

LAND CHANGE IN THE SOUTHERN YUCATÁN AND CALAKMUL BIOSPHERE RESERVE: EFFECTS ON HABITAT AND BIODIVERSITY

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Abstract. The southern Yucatán contains the largest expanse of seasonal tropical forests remaining in Mexico, forming an ecocline between the drier north of the peninsula and the humid Petén, Guatemala. The Calakmul Biosphere Reserve resides in the center of this region as part of the Mesoamerican Biological Corridor. The reserve's functions are examined in regard to land changes throughout the region, generated over the last 40 years by increasing settlement and the expansion and intensification of agriculture. These changes are documented from 1987/1988 to 2000, and their implications regarding the capacity of the reserve to protect the ecocline, forest habitats, and butterfly diversity are addressed. The results indicate that the current landscape matrix serves the biotic diversity of the reserve, with several looming caveats involving the loss of humid forests and the interruption of biota flow across the ecocline, and the amount and proximity of older forest patches beyond the reserve. The highly dynamic land cover changes underway in this economic frontier warrant an adaptive management approach that monitors the major changes underway in mature forest types, while the paucity of systematic ecological and environment–development studies is rectified in order to inform policy and practice.

Key words: *biodiversity; butterfly diversity; Calakmul Biosphere Reserve; land change; remote sensing; seasonal tropical forest; southern Yucatán; tropical deforestation; vegetation structure.*

INTRODUCTION

The southern Yucatán region (SY) of southwestern Quintana Roo and southeastern Campeche is home to the largest expanse of mature, seasonal tropical forests remaining in Mexico (Fig. 1) and part of the largest continuous forest area left in Mesoamerica (Carr 1999). It comprises an important north–south ecological gradient, an ecocline (van der Maarel 1990), connecting the northern most extension of the Petén (Guatemala) humid forest of high endemism (Espadas Manríquez et al. 2003) with the xeric forests to the north. The Calakmul Biosphere Reserve (CBR), covering about one-third of the SY (7225.15 km²), captures this ecocline as part of the MesoAmerican Biological Corridor (MBC). Despite conservation and preservation efforts, the function of this ecocline has been challenged by ongoing forest disturbance that diminishes the extent and increases the fragmentation of mature forest (Lawrence et al. 2004). The SY was opened to significant occupation in the 1960s. The scale of deforestation that

ensued (Achard et al. 1998, Myers et al. 2000) raised international concerns about threats to carbon stocks and to biota and their habitats, leading to the establishment of the CBR in 1989, significant portions of which coincide with agricultural settlements. Land use and land cover changes continue within and beyond the reserve's borders.

Understanding the consequences of land changes on biotic diversity in the SY is complicated by a history of natural and past human disturbances. Hurricanes, operating on the scale of centuries, may blow down significant areas of forest, especially in the eastern part of the region (Boose et al. 2003), with short-term consequences for fauna and flora (Snook 1998). Importantly, the SY was extensively denuded by the ancient Maya prior to their collapse in the region about 1100 years ago (Turner et al. 2003). Subsequently, the forest returned, most likely with significant changes in species abundance (Lambert and Arnason 1981, Gómez-Pompa 1987, Turner et al. 2003). Extensive logging in the last century virtually eliminated mahogany (*Swietenia macrophylla* King) and Spanish cedar (*Cedrela odorata* L.) (Snook 1988, Klepeis 2004). Given this history of disturbance, the seasonal tropical forests of the SY today may be preadapted to disturbance (Whigham et al. 1991).

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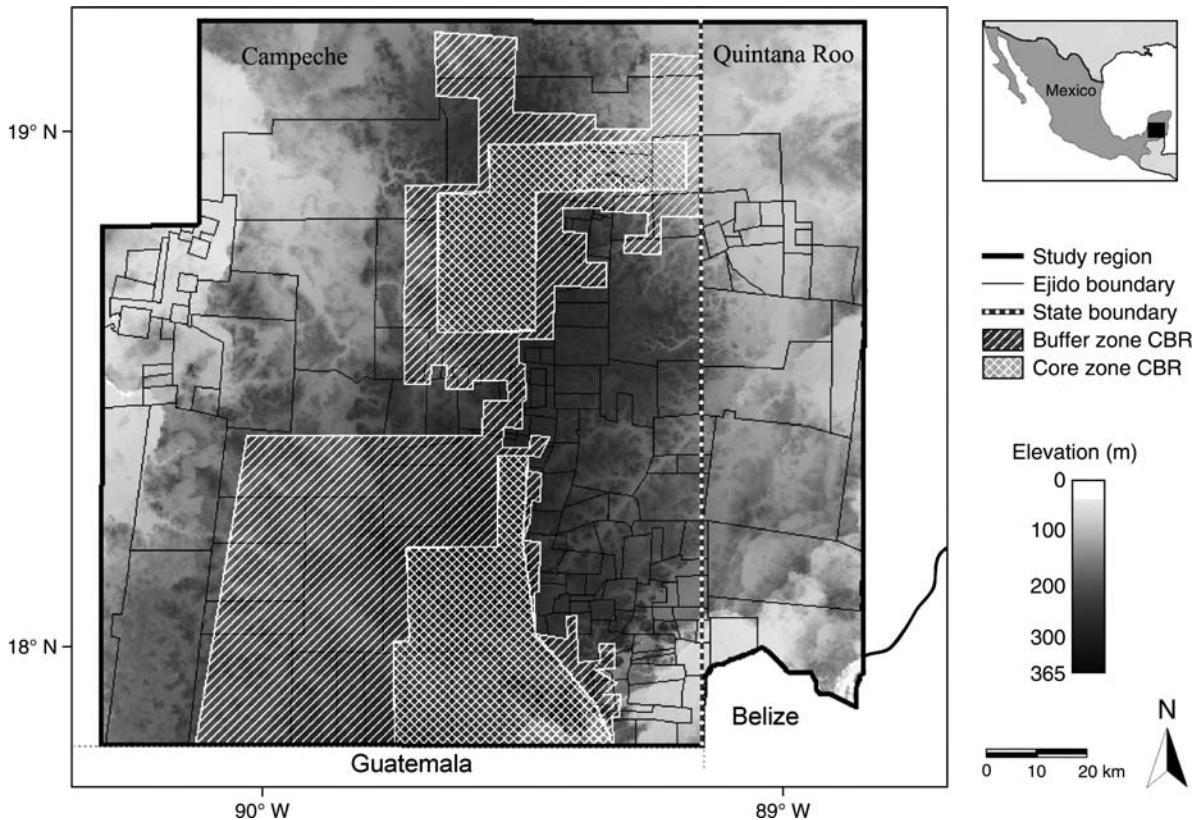


FIG. 1. Topography of the southern Yucatán with the Calakmul Biosphere Reserve (CBR) and ejido boundaries. The ejido boundaries noted are those fully (save one) within the study region. Along with the northern extent of the CBR, these boundaries constitute the analysis area of this study.

Against this background of chronic and episodic disturbances, both natural and anthropogenic, four questions are addressed that are pivotal to understanding the effects of land changes on biotic diversity and the efficacy of the CBR in maintaining this diversity. (1) Are the percentages of forest types comprising the regional ecocline in the SY matched in the CBR? (2) Have the rates and amounts of deforestation and the distribution of disturbance among upland forest types in the SY and CBR differed? (3) How does human disturbance alter forest habitats in terms of landscape pattern, stand structure, and tree species composition? (4) How are butterfly richness and composition affected by vegetation type and time since disturbance?

