with the reduction in the number of species represented by a single individual as described here, change the overall evenness and consequently the diversity of the tree community is also decreased (Chazdon et al. 1998; Magurran 2004). Studies in a Brazilian tropical dry forest (Villela et al. 2006) and other tropical forests (Kammesheidt 1998; Hall et al. 2003; Brown and Gurevitch 2004), have also documented that pioneer species become dominant in logged areas. Increased dominance of pioneer species could have profound implications in future forest management, inducing the loss of marketable timber species or the further colonization by secondary, even weedy species (Parrota et al. 2002; Hall et al. 2003; Brown and Gurevitch 2004; Villela et al. 2006).

Our results suggest that after 10 years of cutting, species richness and diversity are lower than in unlogged counterparts. As timber extraction is ubiquitously performed in the Zona Maya, this activity could slowly erode species richness until a threshold is reached in which plant diversity drops. The reduction in tree diversity could be associated with changes in canopy openness and the differential recruitment of species (Huth and Ditzer 2001; Köhler and Huth 2007). Under logging programs, this loss of species is a challenge for managers. It is possible that this reduction in species diversity could be mitigated by conducting activities such as the thinning of pioneer species, which can temporarily arrest regeneration and establishment of mature forest tree species (Fredericksen and Licona 2000; Holl 2002; Günter et al. 2009; Vargas et al. 2009).

Although our analysis estimated a floristic similarity of about 75% among sites, the MDS plots showed a clear separation of those sites with logging operations from unlogged ones. All those changes were detected in the four DBH classes analyzed in this study, suggesting that logging can affect the tree composition not only of the smaller trees and larger trees, which were affected by a loss of species, but also in intermediate size individuals (our categories 2 and 3), where shifts in composition and dominance were observed.

Logging effects on tree community structure

We documented several changes in the dominance as expressed by the IV in seven of the 14 tree species most harvested in the Maya zone, including *S. macrophylla*, the most valuable timber species in the region. The drop in dominance was associated with the fact that individuals in unlogged sites had greater basal areas, even though more individuals were recorded in logged sites, similar to the pattern documented for African mahogany (*Entandrophragma* sp.) by Hall et al. (2003). Four species showed positive changes in their IV in logged areas. These species are pioneers and the number of individuals was almost double in those areas.

PCA showed higher stump abundance, number of re-sprouting stumps, and liana abundance associated with logged sites. While little can be said in terms of increased number of stumps, regeneration by re-sprouting is an important characteristic of tropical sites (Putz and Brokaw 1989; Whigham et al. 1991; Paciorek et al. 2000; Mostacedo et al. 2009), but which usually results in trees with undesirable architectural characteristics for future forest management. An important increase in the density of these individuals in the future could eventually reduce the value of the forest, and in turn increase the pressure to transform it into a different land use. Increased liana abundance, on the other hand, might also have negative effects on standing trees and could also potentially affect tree regeneration (Gerwing 2001; Pérez-Salicrup 2001; Parrota et al. 2002; Hall et al. 2003).

Forest management and conservation applications

One of the most significant impediments to achieve long-term sustainability of managed forests is the lack of regeneration of commercial tree species (Whitman et al. 1997; Mostacedo and Fredericksen 1999). Our data suggest that the shift in regeneration composition could be the result of both a loss of adult seeding trees and a change in species representation which after logging is dominated by pioneer species.

Although our results show changes in logged forests, timber harvesting in the Mayan zone is a management practice that provides income to the local communities while having a relatively low impact on rainforest, as compared with the more widespread uses of

tropical lands such as cattle ranching in the Neotropics, including Mexico (Dirzo and García 1992). The small reserves in the study *ejidos*, which were used in this study as reference, unlogged sites, help maintain a representative contingent of the species and vegetation structure that was present before modern management. The expansion of this conservation strategy throughout the whole Mayan forests could represent a chance for tree diversity conservation. This could be enhanced by the application of pre-logging practices, such as the establishment of planned roads, liana management, and directional felling of target trees and other silvicultural treatments (Uhl and Vieira 1989; Pereira et al. 2002; Peña-Claros et al. 2008). In addition, post-logging practices such as reforestation programs, forest enrichment, and pioneer species management may ensure availability of propagules, and promote connectivity via regeneration of secondary and tertiary roads allowing both use of resources and biodiversity conservation.

