EFFECTS OF SELECTIVE LOGGING AND SHIFTING CULTIVATION ON THE STRUCTURE AND DIVERSITY OF A TROPICAL EVERGREEN FOREST IN SOUTH-EASTERN MEXICO

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CASTRO-LUNA AA, CASTILLO-CAMPOS G & SOSA VJ. 2011. Effects of selective logging and shifting cultivation on the structure and diversity of a tropical evergreen forest in south-eastern Mexico. In order to make recommendations on forest management, we compared the floristic composition, diversity and physiognomy of a tropical evergreen forest (TEF) vegetation regenerating after two types of past use, namely, selective cutting and shifting cultivation, in Agua Blanca State Park, Mexico. These common types of use caused different kinds of forest disturbances. Plant cover was sampled in 32 quadrats randomly distributed in four stands of logged forest and four stands of secondary vegetation on land previously used for agriculture. A total of 220 species were recorded in 156 genera and 78 families of vascular plants. There were marked differences in the floristic composition, diversity and physiognomy between types of vegetation regenerations. Woody cover, canopy height and canopy cover were significantly higher in the selectively logged TEF than in the secondary vegetation after shifting cultivation, but herbaceous plant cover was comparable between regeneration types. Dominant tree and shrub species were different between regeneration types. The short fallow period for the plots previously used for agriculture resulted in the absence of intermediate regeneration stages, thus, hindering the succession of stands towards floristic composition and structure similar to those of logged TEF. Some alternative types of landuses that could mitigate negative impacts on forest regeneration are also discussed.

Keywords: Landuse, arrested succession, karst, Mesoamerica, Tabasco

CASTRO-LUNA AA, CASTILLO-CAMPOS G & SOSA VJ. 2011. Kesan tebangan memilih serta pertanian pindah terhadap struktur dan kepelbagaian hutan malar hijau tropika di tenggara Mexico. Sebagai usaha membuat pengesyoran tentang pengurusan hutan, kami membandingkan komposisi flora, kepelbagaian dan fisiognomi tumbuhan hutan malar hijau tropika (TEF) yang tumbuh selepas dua jenis penggunaan tanah yang berbeza iaitu tebangan memilih serta pertanian pindah. Kajian dijalankan di Agua Blanca State Park, Mexico. Penggunaan tanah ini mengakibatkan gangguan hutan yang berbeza. Tumbuhan tutup bumi disampel di 32 kuadrat yang bertabur secara rawak di empat dirian hutan sudah kerja dan empat dirian tumbuhan sekunder di kawasan yang dahulunya diguna untuk pertanian. Sebanyak 220 spesies direkod yang tergolong dalam 156 genus serta 78 famili tumbuhan pembuluh. Terdapat perbezaan ketara dalam komposisi flora, kepelbagaian dan fisiognomi antara jenis tumbuhan yang terjana semula itu. Litupan tumbuhan berkayu, ketinggian kanopi serta litupan kanopi lebih besar di TEF yang mengalami tebangan memilih berbanding tumbuhan sekunder selepas pertanian pindah. Bagaimanapun litupan tumbuhan herba agak sama bagi kedua-dua hutan. Spesies pokok serta pokok renek pula berbeza antara kedua-dua jenis hutan. Tempoh rang singkat bagi plot yang dahulunya digunakan untuk pertanian telah menyebabkan tidak wujud peringkat penjanaan semula pertengahan di hutan itu. Ini telah menghalang penggantian dirian dengan komposisi flora serta struktur yang serupa dengan TEF yang telah ditebang secara memilih. Penggunaan tanah alternatif yang dapat mengurangkan impak negatif terhadap penjanaan semula hutan turut dibincangkan.

INTRODUCTION

Tropical forests in Mesoamerica are among the most important diversity hot spots in the world. Covering 0.5% of the earth's land mass, these forests hold 17% of the total diversity of terrestrial species known to date (Davis et al. 1997, Myers et al. 2000). Northern Mesoamerica (Belize, Guatemala and south-eastern Mexico) is distinguished by its complex biogeographic origin

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and by karst topography which is characterised by high permeability and shallowness that limit its capacity to retain rainwater. Soils on karst land are more susceptible to desiccation and fire compared with other neotropical soils (Watson et al. 1997, Condit 1998), and small differences in elevation can intensify the effects of seasonal drought (Brewer et al. 2003). The flora of the region, in spite of its high diversity and high percentage of endemism (Burnham & Graham 1999, Wendt 1993), has received little attention (Kelly et al. 1988, Brewer et al. 2003). The vast majority of floristic studies done in the New World tropical forests has so far concentrated on the south of Mesoamerica and South America. The exception is the Los Tuxtlas Biosphere Reserve in southern Veracruz, Mexico located on substrates of volcanic origin, in contrast to other tropical forests in northern Mesoamerica (Hughes et al. 2000).

In the last few decades the surface area of the tropical forests of Mexico and Central America has decreased dramatically owing to activities such as logging, cattle ranching and agriculture (Brown & Lugo 1990). In this study we focused on changes in the floristic composition, diversity and physiognomy of a tropical evergreen forest modified by shifting cultivation and selective cutting. Shifting cultivation, linked to Mesoamerican cultures since pre-Columbian times, continues to be a fundamental activity in the economy of many indigenous and rural 'mestizo' communities (Challenger 1998, Pope 2001, Toledo et al. 2003). In essence, shifting cultivation consists of cutting down the forest or secondary vegetation, and burning the remaining stems and trunks mainly for growing the 'milpa', which is a mixture of corn, beans, squash and other staple crops grown for the family. The relatively small fields are used for one or two years until the fertility of the soil drops; at which point they are abandoned. After a fallow period usually lasting 10–15 years, the process is repeated (Challenger 1998). Selective cutting in forests of the region has focused mainly on red cedar (*Cedrela odorata*) and mahogany (*Swietenia macrophylla*), both valuable timber species (Pennington 1981, Tropical Science Center 2000). The impact of selective cutting on the floristic composition and physiognomy of tropical forests depends on the cutting intensity, the characteristic of the tree species itself and the ecosystem. For example, changes in the composition of understorey plants were minimal for low intensity selective cutting (Costa & Magnusson 2002, 2003), but changes in floristic composition and diversity were severe when many trees were cut or as a result of indirect effects (i.e. fires) associated with high logging intensity (Siegert et al. 2001, Cochrane et al. 2002).

Fast population growth and migration have also had negative effects on the remnants of the forest. The majority of Mexico's forest (80%) occurs in parks and reserves with limited accessibility, steep slopes and land where agriculture is practically impossible (Sader et al. 2004). Even so, anthropogenic pressure on these natural reserves continues to increase as population density increases and with it, the demand for agricultural and forest products (World Bank 1992, Templeton & Scherr 1997). It has gotten to the point where deforestation rates in some protected areas are higher than in the woods that are managed for lumber extraction (Durán et al. 2007). This has led to the idea that a realistic vision of conservation for these ecosystems is that of ecosystems where a certain degree of use is allowed (Noble & Dirzo 1997). Thus, the impact of human activities on plant communities of the region must be understood in order to develop effective management and conservation strategies.