Taken together, these questions address the central issues concerning land change and reserves identified by Hansen and Defries (2007). Question 1 links to the increasing concern about matching fixed boundaries of reserves to the complex and dynamic human and environmental processes operating on reserves (Wilcove and May 1986, Zimmerer 2000, Naughton-Treves et al. 2003). Question 2 addresses the long-term capacity of the reserve to serve its environmental functions, situated, as it is, in highly dynamic land uses common to economic frontiers in the tropics (Curran et al. 2004,

Moran and Ostrom 2005). Questions 3 and 4 ask if species or communities are tied to key forest types that may be under threat of loss as the forest types decline in area or patch size or become restricted to the reserve. The answers help to identify the importance of conserving forest beyond the CBR.

STUDY AREA

The SY is a 22 000-km², project-defined region that captures the entire CBR and the major forest types of the north-to-south ecocline on the interior meseta, or hilly land, rising above the coastal plains of the Yucatán Peninsula (Fig. 1). The meseta is karstic terrain composed of rolling limestone hills and ridges that range from about 100 to 360 m amsl (above mean sea level). These uplands are punctuated with large solution sinks or *bajos*. The uplands of the meseta are dominated by shallow *redzinas*, whereas the *bajos* hold thick *vertisols* that retain water during the wet season. An *Aw* climate (tropical with pronounced winter dry period) dominates the entire SY, characterized by a precipitation gradient ranging from ~900 mm in the northwest to 1400 mm in the southeast.

These conditions support a seasonal tropical forest differentiated by stature, deciduousness, and the relative

abundance of species (Table 1; see Standley 1930, Lundell 1934, Miranda and Hernández 1963, Pennington and Sarukhán 1968). Selva baja and selva mediana sub/caducifolia (SBMsc) are short- to medium-stature forests with significant dry-season leaf loss. They are considered one forest type in our regional land cover classification because imagery analysis cannot yet distinguish between the short and medium stature. About 61% of the SBMsc in the SY resides in uplands of the drier (900–1000 mm/yr), northwest part of the study region (Lawrence et al. 2004). Selva mediana (SM) dominates the central and south-central parts of the region of intermediate precipitation (1000–1200 mm/yr). It is medium-stature forest with lower dry-season leaf loss than SBMsc (Lawrence 2005). About 81% of selva alta (SA), the taller and more humid forest (1200–1400 mm/yr), resides in the east and south.

Selva baja inundable (SBI; seasonally inundated, short-stature forest) dominates most bajos (Peréz-Salicrup 2004), regardless of their location along the precipitation gradient. Landsat image analysis also reveals a distinctive forest signal, designated here as selva baja (SB; short stature) that appears to exist on transitional ground exhibiting soil moisture conditions intermediate between uplands and bajos. Whether this imagery-based class is ecologically distinct from the other forest types has not yet been determined (Table 1).

For the most part, old upland forests (>25 yr old) of SBMsc, SM, and SA maintain similar species that differ in structure and abundance, apparently in response to variation in soil moisture and past human disturbances (Martínez and Galindo-Leal 2002, Pérez-Salicrup 2004). To date, research has identified only a few plant species restricted to specific forest types.

Systematic studies of fauna in the region are few; those undertaken are biased to the more humid parts of the region or are based on small-area samples. Research undertaken immediately west of the SY, in the humid Río Usumacinta area, indicates that land cover changes (largely deforestation) have reduced the habitats of 32 out of 54 mammals, mostly non-generalist species (Cuarón 2000). Habitat reduction is apparently responsible for the reported low population of jaguar in the CBR (Ceballos et al. 2002). In addition, significant reductions of those species hunted by local inhabitants of the SY have been documented (Escamilla et al. 2000, Weber 2000, Reyna-Hurtado 2002).

Hunting and deforestation has risen dramatically in the SY in concert with increases in a population that rose from 2500 people in 1960 to 37 195 in 2000 (INEGI 2000, Turner et al. 2001), not including illegal squatters in the remote southern portions of CBR. Increased smallholder occupation has been accompanied by high rates of upland deforestation (Roy Chowdhury and Schneider 2004) through increasingly intensive forms of slash-and-burn or swidden cultivation that can incorporate commercial jalapeño (chili) production (Keys 2004). Most agriculture in the SY is undertaken on 97

agricultural ejidos and 14 private ranches (Fig. 1). Deforestation is prohibited on government land (most of the CBR core zone of 2479 km²) and 17 forest extensions ejidos (much of the CBR buffer zone of 4746 km²). With ejidos legally entitled to 22.6% of the CBR, reserve officials work with local communities, as well as governmental agencies and nongovernmental organizations, regarding land management decisions, with mixed success (Klepeis and Vance 2003, Abizaid and Coomes 2004).

METHODS

Land covers and change

Land cover classification was based on analysis of Landsat ETM imagery for 2000 (four georeferenced scenes: Paths/Rows 20/47 and 20/48 ETM; 19/47 and 19/48 TM) covering 18 900 km² or 86% of the SY. The classification of the 2000 imagery involved a stepwise classification process or In-Process Classification Assessment (Eastman et al. 2005). This assessment procedure was used to assess three forms of uncertainty in a maximum likelihood classification: ambiguity because of class inseparability, the presence of mixed pixels, and the presence of unknown classes. Mapping these uncertainties permitted refinement through successive iterations of training site visits until all significant land covers were determined with minimal problems of class separation. Post-classification ground-truth yields a land class accuracy of 88%.

Land cover change analysis was conducted using only one Landsat scene (Path: 20 Row: 47) for the years 1987/1988 (combined owing to cloud coverage), 1995, and 2000. This scene (analysis area) covers 81% of the SY study area and 84% of the CBR, and serves to capture most of the major land cover dynamics underway in the SY. Pre-processing of the non-2000 images was limited to georeferencing each to the 2000 image. In order to overcome problems of temporal and spatial variation in the distribution of moisture, spatial prior knowledge of the undisturbed classes was incorporated into the maximum likelihood procedure in the form of Bayesian prior probability images. This procedure yields a statement of the posterior probability of each pixel belonging to each of the land cover classes that was further modified using the probability distribution of slope preferences for each class. On the assumption that there would be reasonable stability in the undisturbed forest classes, the results derived from the accuracy-assessed image (2000) were propagated to earlier years. A cross-tabulation and spatial cross-classification of these classified images were also performed to reduce illogical transitions between forest classes.

To reduce noise, change analysis was conducted only in areas that were classified as agriculture or secondary forest in any of the years from 1987 to 2000. Land transitions were calculated from 1987/1988 to 1995,

TABLE 1. Area and percentage of land cover types in southern Yucatán (SY) and Calakmul Biosphere Reserve (CBR) in 2000.