References

Bray DB, Merino-Pérez L, Negreros-Castillo P, Segura-Warnholtz J, Torres-Rojo M, Vester HFM (2003) Mexico's community-managed forests as a global model for sustainable landscapes. Conserv Biol 17:672–677

Brose U, Martinez ND, Williams RJ (2003) Estimating species richness: sensitivity to sample coverage and insensitivity to spatial patterns. Ecology 84:2364–2377

Brown K, Gurevitch J (2004) Long-term impacts of logging on forest diversity in Madagascar. Proc Natl Acad Sci USA 101:6045–6049

Cannon CH, Peart DR, Leighton M, Kartawinata K (1994) The structure of lowland rainforest after selective logging in West Kalimantan, Indonesia. For Ecol Manag 67:49–68

Cannon CH, Peart DR, Leighton M (1998) Tree species diversity in commercially logged Bornean rainforest. Science 281:1366–1368

Chao A, Chazdon RL, Colwell RK, Shen T-J (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecol Lett 8:148–159

Chazdon RL, Colwell RK, Denslow JS, Guariaguata MR (1998) Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forest of Northeastern Costa Rica. In: Dallmeier F, Comiskey JA (eds) Forest biodiversity, research, monitoring and modeling. UNESCO and The Partenon Publishing Group, New York, pp 285–309

Christensen NL, Bartuska AM, Brown JH et al (1996) The Report of the Ecological Society of America Committee on the scientific basis for ecosystem management. Ecol Appl 6:665–691

Clinebell RR, Phillips OL, Gentry AH et al (1995) Prediction of neotropical tree and liana species richness from soil and climatic data. Biodivers Conserv 4:56–90

Colwell RK (2005) EstimateS: statistical estimation of species richness and shared species from samples. Ver 7.5. Persistent http://purl.oclc.org/estimates

Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. Philos Trans R Soc Lond Ser B 345:101–118

Condit R, Hubbell SP, Lafrankie JV et al (1996) Species-area and species-individual relationships for tropical trees: a comparison of three 50-ha plots. J Ecol 84:549–562

Costa FRC, Magnusson WE (2003) Effects of selective logging on the diversity and abundance of flowering and fruiting understory plants in Central Amazonian forest. Biotropica 35:103–114

Cottam G (1949) The phytosociology of an oak wood in Southwestern Wisconsin. Ecology 30:271–287

Dickinson MB, Whigham DF, Hermann SM (2000) Tree regeneration in felling and natural treefall disturbances in a semideciduous tropical forest in Mexico. For Ecol Manag 134:137–151

Dirzo R, García MC (1992) Rates of deforestation in Los Tuxtlas, a neotropical area in southeast Mexico. Conserv Biol 6:84–90

Durán R, Campos G, Trejo JG et al (1998) Listado florístico de la Península de Yucatán. Centro de Investigación Científica de Yucatán A. C., México

Feldpausch TR, Jirka S, Passos CAM, Jasper F, Riha SJ (2005) When big trees fall: damage and carbon export by reduced impact logging in southern Amazonia. For Ecol Manag 219:199–215

Fredericksen TS, Licona JC (2000) Invasion of non-commercial tree species after selection logging in a Bolivian tropical forest. J Trop For Sci 13:252–263

Galletti HA (1999) La selva maya en Quintana Roo (1983–1996) trece años de conservación y desarrollo comunal. In: Primack RB, Bray D, Galletti HA, Ponciano I (eds) La selva maya, conservación y desarrollo. Siglo XXI editores, México, pp 53–73

Gentry AH (1982) Patterns of neotropical plant species diversity. J Evol Biol 15:1–84

Gerwing JJ (2001) Testing liana cutting and controlled burning as silvicultural treatments for a logged forest in the Eastern Amazon. J Appl Ecol 38:1264–1276