This study was carried out in the state of Tabasco, Mexico where 90% of the original vegetation has been replaced by pastures for extensive cattle ranching. Specifically, the field work was done in a forest reserve which, in spite of its status as a protected natural area, is under strong exploitation pressure by the surrounding population which causes constant disturbances. Our goal was to compare the effects of two different types of past landuses—selective logging and shifting cultivation—on tropical evergreen forest, and based on this information, offer management advice. We posed the question, how different are the floristic composition and the physiognomy in selectively logged tropical evergreen forest compared with secondary vegetation where shifting cultivation had been practised?

We expected differences in either floristic composition or physiognomy because, even though regeneration after shifting cultivation can occur very rapidly in tropical climates, the practice of rapid crop rotation (less than 16 years before a new slash and burn), might be arresting secondary succession. On the other hand, the 32 years that had elapsed since the relatively less severe disturbance of selective cutting was expected to allow these stands to develop a vegetation structure more similar to that of primary forest.

MATERIALS AND METHODS

Study area

This study was conducted in the Agua Blanca State Park (ABSP), Tabasco, Mexico, a tropical forest reserve with an area of 2025 ha managed by the rural inhabitants of the Manatinero-Palomas 'ejido' (communal land under the stewardship of rural inhabitants for agricultural activities). The study area belongs to the physiographic province of the Sierra de Chiapas Mountain Range and is located between the geographic coordinates 17° 35' to 17° 37' N and 92° 27' to 92° 28' W (Figure 1). The climate is type Am(f) w"i'g according to the Köppen climate classification modified by García (1973): warm (mean annual temperature of 26 °C) and humid with rainfall year round. Mean annual precipitation is 3500 mm, most of which falls during the rainy season (June–November, monthly mean 419.8 mm) with the remainder falling as scattered showers (December–May, monthly mean 174.9 mm) (INEGI 1994).

Eighty per cent of the vegetation in the ABSP is tropical evergreen forest (TEF), located on scarped, rocky terrain that is difficult to access. Most of this forest was disturbed by selective logging in the 1970s, resulting in the proliferation of secondary vegetation (Cruz-Hernández 1999). After the disturbance, local inhabitants used this area for hunting and gathering and this allowed the vegetation to recover.

Currently, shifting cultivation is the most common landuse in the ABSP. Since soils of the ABSP are characterised by a limestone substrate and are very shallow, arable land is limited. Thus, areas where the forest has been cut to establish milpas are still surrounded by logged TEF, although all these characteristics have also resulted in a more rapid rotation of crop plots. As a consequence, it is increasingly difficult to find fragments of secondary vegetation that have been abandoned for more than 15 years.

Vegetation sampling

We selected four sampling sites each that represented the two types of vegetation regeneration after two types of landuse, namely, selective cutting and slash-and-burn cultivation. The sites were selected based on their accessibility and topography. We obtained satellite images from 2001 (NASA Landsat Program 2003:

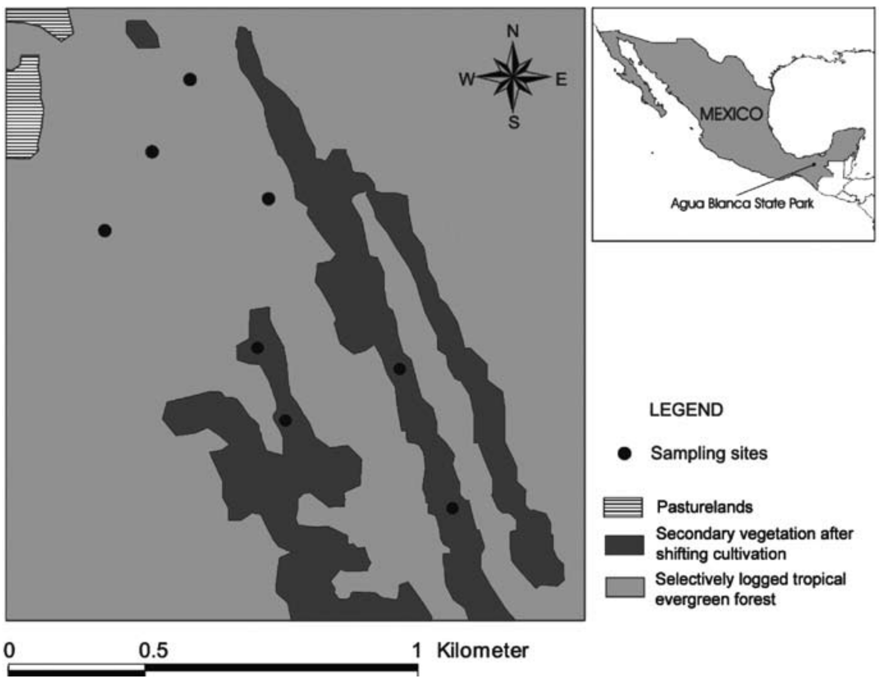

Figure 1 Location of the study area in south-eastern Mexico and the distribution of sites where vegetation was sampled

Landsat ETM+ multispectral, WRS-2, path 022, row 048, orthorectified) and the area of each successional stage was delimited with a combination of bands 5, 2 and 1 using ArcView Geographic Information Systems 3.2 software (GIS, Environmental Systems Research Institute, Redlands, California). The vegetation type at each site was verified during extensive field surveys and information was collected from the local population to obtain the approximate time of abandonment of milpas at the selected sites. For the vegetation regenerating after slash-and-burn cultivation we selected sites that had been abandoned for 5 to 10 years.

To determine the vegetation composition and physiognomy of each type of regeneration, at each of the sites, we randomly set up four 10 × 10 m plots (400 m^2 estimated minimum sampling area), separated by at least 50 m, for a total of 0.16 ha for each regeneration type) to better represent spatial variation (Gotelli & Ellison 2004). Within each plot, we estimated the per cent cover of each woody species using the scale proposed by van der Maarel (1979). We also estimated the following variables representative of the physiognomy of the vegetation: (1) per cent total cover of woody species (trees, shrubs and lianas), (2) per cent total cover of herbaceous species (herbs and vines), (3) per cent cover of the upper canopy, and (4) mean canopy height (van der Maarel 1979). Inside each 100 m^2 plot we randomly placed three 2 × 2 m quadrats in which we recorded herbaceous species cover using the same method as for woody plants. Most of the plant species were identified in the field and when this was not possible, botanical materials were collected, prepared and deposited in the XAL Herbarium at the Instituto de Ecología, A. C., where they were later identified.

Data analysis

For each vegetation type we estimated the evenness index (Magurran 2004), transforming the cover value per species in each quadrat into mean cover value (van der Maarel 1979). We also determined life form (tree, shrub, herb, liana or vine) and regeneration guild for each species. For life form we followed the complementary classifications of Guevara et al. (1994, 2004). To distinguish between lianas and vines we followed Gentry (1991) who described lianas as woody climbers with thick stems and vines as herbaceous climbers with slender stems. We assigned plants to regeneration guilds (primary or secondary vegetation) based on Miranda and Hernández (1963).