Original classes in combined classes	Management areas							
	Area in class (km ²)				Percentage of total management area			
	Core	Buffer	CBR total	SY beyond CBR	Core	Buffer	CBR total	SY beyond CBR
Open land								
Crop cultivation	10.3	34.6	44.9	165.1	0.4	0.7	0.6	1.4
Pasture	2.3	2.6	4.8	73.9	0.1	0.1	0.1	0.6
Bare soil	1.6	3.5	5	57.6	0.1	0.1	0.1	0.5
Large-scale agriculture	0.2	0.6	0.8	29.6	0	0	0	0.3
Settlements/urban	1.9	4.7	6.6	81.7	0.1	0.1	0.1	0.7
Secondary vegetation								
Herbaceous	7.9	22	29.9	268.1	0.3	0.5	0.4	2.3
Shrubby	21.8	35.2	57	389.8	0.9	0.7	0.8	3.3
Arboreous	114.4	183.2	297.6	631.2	4.6	3.9	4.1	5.4
Bracken fern	16.9	27.1	44	237.6	0.7	0.6	0.6	2
Inundated vegetation								
Selva baja inundable (Sbi)	373.4	463.6	837	1722.3	15.1	9.8	11.6	14.8
Tular/Savanna	0.9	1	1.9	36.1	0	0	0	0.3
Transitional forest								
Selva baja (SB)	304.4	884	1188.3	1248.8	12.3	18.6	16.4	10.7
Upland Forest								
Selva baja and mediana sub/caducifolia (SBMsc)	509.1	978.5	1487.6	2063.1	20.5	20.6	20.6	17.7
Selva mediana (SM)	896.3	1715.1	2611.4	3473.9	36.2	36.1	36.1	29.8
Selva alta and mediana (SA)	217.5	389.7	607.2	1161.8	8.8	8.2	8.4	10
Total area	2479.2	4745.9	7225.1					

Note: The data refer to the entire SY imagery assessment area of 18 900.73 km². Percentages are rounded up.

from 1995 to 2000, and from 1987/1988 to 2000 using a cross-tabulation method.

Habitat change: forest structure and species composition

Tree species were identified in 36 forest stands. We sampled 28 secondary forests (2–25 yr old) and eight mature forests over three areas. The driest, northernmost and the wettest, southernmost sites were within 5 km of the reserve. The area of intermediate precipitation was at a distance of 60 km. At each stand, trees >10 cm dbh were sampled in a single 500-m² circular plot, and trees 5–9.9 cm dbh were sampled in a concentric 100-m² plot. Stems 1–4.9 cm were sampled in three 10-m² circular plots between the boundaries of the larger plots (Read and Lawrence 2003). The 10 most abundant species (at least 2% of all stems at a given stand) >1 cm and >5 cm were tallied for each site. The abundant species in secondary and mature forests were then compared. Further study is required to assess differences in rare species.

Along with species composition, the two major characteristics likely to determine habitat value for fauna are the density of stems, especially large trees, and the distribution and variability of canopy heights (James and Wamer 1982, Smith and Shugart 1987, Carey and Johnson 1995, Raman et al. 1998). Algorithms developed by Read and Lawrence (2003) were used to

generate tree heights from diameters for all stems sampled. Differences in tree density and height for each tree size class (1–4.9 cm, 5–9.9 cm, and >10 cm dbh) were determined by two-factor analysis of variance (study area and age class [2–5, 6–10, and 12–25 yr old, and mature forest]). The effect of age class on canopy complexity was analyzed by determining the evenness of tree heights for a given tree diameter size class, within each of the 36 stands. For each stand, trees in the 1–4.9 cm dbh range were allocated into five height classes. The Shannon-Wiener index (Magurran 2004) was used to determine the evenness of the distribution of trees into the five height classes, providing an index of canopy diversity. Higher evenness was taken as an indicator of greater complexity within a canopy layer. Trees 5–10 cm dbh were treated similarly. Trees >10 cm dbh were allocated into 12 bins to match the greater range of heights observed among the largest trees. For each tree size class, differences in evenness were determined by two-factor ANOVA, as before.

Butterfly diversity

On the assumption that deforestation outside the reserve creates a landscape of secondary forests that is less diverse (Lawrence et al. 2004), butterfly species diversity and abundances were measured across the two most common forest types (SBsc, SM) and three age

TABLE 1. Extended.

Management areas					
Percentage of total cover class in SY					
Core	Buffer	CBR total	SY beyond CBR	SY	
				Area (km ²)	% of total
4.9	16.5	21.4	78.6	210	1.1
2.9	3.3	6.1	93.9	78.7	0.4
2.5	5.5	8	92	62.6	0.3
0.6	2.1	2.7	97.3	30.4	0.2
2.2	5.3	7.5	92.5	88.3	0.5
2.7	7.4	10	90	298	1.6
4.9	7.9	12.8	87.2	446.8	2.4
12.3	19.7	32	68	928.8	4.9
6	9.6	15.6	84.4	281.6	1.5
14.4	18.1	32.7	67.3	2559.3	13.5
2.3	2.7	5	95	38	0.2
12.5	36.3	48.8	51.2	2437.1	12.9
14.3	27.6	41.9	58.1	3550.7	18.8
14.7	28.2	42.9	57.1	6085.3	32.2
12.3	22	34.3	65.7	1769	9.4
				18 900.7	

classes (<10-yr-old secondary, >10-yr-old secondary, and mature forest), chosen in relation to structural and compositional differences as observed in the field. Selva baja subcaducifolia (SBsc) was distinguished from the mediana (SMsc) counterpart, unlike in the satellite imagery analysis. Traps with fermenting fruits were set every 50 m along 500-m transects (three transects per forest type × age combination), and specimens were collected from traps and by systematic netting over four days every three months during 1997 (Pozo de la Tijera et al. 2000). Species richness was analyzed with EstimateS (Colwell 2005) for each forest type and age class using Chao 1 and 2, abundance cover estimates (ACE), and incidence cover estimates (ICE) (Chao and Lee 1992; see also Chazdon et al. 1998, O'Hara 2005). Differences among forest types and age classes were tested with Student's *t*. Comparisons of species abundances were also made using a two-factor (age class, forest type), nonparametric permutational multivariate ANOVA (McArdle and Anderson 2001, Anderson 2004a). Data were transformed to the fourth root to diminish the effect of zeroes in the data matrix, and the Bray-Curtis distance index was used for its suitability in describing species abundance (Legendre and Legendre 1998). Additionally, a permutational analysis of multivariate dispersions (PERMDISP; Anderson 2004b) was undertaken to investigate the variability of data within

groups in order to assess the plot-to-plot difference in secondary and mature forest. The same transformation and dissimilarity measures were used as for the PERMANOVA. Finally, a nonmetric multidimensional scaling (nMDS) permitted the examination of the interaction between age class and forest type.

RESULTS

Land cover and change

The differences in the percentages of the mature forest types in CBR and in the SY beyond the reserve are small (Table 1) but statistically significant (tested by means of one-tailed large-sample differences in percentage for each cover type). The SB, SBMsc, and SM types cover 3–6% more ($z = 11.46, 4.99, \text{ and } 9.136963$; all $P < 0.001$) of the CBR than the SY beyond the reserve. The SA and SBi, respectively, cover 1.6% ($z = -3.55, P < 0.001$) and 3.2% ($z = -6.18, P < 0.001$) less (Figs. 2 and 3). As expected, the percentage of open land and secondary vegetation is about 2.4 times less in the CBR than beyond the reserve. Nevertheless, ~491 km² of open land and secondary vegetation exist in the CBR, about 7% of its analysis area (Figs. 4 and 5). Assuming that all lands not in permanent water-marsh and savanna were once mature forest, ~2396 km² or 12.7% of the analysis area has been deforested since the midpoint of last century.

From 1987/88 to 2000, the analysis area witnessed a net increase in both open land and secondary vegetation of ~409 km², mostly drawn from mature forest types rather than successional growth (Table 2). The annual rate of deforestation in this period was 0.2%, but with significant subperiod variability (until 1995, deforestation was 0.4% per year; after 1995, there was 0.1% per year regrowth). By 2000, agricultural lands (cultivated and pasture) and secondary vegetation (largely fallow) came from the reuse of previously farmed land (Table 3). Only ~35% of the total area of agriculture in 2000 was taken directly from mature upland and transitional forest. Overall, 88% of the land that was in secondary vegetation in 1987/88 remained within this class or was cleared again for agriculture. The remaining 12% returned to forest by 2000.