Günter S, Gonzalez P, Alvarez G et al (2009) Determinants for successful reforestation of abandoned pastures in the Andes: Soil conditions and vegetation cover. For Ecol Manag 258:81–91

Gutiérrez-Granados G (2009) Efectos directos e indirectos de la tala selectiva sobre la diversidad vegetal y la interacción planta-mamífero en la selva maya de Quintana Roo. Ph.D. Dissertation, Instituto de Ecología, UNAM, México, p 178

Hall J, Harris DJ, Medjibe V, Asthon PM (2003) The effects of selective logging on forest structure and tree species composition in a Central African forest: implications for management of conservation areas. For Ecol Manag 183:249–264

Holdridge LR (1967) Life zone ecology. Tropical Science Center, San José, Costa Rica

Holl KD (2002) Effect of shrubs on tree seedling establishment in an abandoned tropical pasture. J Ecol 90:179–187

Hortal J, Borges PA, Gaspar C (2006) Evaluating the performance of species richness estimators: sensitivity to sample grain size. J Anim Ecol 75:274–287

Huth A, Ditzer T (2001) Long-term impacts of logging in a tropical rain forest—a simulation study. For Ecol Manag 142:33–51

Jackson SM, Fredericksen TS, Malcolm JR (2002) Area disturbed and residual stand damage following logging in a Bolivian tropical forest. For Ecol Manag 166:271–283

Johns JS, Barreto P, Uhl C (1996) Logging damage during planned and unplanned logging operations in the eastern Amazon. For Ecol Manag 89:59–77

Jongman RHG, ter Braak CJF, van Tongeren OFR (1987) Data analysis in community and landscape ecology. Pudoc, Wageningen, Holand

Kammesheidt L (1998) Stand structure and spatial pattern of commercial species in logged and unlogged Venezuelan forest. For Ecol Manag 109:163–174

Köhler P, Huth A (2007) Impacts of recruitment limitation and canopy disturbance on tropical tree species richness. Ecol Model 203:511–517

Lawes MJ, Griffiths ME, Boudreau S (2007) Colonial logging and recent subsistence harvesting affect the composition and physiognomy of a podocarp dominated Afrotemperate forest. For Ecol Manag 247:48–60

Magurran AE (2004) Measuring biological diversity. Blackwell, Oxford

Makana J-R, Thomas SC (2005) Effects of light gaps and litter removal on the seedling performance of six African timber species. Biotropica 37:227–237

Mostacedo B, Fredericksen TS (1999) Regeneration status of important tropical forest tree species in Bolivia: assessment and recommendations. For Ecol Manag 124:263–273

Mostacedo B, Putz FE, Fredericksen TS, Villca A, Palacios T (2009) Contributions of root and stump sprouts to natural regeneration of a logged tropical dry forest in Bolivia. For Ecol Manag 258:978–985

Negreros-Castillo P, Mize CW (2008) Regeneration of mahogany and Spanish cedar in gaps created by railroad tie extraction in Quintana Roo, México. For Ecol Manag 255:308–312

Negreros-Castillo P, Snook L, Mize CW (2003) Regenerating mahogany (*Swietenia macrophylla*) from seed in Quintana Roo, Mexico: the effects of sowing method and clearing treatment. For Ecol Manag 183:351–362

Olmsted I, Durán R (1990) Vegetación de Sian Ka'na. In: Navarro DL, Robinson JG (eds) Diversidad Biológica en la reserva de la Biosfera de Sian Ka'an Quintana Roo, México. Centro de Investigaciones de Quintana Roo, México, pp 1–13

Paciorek CJ, Condit R, Hubbell SP et al (2000) The demographics of resprouting in tree and shrub species of a moist tropical forest. J Ecol 88:765–777

Panfil SN, Gullison RE (1998) Short term impacts of experimental timber harvest intensity on forest structure and composition in the Chimanes forest, Bolivia. For Ecol Manag 102:235–243