One-way ANOVA was used to test for differences in species richness and evenness and in the physiognomy variables for each regeneration type. Prior to this, all variables measured as percentages were transformed to $\sin^{-1}\sqrt{p}$, where p is proportion. The analyses were done in S-Plus 2000 (MathSoft 1999, Seattle).

Non-metric multidimensional scaling (NMDS) was used to compare the floristic composition of vegetation in the sampling plots (Clarke 1993). NMDS is a robust ranking technique that graphically demonstrates similarity in species ensembles between sites, without making any assumption of a linear relationship between variables (McCune & Mefford 1999). For this, we constructed a similarity matrix with the Bray–Curtis coefficient for untransformed data, using the cover value for each woody and herbaceous species in each 10 × 10 m plot. We ran 1000 iterations and estimated the success of the ranking as a function of the stress value obtained, where low stress values (< 0.1) indicate that the sample ranking is a good representation of the similarity between vegetation plots, while high stress values (> 0.25) indicate the opposite (Clarke & Warwick 2001).

To test the statistical validity of the ranking results of the NMDS, we used an analysis of similarity (ANOSIM) (Clarke 1993). The similarity rank R_{ANOSIM} is a relative measure of the separation between groups that have been defined a priori. Zero indicates that there is no difference between groups, while a value of 1 indicates that all samples within the same group are more similar to each other than they are to those in the other groups. The taxa responsible for similarity, as well as those responsible for dissimilarity between the logged tropical evergreen forest (LTEF) and the secondary vegetation after cultivation were determined using the SIMPER algorithm of the PRIMER program (Clarke 1993). All of these analyses were done using PRIMER version 5 software (2001).

RESULTS

General description of the vegetation

In total, we recorded 220 species of vascular plants, belonging to 156 genera and 78 botanical families (Appendix). The families with the highest species richness were Fabaceae (25), Rubiaceae (11), Arecaceae (10) and Araceae (10). Herbaceous plants (76 species) were the greatest life form followed by shrubs (49), trees (73), vines (13) and lianas (9) (Appendix).

Selectively logged tropical evergreen forest (LTEF)

This type of vegetation comprised mainly primary species. Cover values were high for tree species with some reaching 36 m in height. The most representative families were Araceae, Arecaceae, Acanthaceae, Meliaceae and Sapotaceae. In LTEF we recorded a high value for floristic richness (138 species) and canopy cover was 83.6%. LTEF had the greatest richness of primary species (99 species), mostly herbaceous plants and trees (Appendix). We identified five layers. The upper canopy comprised trees that were 30–36 m tall and dominated by *Dialium guianense*, *Poulsenia armata* and *Quararibea funebris*. The second arboreal layer had trees 19.1–29.9 m in height, with *Guarea* sp. and *Q. funebris* being the most dominant. The third layer was 7.1–19 m in height with dominant species *Decaxyz sparzae*, *Guarea* sp. and *Q. funebris*. The fourth layer was dominated by *Astrocaryum mexicanum*, *Rinorea guatemalensis*, *Faramea occidentalis* and *Louteridium mexicanum*. The herbaceous layer was characterised by shade tolerant species such as *Anthurium pentaphyllum*, *Dieffenbachia seguine*, *Heliconia aurantiaca* and *Sageretia elegans*, as well as five species in the Arecaceae family.

Secondary vegetation after cultivation

This vegetation type was dominated by secondary species. With a relatively low canopy this vegetation type had high proportions of herbaceous plants, vines and lianas. The most characteristic families were Poaceae, Asteraceae, Euphorbiaceae and Smilacaceae, which were exclusive to, or had the highest cover values in this type of vegetation.

Plant species richness was 126 and herbaceous plants were the most common life form, although trees and shrubs were also important (Figure 2). There were three layers with relatively disperse canopy (33.8% cover) and, where trees reached 15 m tall, mainly dominated by *Heliocarpus mexicanus*, *Cochlospermun vitifolium* and *Cecropia obtusifolia*. The second layer comprised mainly trees 4.1–9.9 m in height, with *Bursera simaruba*, *Cupania dentata*, *H. mexicanus* and *Trema micrantha* as dominants. The lowest layer was dominated by the woody species *Casearia corymbosa*, *Piper aduncum* and *Cordia alliodora*, and by the herbaceous plants *Desmodium axillare*, *Heliconia latispatha*, *Lasiacis divaricata* and *Maranta arundinacea*.

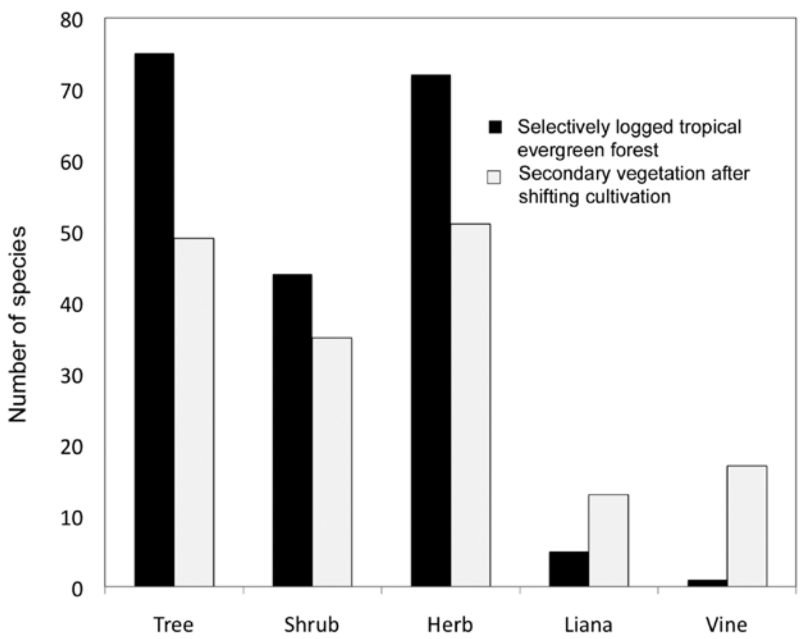

Figure 2 Distribution of life forms in the logged tropical evergreen forest and secondary vegetation after shifting cultivation

Diversity, physiognomy and floristic similarity of the regeneration types

The species evenness of the secondary vegetation was significantly greater than that of the LTEF, but there were no significant differences in species richness between regeneration types (Table 1). For physiognomy, there were no significant differences in the per cent cover of herbaceous plants between the two regeneration types, but per cent cover by woody plants, canopy height and canopy cover were significantly greater in LTEF (Table 1).