These dynamics varied within and beyond the reserve, especially on agricultural ejidos and ranches (Fig. 5, Table 2). By 2000 the net increase in open lands within the core, buffer, and non-reserve areas was 0.04%, 0.12%, and 0.49%, respectively (Table 2), recalling that deforestation began previous to 1987/88. The net losses of intact upland vegetation were 0.84%, 0.70%, and 2.55%, respectively (Table 2). Secondary growth, mostly fallow, and lands taken by bracken fern increased in area throughout the SY by 2.42% (Table 2). More than 67% (or 274 km²) of the 412 km² loss in mature forests took place among the three upland types: 36% SM, 35% SBMsc, and 29% SA. These forests were cut in the core

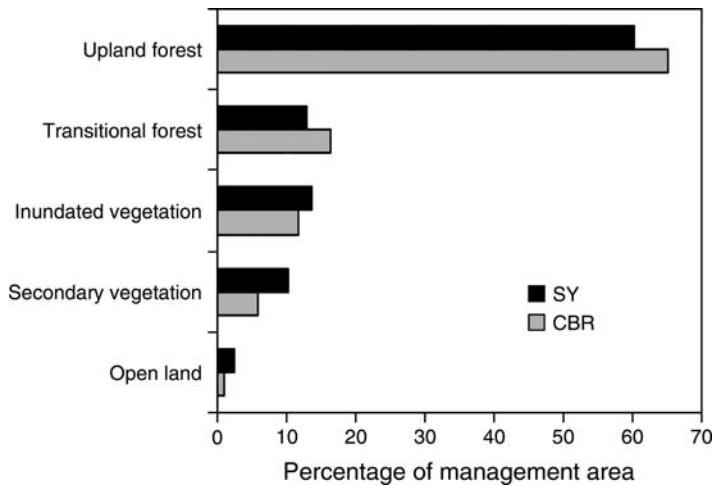


FIG. 2. Percentages of land cover types in the southern Yucatán outside the reserve (SY) and corresponding percentages in Calakmul Biosphere Reserve (CBR).

(17 km²) and buffer (27 km²) of the CBR, and in the SY beyond the reserve (230 km²; Tables 2 and 3).

Habitat change: forest structure and species composition

Fifty-eight tree species were among the 10 most common species per plot. Only nine of these (15%) were relatively abundant in both mature and secondary forests (Appendix A). Twenty-four were among the top 10 only in secondary forests, and 17 were common only in mature forests.

The density of stems <5 cm dbh was twice as high in young (<10-yr-old) as in old forests (Table 4). Stems 5–9.9 cm dbh, which make up the understory in mature forest, were less dense in young secondary than in mature forest (by 28–56%), but did not differ significantly between mature and old secondary forests (12–25 yr old). However, the density of trees >10 cm dbh, those that make up the canopy, was 38% lower in 12–25 year old secondary forests than in mature forest.

Maximum canopy height for all secondary forests was 40% lower than that of mature forest (15 m vs. 26 m) and did not differ substantially between the youngest and the oldest secondary forest because of relic trees that occasionally survive the burn prior to cultivation. For

stems 1–4.9 cm dbh, mean height did not differ between old secondary and mature forests. For stems 5–9.9 cm dbh, however, mean height was 18% lower in old secondary forest (6.2 m vs. 7.6 m), and for trees >10 cm dbh, mean canopy height was 31% lower (8.7 m vs. 12.6 m) (Table 4).

Canopy complexity increased with forest age. Even with relic trees contributing to canopy complexity, among trees >10 cm dbh, evenness was 2.5–7.5 times as great in mature forest as in secondary forest (Table 4). The evenness of heights for trees 5–9.9 cm dbh was only 1.3–2.0 times as great in mature as in secondary forest. Height evenness of stems 1–4.9 cm dbh was 12% lower in 2–5 year old secondary forests than in mature forest, and it did not differ between 12–25 year old secondary forest and mature forest. Canopy complexity in secondary forests declined with increasing tree size class, an outcome expected in young, even-aged stands. In contrast, canopy complexity increased from the smallest to the largest tree size class in mature forest.

Butterfly diversity

More than 60% of the species in the butterfly database were shared between SBsc (Appendix B) and SM (75 out

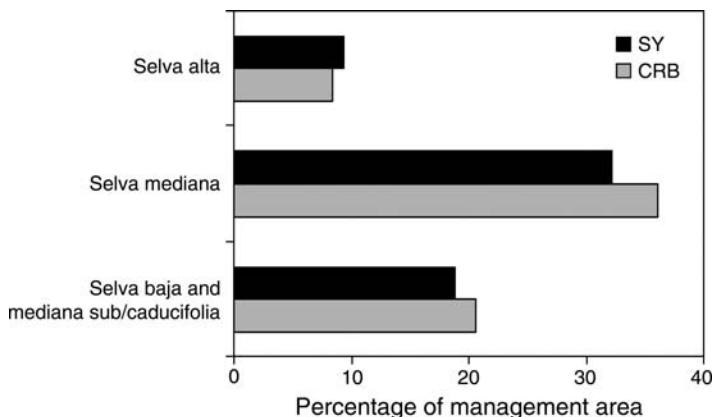


FIG. 3. Percentages of upland forest types in the southern Yucatán outside the reserve (SY) and corresponding percentages in Calakmul Biosphere Reserve (CBR).

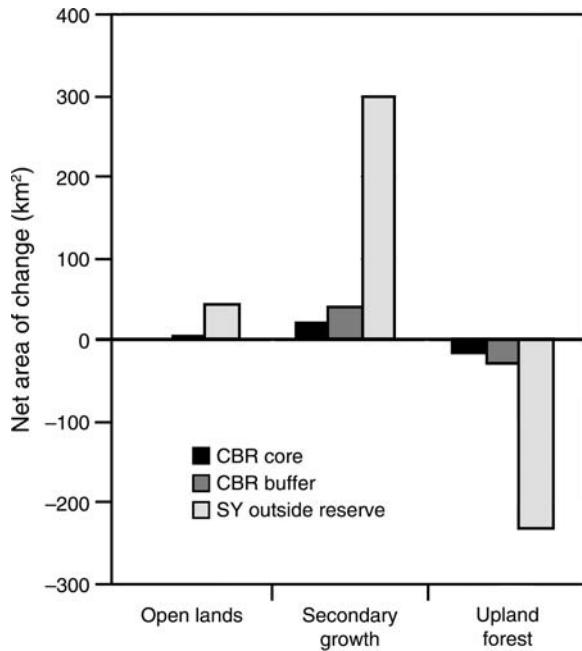


FIG. 4. Change in land cover (gain or loss in area) in the southern Yucatán and Calakmul Biosphere Reserve, 1987/1988 to 2000, including changes outside the management area.

of 123 species), with 21 unique to SM and 27 to SBsc. Species exclusive to one type or another were rare (<0.1% of the observations). Similarly, about 60% of the species were shared between mature and secondary forest for both SBsc and SM. Secondary forests, however, tended to hold more unique species than mature forest (34 vs. 15 in SBsc and 37 vs. 9 in SM). Most of these unique species were rare as well. In both SM and SBsc, only *Polygonus savigny savigny* was unique to mature forest and less rare (represented by >0.1% of the individuals). Unique for secondary vegetation in both forest types and less rare were *Nessaea aglaura aglaura*, *Siproeta stelenes biplagiata*, *Taygetis thamyra*, and *Ypthimoides renata*.