Parrota JA, Francis JK, Knowles OH (2002) Harvesting intensity affects forest structure and composition in an upland Amazonian forest. For Ecol Manag 169:243–255

Peña-Claros M, Peters EM, Justiniano MJ et al (2008) Regeneration of commercial tree species following silvicultural treatments in a moist tropical forest. For Ecol Manag 255:1283–1293

Pereira R, Zweede J, Asner GP, Keller M (2002) Forest canopy damage and recovery in reduced-impact and conventional selective logging in eastern Para, Brazil. For Ecol Manag 168:77–89

Pérez-Salicrup DR (2001) Effect of liana cutting on tree regeneration in a liana forest in Amazonian Bolivia. Ecology 82:389–396

Pérez-Salicrup DR (2004) Forest types and their implications. In: Turner BL II, Geoghegan J, Foster DR (eds) Integrated land-change science and tropical deforestation in the southern Yucatán: Final frontiers. Oxford University Press, Oxford, pp 63–80

Phillips O, Miller JS (2002) Global patterns of plant diversity: Alwyn H. Gentry's Forest Transect Data Set. Monographs in systematic botany from the Missouri Botanical Garden. Missouri Botanical Publisher, St. Louis

Pinard MA, Barker MG, Tay J (2000) Soil disturbance and post-logging forest recovery on bulldozer paths in Sabah, Malaysia. For Ecol Manag 130:213–225

Putz FE, Brokaw NVL (1989) Sprouting of broken trees on Barro Colorado Island, Panama. Ecology 70:508–512

Snook LK (1999) Aprovechamiento sostenido de la caoba (Swietenia macrophylla, King) en las selvas de la península de Yucatán México. In: Primack RB, Bray D, Galletti HA, Ponciano I (eds) La selva maya, conservación y desarrollo. Siglo XXI editores, México, pp 98–119

Sokal RR, Rohlf FJ (1995) Biometry. Freeman, New York

ter Steege H, Welch I, Roderick Z (2002) Long-term effect of timber harvesting in the Bartica Triangle, Central Guyana. For Ecol Manag 170:127–144

ter Steege H, Pitman N, Sabatier D et al (2003) A spatial model of tree α-diversity and tree density for the Amazon. Biodivers Conserv 12:2255–2277

Toledo M, Poorter L, Peña-Claros M et al (2011) Climate is a stronger driver of tree and forest growth rates than soil and disturbance. J Ecol 99:254–264

Toledo-Aceves T, Purata-Velarde S, Peters CM (2009) Regeneration of commercial tree species in a logged forest in the Selva Maya, Mexico. For Ecol Manag 258:2481–2489

Trejo I, Dirzo R (2002) Floristic diversity of Mexican seasonally dry tropical forests. Biodivers Conserv 11:2048–2063

Uhl C, Vieira ICG (1989) Ecological impacts of selective logging in the Brasilian Amazon: a case study from the Paragominas region of the state of Para. Biotropica 21:98–106

Vargas R, Allen EB, Allen MF (2009) Effects of vegetation thinning on above- and belowground carbon in a seasonally dry tropical forest in Mexico. Biotropica 41:302–311

Verissimo A, Barreto P, Mattos M, Tarifa R, Uhl C (1992) Logging impacts and prospects for sustainable forest management in an old Amazonian frontier: the case of Paragominas. For Ecol Manag 55:169–199

Villela DM, Nascimento MT, Aragão LEOC, Gama DM (2006) Effect of selective logging on forest structure and nutrient cycling in a seasonally dry Brazilian Atlantic forest. J Biogeogr 33:506–516

Webb EL (1997) Canopy removal and residual stand damage during controlled selective logging in lowland swamp forest of northeast Costa Rica. For Ecol Manag 95:117–129

Whigham DF, Olmsted I, Cabrera E et al (1991) The impact of hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the northeastern Yucatan peninsula. Biotropica 23:434–441

Whitman AA, Brokaw NVL, Hagan JM III (1997) Forest damage caused by selection logging of mahogany (Swietenia macrophylla) in northern Belize. For Ecol Manag 92:87–96