NMDS ranking revealed that, based on cover, the plots clearly fell into two groups: one corresponding to LTEF and the other to secondary vegetation after cultivation (Figure 3). The stress value was 0.14 and this indicated that the ordination of the two axes used in Figure 3 was reliable. The floristic compositions of the LTEF and the secondary vegetation were markedly different ($R_{ANOSIM} = 0.923$, $p < 0.001$). The SIMPER analysis gave a value of mean dissimilarity between vegetation types of 98.33% while mean similarity between LTEF plots was 28.92, and similarity between secondary

Table 1 Summarised ANOVA tables for vegetation structure variables compared between logged tropical evergreen forest and secondary succession after shifting cultivation

Response variable	Source of variation	Degrees of freedom	Mean square	F	p
Species richness[a]	Regeneration type	1	1.086^{-5}	0.002	0.97
	Error	30	6.019^{-3}		
Evenness[b]	Regeneration type	1	0.043	17.58	2.20^{-4}
	Error	30	0.002		
Per cent cover of herbaceous plants[c]	Regeneration type	1		0.33	
	Error	30			
Per cent cover of woody plants[c]	Regeneration type	1	943.7	7.55	0.57
	Error	30	124.9		
Per cent canopy cover[c]	Regeneration type	1	8256.5	116.20	7.74^{-12}
	Error	30	71.05		
Canopy height	Regeneration type	1	2.15	73.68	1.41^{-9}
	Error	30	0.03		

[a]log (S); [b]evenness index; [c]$\sin^{-1}\sqrt{proportion}$

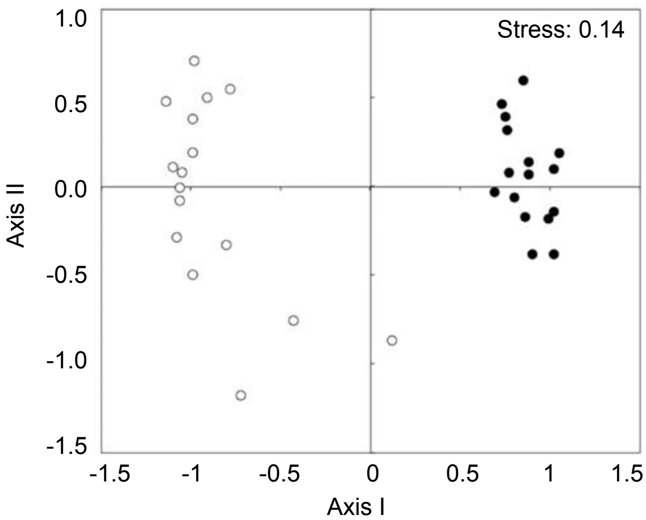

Figure 3 Rank of the plant plots according to non-metric multidimensional scaling (NMDS), showing differences in floristic composition between the two types of vegetation regeneration; secondary vegetation (black dots) and selectively logged tropical evergreen forest (clear dots)

vegetation plots was 18.84%. The species that contributed most to the similarity within LTEF and secondary vegetation samples, as well as the dissimilarity between them are listed in Table 2.

DISCUSSION

Results of this study showed that the floristic composition, diversity and physiognomy of the selectively logged TEF were markedly different from those of the secondary vegetation growing in abandoned plots after slash-and-burn cultivation. There were few species in common between the two vegetation types and it appeared that these differences resulted from the distinct processes of forest regeneration that occurred depending on the disturbance factor and the history of landuse. Secondary vegetation grew in plots where the TEF had been completely removed, suggesting that different colonisation phases by pioneer species occurred (Wijdeven & Kuzee 2000). In LTEF, in contrast, disturbance from selective cutting left most of the individual trees alive, allowing the damaged vegetation to resprout (Turner et al. 1998, Chazdon 2003).

It has been reported that under low extraction intensity, some forest recovers rapidly after selective cutting (Malcolm & Ray 2000, Pinard et al. 2000). However, in some of the LTEF plots we found trees and shrubs characteristic of secondary vegetation (e.g. *Acalypha diversifolia* and *Cecropia obtusifolia*), as well as physical evidence of disturbance (i.e. lower canopy cover) as long as 30 years after the trees had been cut. It is important to remember that the TEF occurs on a limestone substrate (Castillo & Zavala 1996) and this could be slowing down the recovery of the vegetation. This type and texture of soil can retard and even stop the process of succession towards a mature forest (Chazdon 2003, Paul et al. 2004). As the density of large trees reduced, large gaps opened in the vegetation and caused proliferation or disappearance of certain species, especially in the understorey (Capellotto et al. 2002, Smith 1987). For example, *A. mexicanum* was dominant in the less disturbed LTEF plots but was absent or very rare in plots with the highest degree of deterioration from selective cutting (i.e. lower canopy cover). In contrast, *L. mexicanum* was abundant in the plots showing the greatest signs of disturbance. The explanation for these contrasting results is that *A. mexicanum,* a shade-loving species that reproduces at the age of about 39 years old, is one of the most characteristic species of well-conserved forests in the region (Piñero et al. 1984, Purata 1986, Sarukhán 1980). *Louteridium mexicanum,* however, has been favoured by its ability to colonise sites with limestone substrates that have been disturbed by selective cutting (García-Rosales 1999).

Species turnover between vegetation types was high. There was scarcity of seedlings of late successional and primary species in the plots where shifting cultivation had been carried out. However, tropical forest on land used for this type of agriculture showed rapid recovery (Uhl 1987, Guariguata & Ostertag 2001, Makana & Thomas 2006). This may be a result of the intense use of the soil since some parts of the ABSP have been used intermittently since 1965, causing a drastic decrease in the level of organic material in the soil (Castillo & Zavala 1996). Repeated use of the soil prevents the regeneration of tropical forest from reaching mature successional stages, thus, impoverishing the nutrient content (Guariguata et al. 1997, Ferguson et al. 2003, Dieckmann et al. 2007). This will in turn cause changes in plant species composition (Lawrence et al. 2005).

It is likely that other factors, both biotic (i.e. predation) and abiotic (i.e. microclimate and soil characteristics) are affecting the germination and seedling establishment of the primary forest in the abandoned plots of the ABSP. Limestone substrate and karst terrain are very susceptible to desiccation and fire during the dry season and periods of drought; these conditions kill the seedlings and saplings of the more sensitive species (Watson et al. 1997, Condit 1998, Brewer et al. 2003). Distance to seed source is also very important to the development of floristic composition in abandoned plots (Purata 1986) because vast expanses that are devoid of trees are usually not visited by bats and birds, the main seed dispersers in tropical regions (Galindo-González et al. 2000). However, the LTEF vegetation in the present study area was close to the areas that had been deforested and had high abundance of bats (Castro-Luna et al. 2007) and birds in its secondary vegetation (AA Castro-Luna, personal observation). Medium size and large mammals (peccaries, deer and tapir) have been extirpated from the study area by hunting. Given that these animals are the main vectors of large-seeded plants, this may cause the low recruitment of late successional stage and primary plants in the area

Table 2 Species making the greatest contribution to similarity within sites in tropical evergreen forest undergoing two types of regenerations