Despite a considerable sampling effort (>1300 individuals collected in more than 40 sampling days in each forest-age combination), species accumulation curves did not reach an asymptote (Fig. 6). The inclination of the curves suggests that young secondary and mature SBsc would achieve similar richness with continued sampling, but old secondary SBsc would saturate at a lower level (Fig. 6A). The curves for SM (Fig. 6B), however, suggest that near-complete richness is reached in young secondary forest and would increase with continued sampling in mature and old secondary growth.

Other estimators of species richness (Fig. 7) confirm this pattern. With the exception of the ACE estimator, all are higher for SBsc <10 years than for mature and

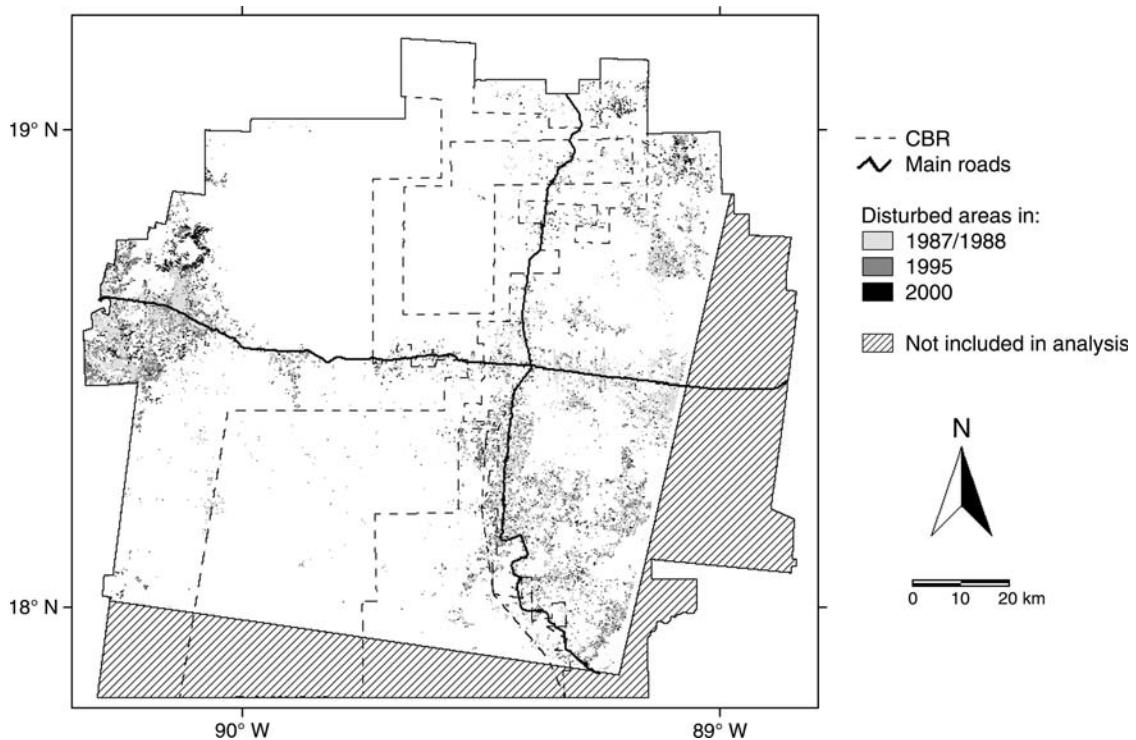


FIG. 5. Areas in agriculture or secondary vegetation from 1987/1988 to 2000 in the Western Landsat Scene. All areas exposed for each date remained in cultivation or early stages of fallow in 2000. Note that 84% of the CBR is captured in this Landsat scene.

TABLE 2. Changes (1987–2000) in area of land cover classes, by reserve and non-reserve status based on Western Landsat TM Image.

Class description	Change between 1987/1988 and 2000 (km ²)			
	Total in SY	CBR core	CBR buffer	Outside reserve
Open lands	49.83	0.86	4.46	44.52
Net area change	49.83 (0.34)	0.85 (0.04)	4.46 (0.12)	44.52 (0.49)
Total area in 2000	350.10 (2.36)	14.04 (0.71)	37.33 (0.97)	298.74 (3.31)
Secondary growth (SG)				
Herbaceous secondary	91.05	4.81	13.34	72.90
Shrubby secondary	26.53	-1.82	-1.32	29.67
Arboreal secondary	193.40	16.76	23.94	152.70
Bracken fern	48.41	2.01	2.91	43.49
Net area change in SG	359.40 (2.42)	21.76 (1.10)	38.87 (1.01)	298.77 (3.31)
Total area SG in 2000	1430.01 (9.62)	139.48 (7.03)	238.92 (6.22)	1051.62 (11.65)
Seasonally inundated forest				
Selva (S.) baja inundable	-84.14	-4.92	-9.61	-69.61
Net area change	-84.14 (-0.57)	-4.92 (-0.25)	-9.61 (-0.25)	-69.61 (-0.77)
Total area in 2000	1627.98 (10.96)	298.73 (15.06)	370.59 (9.64)	958.66 (10.62)
Transitional forest				
S. baja	-53.64	-1.52	-7.31	-44.81
Net area change	-53.64 (-0.36)	-1.52 (-0.08)	-7.31 (-0.19)	-44.81 (-0.50)
Total area in 2000	1960.54 (13.20)	241.52 (12.17)	692.40 (18.01)	1026.62 (11.37)
Upland forests (UF)				
S. baja and mediana sub/caducifolia	-95.63	-0.75	-5.79	-89.08
S. mediana	-98.39	-12.63	-12.50	-73.26
S. alta	-79.76	-3.26	-8.65	-67.84
Net area change in UF	-273.78 (-1.84)	-16.64 (-0.84)	-26.94 (-0.70)	-230.20 (-2.55)
Total area UF in 2000	9471.98 (63.75)	1290.36 (65.03)	2504.44 (65.16)	5677.18 (62.87)
Total area, all classes	14 857.87	1984.16	3843.74	9029.97

Notes: See Table 1 for a description of the classes. The percentage of the total area per column is given in parentheses; 4042.86 km² of the southern Yucatán (SY) imagery analysis region resides beyond the western scene (see Fig. 2).

SBsc >10 years. The SM <10 years has the lowest richness, and mature SM is richer than, or as least as rich as, SM >10 years, again except for the ACE estimator. This last estimator may be biased by its inclusion of species abundance (O'Hara 2005); thus we consider the ICE and Chao 2 as better estimators (Chazdon et al. 1998). The difference between a low actual and high estimated value for mature SM is explained by both the relatively low number of individuals and the high plot-to-plot differences resulting in the analysis of dispersion.

The PERMANOVA showed a significant interaction between vegetation types and ages ($F = 2.81$, $df = 1,2$, interaction $df = 2$, $P = 0.0006$), caused by these described patterns of butterfly diversity during forest development in the two vegetation types. An analysis of dispersion showed that butterfly communities were more heterogeneous in mature than in secondary forests. Furthermore, the butterfly communities were more distinct between forest ages in SBsc than in SM. In particular, <10 year-old and >10 year-old SM were not as distinctive compared to their SBsc counterparts. The nMDS

TABLE 3. Land cover transitions in area from 1987/1988 to 2000: Western Landsat TM Scene only, with percentages (within-column) given in parentheses.

Land cover classes in 2000	Transitions (km ²) from land cover classes in 1987/1988				
	Agriculture	Secondary vegetation	Inundated vegetation	Transitional forest	Upland forest types
Agriculture	134.66 (42.4)	64.46 (6.1)	27.55 (1.6)	27.21 (1.4)	96.21 (1.0)
Secondary vegetation	119.06 (37.5)	868.14 (81.6)	71.28 (4.2)	58.44 (2.9)	313.07 (3.2)
Inundated vegetation	6.57 (2.1)	10.63 (1.0)	1607.90 (94.2)	0.48 (0.0)	2.35 (0.0)
Transitional forest (Selva baja)	11.38 (3.6)	22.95 (2.2)	0.09 (0.0)	1926.10 (95.7)	0.00 (0.0)
Upland forest types	45.96 (14.5)	98.22 (9.2)	0.59 (0.0)	0.00 (0.0)	9327.19 (95.8)

Notes: Some transitions are not possible, such as the shift of upland vegetation to bajo vegetation. Image analysis, however, is affected by major differences in the amount and timing of precipitation. Even controlling for dates, precipitation differences trigger subtle shifts in certain signals, especially for selva baja, which is a transition type between upland and bajo. Also, the transition from agriculture to upland forest in the time allotted is not possible. These "errors" are reported here rather than being masked by various transition rules.

TABLE 4. Density, height, and complexity (mean \pm SE) of secondary and mature upland forests.

Forest parameter	Age class			
	2–5 yr old	6–10 yr old	12–25 yr old	Mature
Density (stems/ha)				
1–5 cm dbh	22 800 ^a \pm 2240	17 600 ^{ab} \pm 2150	14 600 ^{bc} \pm 2190	10 200 ^c \pm 2320
5–10 cm dbh	690 ^a \pm 200	1140 ^{ab} \pm 190	1480 ^{bc} \pm 200	1580 ^c \pm 210
>10 cm dbh	73 ^a \pm 83	116 ^a \pm 81	552 ^b \pm 82	884 ^c \pm 87
Mean height (m)				
1–5 cm dbh	3.4 ^a \pm 0.0	3.60 ^b \pm 0.0	3.70 ^c \pm 0.0	3.60 ^{bc} \pm 0.1
5–10 cm dbh	6.1 ^{ab} \pm 0.1	6.0 ^a \pm 0.1	6.2 ^b \pm 0.1	7.6 ^c \pm 0.1
>10 cm dbh	8.4 ^a \pm 0.4	8.1 ^a \pm 0.3	8.6 ^a \pm 0.1	12.6 ^b \pm 0.1
Canopy height (m)†	7.2 (8.9)	8.5 (8.6)	11.1 (11.2)	16.0
Canopy complexity‡				
1–5 cm dbh	1.09 ^a \pm 0.05	1.14 ^{ab} \pm 0.04	1.23 ^b \pm 0.04	1.24 ^b \pm 0.07
5–10 cm dbh	0.57 ^a \pm 0.14	0.89 ^{bc} \pm 0.07	0.87 ^b \pm 0.08	1.17 ^c \pm 0.08
>10 cm dbh	0.46 ^{bc} \pm 0.21	0.23 ^c \pm 0.11	0.73 ^b \pm 0.13	1.76 ^a \pm 0.14

Notes: Heights were predicted from stem diameter. Different letters indicate significant differences between age classes for a given parameter measured within a given size class of tree (by row). Marginal means are presented from a two-factor ANOVA (by age class and study area).

† Data reported are the 90th percentiles for heights among all trees measuring >5 cm dbh for 2–5 year old forests, and >10 cm dbh for all other age classes, after removing relic trees (palms). Data with relic trees included are in parentheses.

‡ As measured by the Shannon-Wiener diversity index of evenness.

ordinations showed that mature forest plots were grouped and separated from secondary forest plots (at the 70% level of similitude).

DISCUSSION

Land cover and change

The current percentage of mature forest types in CBR and the SY beyond the CBR appear similar, suggesting that the reserve's boundaries capture the regional ecocline (Question 1) and the biotic diversity it houses. The in-out boundary differences for all upland forest types are significant, however. Recognizing that substantial losses of higher stature and more humid SM and SA have taken place beyond the reserve, these results suggest that, compared to an "undisturbed" ecocline, the CBR holds less of the humid SA and matches well the SM. Given this difference, the ability of the CBR to maintain the biotic diversity of the ecocline may hinge on the minimal area of each upland forest type required for this maintenance (largely unknown) and the amount of these types in proximity to the CBR.

The rate of deforestation in the SY was high from 1987 to 2000 (0.2% per year). The last six years of that period, however, displayed a modest reversal; deforestation declined and some older succession was permitted to return to mature forest state (Question 2). This last trend may reflect CBR policies aimed at halting deforestation, recalling that loss rates outside the reserve were 2.2-fold (SM) to 8.6-fold (SBMsc) higher than those inside the reserve; but it also may reflect the thin markets operating in this agricultural frontier or the role of household life cycles (Roy Chowdhury and Turner 2006). Regardless of the causes, tropical reserves in economic frontiers invariably confront ebbs and flows in

surrounding land cover changes (Naughton-Treves et al. 2003, Curran et al. 2004, Moran and Ostrom 2005) and, thus, shifts in land use pressures along or within the borders of reserves. Indeed, observations subsequent to 2000 hint that deforestation may be on the increase again in the SY.

All major forest types decreased in area over the study period for the SY at large (Question 2), despite farmers' claims to prefer upland types and perhaps reflecting the use of seasonal wetlands for pasture. It is noteworthy, however, that deforestation in the reserve proper focused on upland forest types of the ecocline, especially the SM and SA. The small amount of the humid SA in the reserve raises concerns, given its losses (6%) outside the reserve over the study period as well as losses in the reserve (4%).

Habitat change: forest structure and species composition

Little overlap exists among the most common tree species of mature and secondary forest. If land change continues, the 16 species found predominately in mature forests are at risk of becoming scarce outside the CBR (Question 3). Reductions in population size over the entire SY (inside and outside of the reserve) could ultimately threaten these species in the reserve, but extinction is less likely because they are such common species in mature forest. For rare plant species, however, loss of mature forest habitat outside the reserve may diminish the resilience of populations within the reserve, especially for species in the SA (Hansen and DeFries 2007).

The species that will ultimately dominate mature forest can be present at low abundance during succession in these upland forests (Pérez-Salicrup 2004).