Species	LF	RG	Selectively logged tropical evergreen forest				Secondary vegetation after shifting cultivation			
			S1	S2	S3	S4	S1	S2	S3	S4
Rinorea guatemalensis	S	P	28.2	5.2	23.5					
Astrocaryum mexicanum	S	P	22.2		12.3					
Guarea sp.	T	P	19.9			18.4				
Spondias radlkoferi	T	P	12.2					2.7		5.4
Rubiaceae	T	U	9.6							
Faramea occidentalis	S	P		22.8		9.5				
Louteridium mexicanum	S	S		12.8		7.9				
Acalypha diversifolia	S	S		12.8			25	5.9	7.7	
Quararibea funebris	T	P		11.6	29.2	17.1				
Mirandea sylvatica	H–S	P		11.2						
Hyperbaena jalcomulcensis	T	P		10.9						
Syngonium sp.	H	S		5.2						
Poulsenia armata	T	P			12.8					
Dialium guianense	T	P			6.9	12.6				
Hyperbaena mexicana	T	P			5.8					
Tradescantia zanonia	H	P				8.4				
Aphelandra aurantiaca	H	P				8				
Pouteria unilocularis	T	P				5.6				
Anthurium pentaphyllum	V	P				5.6				
Cupania dentata	T	S					14.5		12.5	3
Leucaena glauca	T	S					10.6			
Hamelia patens	S	S					8.6	16.3	6.7	7
Heliocarpus mexicanus	T	S					8.3	41	10	18.8
Lantana camara	S	S					7.9			
Tragia sp1.	H	S					4.9			
Melanthera nivea	H	S					4.7			
Scleria bracteata	H	S					4.2	8.9		
Cochlospermun vitifolium	T	S					2.3		14.4	
Heliconia latisphata	H	S						7.8	5.7	
Dalbergia brownei	S	S						4.6		
Acacia angustissima	T	S						3.3		
Senna quinquangulata	S	S							14.4	
Guazuma ulmifolia	T	S							8.1	
Vernonia patens	S	S							7.2	
Machaerium kegelii	L	S							4.4	
Verbesina sp.	S	S								11.5
Trema micrantha	T	S								11.2
Bursera simaruba	T	S								9.7
Cecropia obtusifolia	T	S								9.7
Piper hispidum	S	S								8.8
Phylodendron tripartitum	H	S								7.5
Cumulative percentage			92.1	92.5	90.6	93	91.2	90.6	91.2	92.6

Values are the percentages obtained using the SIMPER algorithm. Sampling sites for each regeneration type were consecutively named S1, S2, S3 and S4. LF = life form (T = tree; S = shrub; H = herbaceous plant; V = vine; L = liana); RG = regeneration guild (P = primary; S = secondary; U = unknown)

(Wunderle 1997). This has not yet been tested in the ABSP, but owing to the strong plant–animal interaction in the Los Tuxtlas Biosphere Reserve in Mexico, the disappearance of megafauna has had a negative effect on plant species composition of primary forests (Dirzo & Miranda 1990).

Implications for conservation and forest management

In the ABSP the status of the forest reserve, along with the mountainous terrain and its thin rocky soil, has favoured the conservation of the once logged tropical evergreen forest. However, the short fallow period for the plots that were used for agriculture has resulted in the absence of intermediate regeneration stages, with poor representation of the species characteristic of those stages. Thus, it is recommended that communal farmers allow some plots to complete their regeneration right up to the stage of mature secondary vegetation; there would then be more than just two classes of vegetation (e.g. the selectively logged forest and early secondary vegetation). The reduction in the fallow time of soils used for shifting cultivation appears to be a widespread problem in tropical regions (Dalle & de Blois 2006). Thus, future studies should focus on finding alternate uses for these soils in order to lighten the pressure on wooded land in the tropics.

With the current degree of landuse in the park, the logged TEF is still well preserved and can act as a genetic reservoir for regeneration should farmers change to a way of making a living other than shifting cultivation. It is important to mention that ecotourism is an alternative landuse with high potential for this region because there is a 5200 m long cave system (Pisarowicz 1988) as well as a natural spring that runs over rough terrain, creating pools and waterfalls. As tourist development programmes emerge and more people become involved, dependence on agriculture could decrease and with it, the pressure on the land (Ellis & Porter-Bolland 2008). Moreover, it should be noted that limestone soils are very common in the Mesoamerican biodiversity hotspot, the Caribbean and the Brazilian Cerrado. This is why information provided by this study as well as management recommendations can be extended to other places with similar characteristics.

Another aspect that has not yet been considered for the management of the park is payment for environmental services. This should be an interesting alternative for the conservation of the forests in the region given that current policies encourage these strategies (Alix-García et al. 2005). This has been done in some parts of the Yucatan Peninsula and with rational use of alternative forest resources (e.g. the cultivation of *Chamaedorea* palms) or agroforestry (Bhagwat et al. 2008), the quality of life of the rural inhabitants can be improved and at the same time increase their commitment to conserve the resources under their stewardship.

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Appendix Floristic list for two types of tropical evergreen forest regeneration studied in the Agua Blanca State Park in Tabasco, Mexico

FAMILY[1] *Species*	LTEF	SV	LF	RG
PTERIDOPHYTA				
ADIANTACEAE				
Adiantum pulverulentum L.	0.19 ± 0.73	-	H	P
Hemionitis palmata L.	-	1.17 ± 3.40	H	S
ASPLENIACEAE				
Asplenium alatum Humb. and Bonpl. ex Willd.	0.002 ± 0.008	-	H	P
Asplenium delitescens (Maxon). L.D. Gómez	0.004 ± 0.01	-	H	P
Asplenium sp.	0.002 ± 0.008	-	H	P
LOMARIOPSIDACEAE				
Lomariopsis recurvata Fée	1.30 ± 5.21	-	T	P
NEPROLEPIDACEAE				
Nephrolepis biserrata (Sw.) Schott	0.002 ± 0.008	-	H	P
POLYPODIACEAE				
Genus not determined	-	0.002 ± 0.008	H	U
Genus not determined	0.36 ± 1.46	-	H	U
PTERIDACEAE				
Pteris altissima Poir.	0.002 ± 0.008	-	H	P
SCHYZACEAE				
Lygodium heterodoxum Kunze	0.04 ± 0.11	5.97 ± 6.64	V	S
Lygodium venustum Sw.	-	0.18 ± 0.73	V	S
TECTARIACEAE				
Ctenitis melanosticta (Kunze) Copel.	0.41 ± 1.56	0.39 ± 1.56	H	P
Tectaria heracleifolia (Willd.) Underw.	0.002 ± 0.008	-	H	P
THELYPTERIDACEAE				
Thelypteris toganetra A.R. Sm.	-	0.61 ± 1.79	H	S
LILIOPSIDA				
ARACEAE				
Anthurium pentaphyllum (Aubl.) G. Don	3.89 ± 6.20	0.18 ± 0.73	V	P
Anthurium podophyllum (Cham. and Schltdl.) Kunth	4.30 ± 7.63	1.74 ± 5.08	H	P
Anthurium schlechtendalii Kunth	0.006 ± 0.01	-	H	P
Dieffenbachia seguine (Jacq.) Schott	4.02 ± 7.82	-	H	P
Philodendron radiatum Schott	0.002 ± 0.008	-	V	P
Philodendron tripartitum (Jacq.) Schott	0.61 ± 1.67	11.38 ± 28.30	V	P
Rhodospatha cf. wendlandii Schott	1.30 ± 5.21	-	H	P
Spathiphyllum cochlearispathum (Liebm.) Engl.	0.78 ± 3.13	-	H	P
Syngonium chiapensis Matuda	0.21 ± 0.73	-	H	P
Syngonium podophyllum Schott	0.004 ± 0.01	2.54 ± 5.51	V	P
ARECACEAE				
Astrocaryum mexicanum Liebm.	20.08 ± 22.53	0.006 ± 0.03	S	P
Chamaedorea elegans Mart.	0.01 ± 0.02	-	H	P