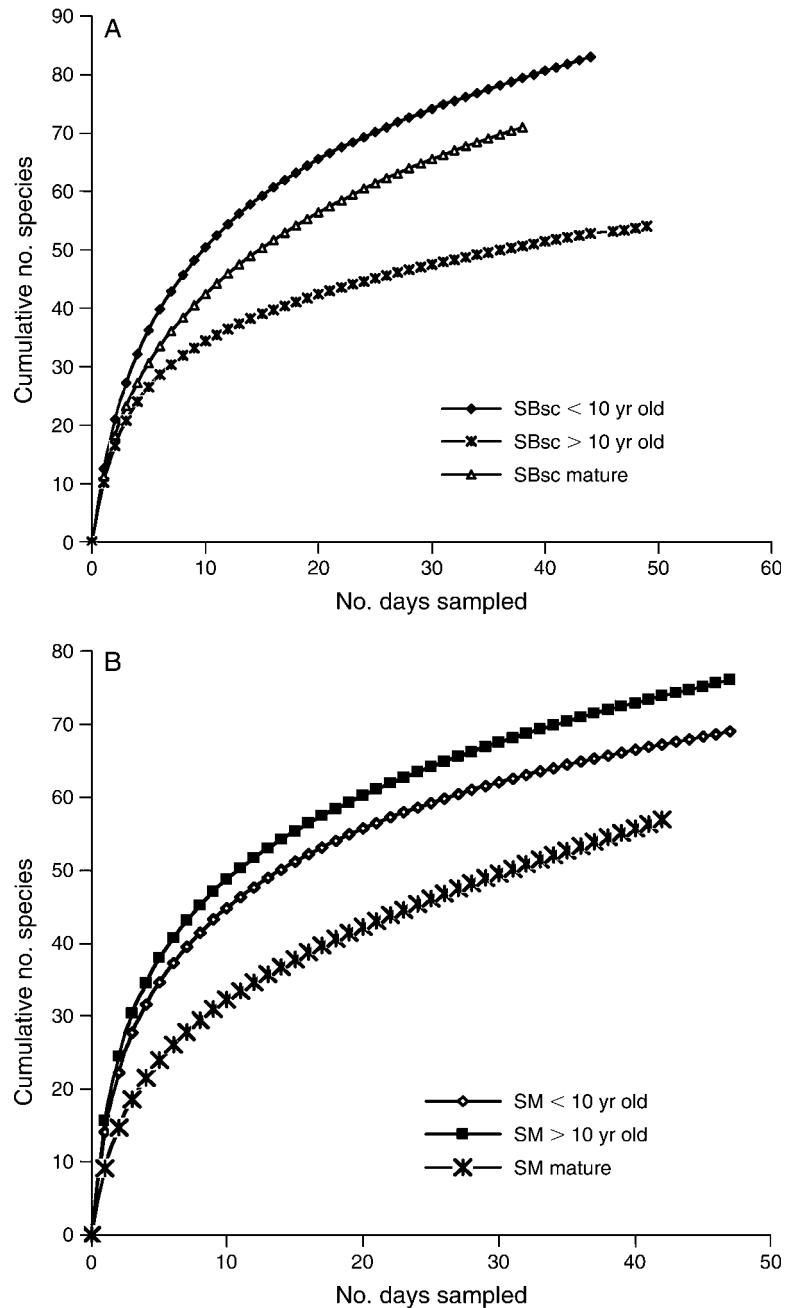


FIG. 6. Accumulation curves of species per number of days sampled in two forest types (selva mediana sub/caducifolia [SBsc] and selva mediana [SM]), and in different age classes (<10 years old, secondary forest >10 years old, and mature forest). Curves were constructed with "S obs" from EstimateS (Colwell 2005).

Recovery of species composition, but not abundances, thus may occur within 25–30 years under ideal conditions (Turner et al. 2001). The dissimilarity in dominant species between mature and secondary forest suggests that those conditions are not often met under the current fallow regime. The presence of late-successional species that can regenerate by sprouting contributes to the overlap between species dominant in mature

and secondary forest. Additionally, colonization by late-successional species dependent on seed dispersal is facilitated by the current proximity of mature forest tracts outside of the reserve, much of them preserved within larger ejidos providing land managers the option to do so. Repeated parcel use and a shortened fallow, especially in smaller (or land-sparse) ejidos, are likely to preclude successful reproduction by some late-succes-

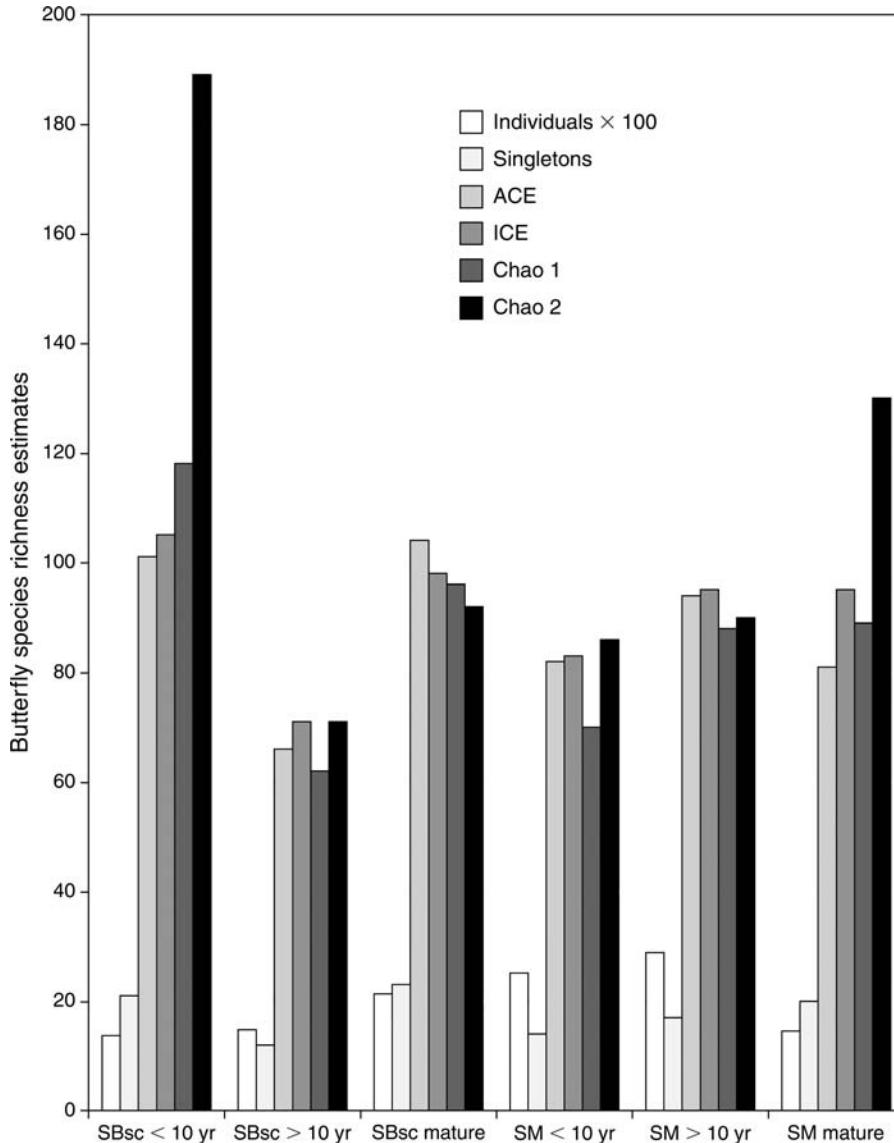


FIG. 7. Estimated species richness as abundance cover estimate (ACE), incidence cover estimate (ICE), and two Chao indices, numbers of individuals and numbers of species with only one individual (singletons) of butterflies compared between selva mediana (SM) and selva baja subcaducifolia (SBsc) and within forest types by age. Data were calculated in EstimateS (Colwell 2005). Differences between Chao indexes are significant ($P < 0.005$) in Student's t tests within each forest type. Differences in Chao 1 and 2 between mature forest types are also significant.

sional species. Thus, for some species, secondary forest will function as a sink habitat. Maintaining a diverse species pool outside the reserve depends entirely on the scale of fragmentation that currently leaves mature forest and disturbed lands in close proximity (Schneider 2004). At the ejido scale, as mature forest is pushed farther from the centers of human disturbance, especially east of the CBR, local biodiversity will diminish (Lawrence 2004). On a larger, landscape scale, forested areas of the Petén (Guatemala) to the south will continue to be a source for mature forest species in addition to the reserve. Whether these species can

successfully disperse to the broader region remains an important question.

Although tree biodiversity seems to be intact, the relative abundance of species has shifted, and will continue to do so, with some local extinctions. Furthermore, fallow-based agriculture currently creates patches of forest with more small stems, fewer medium and large trees, and lower and less variable tree canopies. In older secondary forest, the understory recovers much of its former structure, but embodies less natural variability. The upper canopy remains substantially diminished in tree density, height, and complexity.