(continued)

Appendix (continued)

FAMILY[1] *Species*	LTEF	SV	LF	RG
Chamaedorea ernesti-augusti H. Wendl.	1.60 ± 3.60	-	H	P
Chamaedorea oblongata Mart.	1.96 ± 6.34	0.002 ± 0.008	H	P
Chamaedorea sp.1	0.78 ± 3.13	-	S	P
Chamaedorea sp. 2	0.55 ± 1.60	0.002 ± 0.008	H	P
Chamaedorea tepejilote Liebm.	1.30 ± 5.21	-	H	P
Cryosophila argentea Bartlett	1.18 ± 4.69		S	P
Desmoncus orthacanthos Mart.	0.80 ± 3.12	1.72 ± 5.04	H-S	P
Genus not determined	1.17 ± 2.52	-	H	U
COMMELINACEAE				
Gibasis sp.	0.21 ± 0.73	0.004 ± 0.02	H	S
Tradescantia zanonia (L.) Sw.	3.78 ± 8.34	-	H	P
COSTACEAE				
Costus pictus D. Don ex. Lindl.	0.002 ± 0.008	0.002 ± 0.008	H	P
CYPERACEAE				
Rhynchospora radicans (Schltdl. & Cham.) H. Pfeiff.	-	0.42 ± 1.58	H	S
Scleria bracteata Cav.	-	10.91 ± 16.09	H	S
DIOSCOREACEAE				
Dioscorea composita Hemsl.	-	0.39 ± 1.56	L	S
HELICONIACEAE				
Heliconia aurantiaca Ghiesbr.	2.10 ± 5.89	-	H	P
Heliconia latispatha Benth.	-	16.70 ± 25.87	H	S
Heliconia uxpanapensis C. Gutiérrez Báez	-	1.17 ± 3.40	H	S
Heliconia vaginalis Benth.	2.42 ± 7.32	0.18 ± 0.73	H	S
MARANTACEAE				
Calathea lutea G. Mey	-	1.17 ± 4.69	H	S
Maranta arundinacea L.	0.002 ± 0.008	1.35 ± 3.25	H	S
Stromanthe macrochlamys (Woodson & Standl.) H. Kenn. & Nicolson	1.19 ± 3.39	4.43 ± 7.41	H	S
ORCHIDACEAE				
Lycaste sp.	0.002 ± 0.008	-	H	P
Oeceoclades maculata (Lindl.) Lindl.	0.002 ± 0.008	0.42 ± 1.64	H	S
Genus not determined	0.002 ± 0.008	-	H	U
Genus not determined	-	0.002 ± 0.008	H	U
Sobralia sp.	0.002 ± 0.008	-	H	P
POACEAE				
Ichnantus sp.	-	2.80 ± 10.39	H	S
Lasiacis divaricata (L.) Hitchc.	-	1.01 ± 2.11	H	S
Lasiacis oaxacensis (Steud.) Hitchc.	-	0.02 ± 0.09	H	S
Lasiacis procerrima Hitchc.	-	0.18 ± 0.73	H	S
Lasiacis rugelii Hitchcock	-	0.60 ± 2.29	H	S
Panicum fasciculatum Sw.	-	0.82 ± 1.79	H	S
Panicum maximum Jacq.	-	0.39 ± 1.56	H	S

(continued)

Appendix (continued)

FAMILY[1] *Species*	LTEF	SV	LF	RG
MAGNOLIOPSIDA				
ACANTHACEAE				
Aphelandra aff. speciosa Brandegee	3.91 ± 15.63	-	S	P
Aphelandra aurantiaca (Scheidw.) Lindl.	3.95 ± 8.94	-	H	P
Justicia campechiana Standl.	0.21 ± 0.73	0.97 ± 3.16	H	S
Louteridium mexicanum (Baill.) Standl.	12.57 ± 23.24	-	S	S
Mirandea sylvatica Acosta	5.81 ± 10.87	-	H-S	P
AMARANTACEAE				
Iresine celosia L.	-	0.07 ± 0.13	H	S
ANACARDIACEAE				
Spondias radlkoferi Donn. Sm.	10.94 ± 29.89	5.71 ± 7.48	T	S
ANNONACEAE				
Stenanona stenopetala (Donn. Sm.) G.E. Schatz.	2.41 ± 9.36	-	T	P
APOCYNACEAE				
Stemmadenia donnell-smithii (Rose) Woodson	3.91 ± 15.63	-	T	P
Stemmadenia sp.	-	0.06 ± 0.25	T	P
ARALIACEAE				
Dendropanax arboreus (L.) Decne. & Planch.	14.46 ± 30.25	0.55 ± 2.19	T	P
ASTERACEAE				
Clibadium arboreum Donn. Sm.	-	1.72 ± 5.04	S	S
Melanthera nivea (L.) Small	-	3.50 ± 7.97	H	S
Verbesina turbacensis Kunth	-	0.006 ± 0.03	S	S
Vernonia patens Kunth	-	5.23 ± 8.34	S	S
Zexmenia serrata La Llave	-	3.52 ± 10.20	S	S
BEGONIACEAE				
Begonia heracleifolia Schltdl. & Cham.	-	0.01 ± 0.03	H	P
BIGNONIACEAE				
Amphitecna apiculata A.H. Gentry	1.25 ± 4.67	0.006 ± 0.03	T	P
Tabebuia chrysantha (Jacq.) G. Nicholson	-	0.006 ± 0.03	T	P
BOMBACACEAE				
Pseudobombax sp.	-	0.006 ± 0.03	T	P
Quararibea funebris (La Llave) Vischer	34.38 ± 39.06	-	T	P
BORAGINACEAE				
Cordia alliodora (Ruiz & Pav.) Oken	0.006 ± 0.03	2.48 ± 9.34	T	S
BURSERACEAE				
Bursera simaruba (L.) Sarg.	1.17 ± 4.69	6.05 ± 11.21	T	S
CACTACEAE				
Epiphyllum caudatum Britton & Rose	0.18 ± 0.73	-	V	P
CAPPAREACEAE				
Crataeva tapia L.	0.01 ± 0.03	-	T	P
CARICACEAE				
Jacaratia dolichaula (Donn. Sm.) Woodson	-	2.34 ± 6.40	T	P
CECROPIACEAE				
Cecropia obtusifolia Bertol.	1.17 ± 4.69	11.10 ± 13.36	T	S
CELASTRACEAE				
Genus not determined	-	1.17 ± 4.69	S	U

(continued)

Appendix (continued)

FAMILY[1] *Species*	LTEF	SV	LF	RG
Genus not determined	5.47 ± 21.88	-	T	U
Rhacoma eucymosa (Loes. & Pittier) Standl.	0.55 ± 2.19	-	S	P
COCHLOSPERMACEAE				
Cochlospermum vitifolium (Willd.) Spreng.	-	19.98 ± 26.39	T	S
COMBRETACEAE				
Combretum fruticosum (Loefl.) Stuntz	-	1.17 ± 4.69	L	S
Terminalia amazonia (J.F. Gmel.) Exell	1.27 ± 4.67	0.006 ± 0.03	T	P
CLUSIACEAE				
Rheedia edulis (Seem.) Planch. & Triana	0.01 ± 0.03	-	T	P
CUCURBITACEAE				
Melothria pendula L.	-	1.95 ± 1.73	V	S
Momordica charantia L.	-	0.02 ± 0.08	V	S
ELAEOCARPACEAE				
Sloanea meianthera Donn. Sm.	0.54 ± 2.19		T	P
EUPHORBIACEAE				
Acalypha diversifolia Jacq.	6.25 ± 17.68	32.09 ± 32.12	S	S
Dalechampia spathulata (Scheidw.) Baill	0.97 ± 2.69	-	H	P
Euphorbia heterophylla L.	-	0.002 ± 0.008	H	S
Poinsettia heterophylla (L.) Klotzsch & Garcke	-	0.79 ± 3.12	H	S
Sapium nitidum (Monach.) Lundell	-	4.69 ± 12.81	T	S
Sapium sp.	-	0.55 ± 2.19	T	S
Tragia sp 1.	-	3.66 ± 8.34	H	S
Tragia sp 2.	-	0.004 ± 0.01	V	S
FABACEAE				
Acacia angustissima (Mill.) Kuntze	-	6.41 ± 13.13	T	S
Acacia cornigera (L.) Willd	0.006 ± 0.03	1.73 ± 5.04	S	S
Acacia mayana Lundell	1.17 ± 4.69	-	T	P
Bauhinia sp.	0.006 ± 0.03	0.006 ± 0.03	S	P
Calliandra tergemina (L.) Benth	1.16 ± 2.97	0.55 ± 2.19	T	P
Cynometra retusa Britton & Rose	3.91 ± 15.62	-	T	P
Dalbergia brownei (Jacq.) Schinz	-	6.05 ± 11.21	S	S
Desmodium axillare (Sw.) DC.	-	3.64 ± 7.31	H	S
Desmodium incanum DC.	-	0.23 ± 0.81	H	S
Dialium guianense (Aubl.) Sandwith	27.03 ± 39.32	-	T	P
Erythrina americana Mill.	-	0.006 ± 0.03	T	S
Inga pavoniana G. Don	-	3.51 ± 10.20	T	S
Inga spuria Humb. & Bonpl. ex Willd.	-	2.34 ± 9.38	T	S
Leucaena glauca Benth.	-	10.17 ± 21.39	T	S
Lonchocarpus aff. guatemalensis Benth	1.17 ± 4.69	-	T	P
Lysiloma divaricata Hook & Jackson	5.47 ± 21.88	-	T	P
Lysiloma sp.	5.47 ± 21.88	1.17 ± 4.69	T	P
Machaerium kegelii Meisn.	-	3.28 ± 6.56	L	S
Mimosa sp.	0.006 ± 0.03	0.006 ± 0.03	S	U
Pithecellobium furcatum Benth.	0.006 ± 0.03	0.81 ± 2.25	T	S
Senna fruticosa (Mill.) H.S. Irwin & Barneby	-	2.35 ± 9.37	S	S
Senna quinquangulata (Rich.) H.S. Irwin & Barneby	-	8.59 ± 19.21	S	S

(continued)

Appendix (continued)

FAMILY[1] *Species*	LTEF	SV	LF	RG
Stizolobium pruriens (L.) Medick.	-	0.18 ± 0.73	V	S
Swartzia guatemalensis (Donn. Sm.) Pittier	2.35 ± 9.37	-	S	P
Zygia sp.	1.17 ± 4.69	-	T	P
FLACOURTIACEAE				
Casearia corymbosa Kunth	0.55 ± 2.19	1.16 ± 2.97	T-S	S
Zuelania guidonia (Sw.) Britton & Millsp.	1.17 ± 4.69	2.41 ± 9.36	T	S
GESNERIACEAE				
Drymonia serrulata (Jacq.) Mart.	-	0.002 ± 0.008	V	P
HIPPOCRATACEAE				
Pristimera celastroides (Kunth) A.C. Sm.	-	0.006 ± 0.03	L	P
LAURACEAE				
Genus not determined	3.91 ± 15.63	-	T	U
Genus not determined	3.91 ± 15.63	-	T	U
Genus not determined	2.36 ± 9.37	-	S	U
LOGANIACEAE				
Spigelia humboldtiana Cham. & Schltdl.	-	0.004 ± 0.01	H	S
MALPIGHIACEAE				
Bunchosia lanceolata Turcz.	1.18 ± 4.69	0.62 ± 2.18	S	S
Malpighia glabra L.	-	0.61 ± 2.19	S	S
Stigmaphyllon lindenianum A. Juss	-	0.002 ± 0.008	V	S
MALVACEAE				
Gossypium hirsutum L.	-	0.18 ± 0.73	H	S
MELASTOMATACEAE				
Clidemia petiolaris (Schltdl. & Cham.) Schltdl. ex Triana	-	0.006 ± 0.03	S	S
Conostegia xalapensis (Bonpl.) D. Don ex DC.	-	1.72 ± 5.04	T	S
Miconia impetiolaris (Sw.) D. Don ex DC.	0.02 ± 0.04	-	S	P
MELIACEAE				
Guarea grandifolia DC.	0.006 ± 0.03	-	T	P
Guarea sp.	29.46 ± 34.48	-	T	P
Trichilia sp.	2.35 ± 9.37	1.09 ± 2.99	T	P
MEMESILACEAE				
Mouriri myrtilloides (Sw.) Poir.	0.58 ± 2.18	-	S	P
MENISPERMACEAE				
Hyperbaena mexicana Miers	7.43 ± 16.49	-	T	P
Hyperbaena aff. jalcomulcensis Pérez & Cast.-Campos	6.25 ± 17.68	-	T	P
MORACEAE				
Brosimum alicastrum Sw.	6.78 ± 22.02	-	T	P
Ficus obtusifolia Kunth	2.34 ± 9.38	-	T	P
Ficus sp.	-	0.006 ± 0.03	T	P
Genus not determined	0.02 ± 0.08		T	P
Poulsenia armata (Miq.) Standl.	17.58 ± 34.99	-	T	P
Trophis mexicana (Liebm.) Bureau	2.34 ± 9.38	-	T	P
MYRSINACEAE				
Ardisia paschalis Donn. Sm.	0.02 ± 0.04	-	S	P

(continued)

Appendix (continued)

FAMILY[1] *Species*	LTEF	SV	LF	RG
Genus not determined	3.91 ± 15.63	-	T	P
Icacorea sp.	0.006 ± 0.03	-	H	P
MYRTACEAE				
Eugenia sp 1.	0.006 ± 0.03	-	S	P
Eugenia sp 2.	0.03 ± 0.05	-	S	P
NYCTAGINACEAE				
Pisonia aculeata L.	0.006 ± 0.03	-	S	P
OCHNACEAE				
Ouratea crassinervia Engl.	0.02 ± 0.04	-	T	P
PASSIFLORACEAE				
Passiflora coriacea Juss.	-	0.21 ± 0.81	V	S
PIPERACEAE				
Peperomia granulosa Trel.	0.19 ± 0.75	-	H	P
Piper amalago L.	2.11 ± 5.88	-	H	P
Piper auritum Kunth	-	1.30 ± 5.21	H	S
Piper aduncum L.	0.18 ± 0.73	10.57 ± 13.41	S	S
POLYGONACEAE				
Coccoloba barbadensis Jacq.	-	1.17 ± 4.69	S	S
Coccoloba sp.	-	0.06 ± 0.25	T	U
RANUNCULACEAE				
Clematis dioica L.	-	0.002 ± 0.008	V	S
RHAMNACEAE				
Sageretia elegans (KunB.) Brongn.	1.83 ± 5.00	0.08 ± 0.25	S	S
ROSACEAE				
Licania platypus (Hemsl.) Fritsch.	1.23 ± 4.68	-	T	P
RUBIACEAE				
Alseis yucatanensis Standl.	1.72 ± 5.04	-	T	P
Borreria laevis (Lam.) Griseb	-	0.002 ± 0.008	H	S
Faramea occidentalis (L.) A. Rich.	17.41 ± 19.68	-	S	P
Hamelia patens Jacq.	-	28.03 ± 20.79	S	S
Posoqueria latifolia (Rudge) Roem. & Schult.	9.93 ± 25.90	-	T	P
Psychotria sp 1.	-	0.01 ± 0.03	T	P
Psychotria sp 2.	0.06 ± 0.25	-	S	P
Psychotria limonensis K. Krause	-	0.002 ± 0.008	S	P
Psychotria pleuropoda Donn. Sm.	0.18 ± 0.73	-	H	P
Randia sp.	5.47 ± 21.88	-	L	P
Genus not determined	9.38 ± 26.02	-	T	U
RUTACEAE				
Esenbeckia pentaphylla (Macfad.) Grises.	1.18 ± 4.68	0.06 ± 0.25	T	P
Decazyx esparzae F. Chiang	11.73 ± 25.90	-	T	P
Zanthoxylum kellermanii P. Wilson	-	1.18 ± 4.68	S	S
SAPINDACEAE				
Cupania dentata DC.	-	23.27 ± 26.33	T	S
Paullinia pinnata L.	0.76 ± 1.77	1.08 ± 1.90	L	P
Paullinia sp.	0.04 ± 0.11	-	H	P
Paullinia tomentosa Jacq.	0.03 ± 0.08	0.97 ± 3.16	L	S

(continued)

Appendix (continued)

FAMILY[1] *Species*	LTEF	SV	LF	RG
Genus not determined	0.006 ± 0.03	-	S	P
Serjania mexicana (L.) Willd.	-	3.65 ± 9.40	V	S
SAPOTACEAE				
Manilkara zapota (L.) P. Royen	1.91 ± 5.02	-	T	P
Peteniodendron belizense Lundell	0.55 ± 2.19	-	S	P
Pouteria unilocularis (Donn. Sm.) Baehni	1.18 ± 4.69	-	T	P
SMILACACEAE				
Smilax aff. regelii Killip & C.V. Morton	-	1.17 ± 3.40	V	S
Smilax aristolochiaefolia Miller	-	0.02 ± 0.08	V	S
Smilax mollis Humb. & Bompl. ex Willd.	-	0.18 ± 0.73	V	S
SOLANACEAE				
Cestrum glanduliferum Kerber ex Francey	0.006 ± 0.02	-	S	S
Cestrum megalophyllum Dunal	0.006 ± 0.02	-	T	P
Solanum umbellatum Mill.	-	0.01 ± 0.03	S	S
STERCULIACEAE				
Sterculia mexicana R. Br.	5.48 ± 21.87	-	T	P
Guazuma ulmifolia Lam.	-	9.38 ± 26.02	T	S
TILIACEAE				
Heliocarpus mexicanus (Turcz.) Sprague	-	46.88 ± 33.93	T	S
ULMACEAE				
Trema micrantha (L.) Blume	-	15.63 ± 20.54	T	S
URTICACEAE				
Urera elata (Sw.) Griseb.	5.08 ± 16.01	1.17 ± 4.69	T	S
VERBENACEAE				
Aegiphila monstrosa Moldenke	1.17 ± 4.69	-	S	S
Lantana camara (L.) L.H. Bayley	-	8.84 ± 17.84	S	S
Genus not determined	-	10.70 ± 22.30	T	S
VIOLACEAE				
Rinorea guatemalensis (S. Watson) Bartlett	33.98 ± 27.67	-	S	P
Rinorea hummelii Sprague	0.006 ± 0.03	-	S	P
VITACEAE				
Cissus sicyoides L.	-	2.37 ± 4.41	L	S
Vitis tiliifolia Hump. & Bonpl. ex Roem. & Schult.	-	2.11 ± 5.88	L	S
ZAMIACEAE				
Zamia loddigessii Miq.	0.006 ± 0.01	0.03 ± 0.08	H	P
UNKNOWN FAMILIES				
Unknown tree 1	5.46 ± 21.88	-	T	U
Unknown tree 2	5.47 ± 21.88	-	T	U
Unknown tree 3	3.91 ± 15.63	-	T	U
Unknown tree 4	0.006 ± 0.03	-	T	U
Unknown tree 5	1.17 ± 4.69	-	T	U
Unknown tree 6	5.47 ± 21.88	-	T	U

[1]Taxonomic nomenclature follows Cronquist (1988) and authorities are abbreviated according to Brummitt and Powell (1992). Values are mean cover (± SD) for the 16 plots 10 × 10 m (four in each of the four sites selected in each type of regeneration). Per cent cover for each species was calculated using van der Maarel's (1979) procedure. LTEF = logged tropical evergreen forest; SV = secondary vegetation after shifting cultivation; LF = life form (T = tree; S = shrub; H = herbaceous plant; V = vine; L = liana); RG = regeneration guild (P = primary; S = secondary; U = unknown)