Structural complexity at the scale of the patch is diminished.

Butterfly diversity

The SM and SBsc each have unique species. Although it is not clear-cut from the evidence, the SM is probably the richer forest type. Estimated diversity in the two mature forest types is higher than in secondary forest (Question 4), in part due to important plot-to-plot differences. These results must be evaluated against the background of the actual landscape wherein butterflies have the possibility of moving between mature and secondary forest because of their nearness. We suspect that butterfly species richness in secondary forest is partly due to a source–sink relationship with mature forest in the same landscape. An indication is given by species like *Fountainea eurypyle confusa* and *Anaea troglodyta aidea*, which are mostly found in mature forests where they probably live during part of their life cycle, but are also found, to a lesser degree, in secondary forests. This source–sink relationship creates less predictable species assemblages, which explains why, in SM, the apparently richer secondary forest (at the landscape level) is clearly less diverse from plot to plot, compared to mature forest.

Forest disturbance appears to affect butterflies in the SM differently than in the SBsc. There is a considerable decrease in species with the transition from mature to secondary forest in SBsc, despite an increase in the early-successional stages, explained by the abundance of flowering herbs in young SBsc. The loss in secondary forest is less and the recovery seems faster in SM. The fact that SM is the professed favored forest type by local farmers, however, raises questions about the longer term threats to this ecosystem.

These questions noted, the current mosaic of secondary and mature forests in SY beyond the reserve apparently affords a large degree of resilience for the butterfly population. Any effects of the landscape outside the reserve on butterflies inside the reserve could not be detected in this research. The mature forest types, however, are commonly the exclusive host to some species, especially the SA (Maya Martinez et al. 2005). Sustained losses of mature forest in the SY, therefore, suggest reductions in butterfly diversity. Furthermore, diminished variability in the understory and lower structural diversity, even in older successional forest, suggest a reduction in potential butterfly habitats (Schulze et al. 2001). Butterfly diversity in the reserve may depend primarily on the capacity of the reserve system to protect its mature forest.

Scope and limitations

Further accuracy assessments of the remote-sensing land classification are required, owing to the paucity of test sites in the far northwest portion of the region, which is isolated and difficult to access. In addition, the characteristics of the imagery-defined SB forest type

need to be assessed in the field. Finally, to explore the relationship between deforestation rates and fallow dynamics, improvement in the separation of late-successional forest (~15–25 yr) from older forest growth is required.

A much larger sampling effort, with attention to rare as well as common species, is essential to better delimit the character of the ecocline and the current status of, and risks to, tree diversity. A small bias in the butterfly data may exist due to the methodology employed: all traps were hung at a standard height and were expected to sample a fixed volume of the forest. This volume was a relatively smaller percentage of potential volume in the higher SM than in the lower SBsc, and in the mature than in the secondary forests. Furthermore, some transects included very small patches of mature forest. A clearer idea of which species are “typically” mature forest species vs. secondary forest species should include more autoecological data (Vester and Cleef 1998, Vester and Calmé 2003).

Conclusions: management and research implications

After nearly a millennium of sparse habitation and use, the forests of SY have witnessed significant human disturbance, as evident in the other cases included in this special issue, prompting the establishment of the CBR and MBC to serve various environmental functions. The most pressing concern for the preservation of biotic diversity in the CBR and the SY is to maintain the matrix and connectivity of different forest types comprising the north-to-south ecocline from dry to humid conditions. The reserve’s role in the MBC is predicated on the assumption that the flow of biota across this ecocline is maintained. Of the mechanisms that link land use change outside reserves to biodiversity inside reserves (suggested by Hansen and DeFries 2007), the CBR would appear to be most at risk due to a reduction in effective ecosystem size, loss of critical habitats, expansion of barriers to the movement of biota, and an increase in exposure of biota to humans. Recognizing the paucity of current work directly addressing these issues in the SY, this study provides several insights.

Conditions of land change in the reserve and beyond that would lead to a tipping point in the maintenance of biotic diversity are not known, but clearly depend on the amount and distribution of mature forest. The butterfly analysis suggests that the current forest matrix in the SY may not diminish butterfly diversity in the reserve. In contrast, this same matrix may be affecting the population of the jaguar. The estimated population of this top predator in the CBR (482 jaguars; Ceballos et al. 2002) is below the species’ persistence level of 500 or more (Lande 1988). The persistence of this species in the reserve will apparently depend on the success of individuals living beyond the reserve. This success is questionable, given the scale of habitat disturbance in the SY, especially of mature forest that has been cut over

the past 40 years. Other fauna are likely to be affected by the losses in the upland forest types of the regional ecocline, including SM and SA, which may serve as a source for more marginal populations in drier areas and as a seasonal refuge for migrating animals. Deforestation has been accompanied by a 14-fold increase in human population since 1960, which amplifies hunting and stresses faunal species in the SY (Escamilla et al. 2000). It has also been accompanied by increasing amounts of dry-season burning for cultivation, significantly enlarging the area under bracken fern, with implications for fauna as well (Schneider 2006).

Whether the CBR alone can preserve sufficient amounts of each forest type of the ecocline to serve its role in the MBC remains an open question. The answer resides partly in the amount of deforestation, especially of SM and SA, and partly in the spatial arrangement of that deforestation. In this regard, perhaps the greatest threat to biodiversity in the CBR is the nearly 10 km wide swath of deforestation aligned along the north-south and east-west highways. The east-west swath, separating drier from wetter areas, may significantly reduce migration pathways, reducing the effectiveness of the CBR as a local reservoir of biodiversity and as a critical link between xeric and humid habitats for the MBC.

Agriculture appears to be intensifying, changing nutrient dynamics to reduce crop yields and the rate of forest regeneration (Lawrence et al. 2004). Various unproven land management schemes are underway (Roy Chowdhury and Turner 2006) that may reduce the ecological integrity of the non-reserve forest matrix (Mayfield and Daily 2005). Beyond the SY, the supra-regional scale of deforestation-agriculture may be reducing local precipitation in the SY and CBR (Malizia 2006), enlarging the southern reach of SBMsc and potentially reducing the amount of humid forests in the CBR ecocline.

The unknowns concerning the consequences of these observations and their impacts on biotic diversity in the reserve, especially spatial and temporal population dynamics, are large. The evidence presented here regarding upland forest changes, habitat consequences, and butterfly diversity, however, suggest that landscape-level changes and processes may hold the key to the ecocline and biota questions, including the number, size, and distribution of patches of older growth forest outside the reserve. This observation, coupled with the unknowns and the synergy among the biophysical and human dimensions of land change in the SY and the CBR, point to the need for "adaptive management." Such a course requires close observations of the change trajectories in specified forest types, including metrics of landscape patterns and studies of targeted taxa, including sensitive fauna (Morales Rosas and Magaña Rueda 2001, Naughton-Treves et al. 2003). Improved information about regional dynamics in the coupled human-environment system, including satellite imagery assess-

ment, is especially important. Monitoring changes in land cover, however, must be matched by systematic studies of biodiversity and the ecological processes that connect biodiversity with different land users across the ecocline. These shortcomings notwithstanding, the results of this study suggest that a possible "small loss, big gain" outcome (DeFries et al. 2007) might follow from reducing the loss of the humid SA in the SY and CBR by substituting alternative household income strategies in order to preserve this critical forest type.

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LITERATURE CITED

- Abizaid, C., and O. T. Coomes. 2004. Land use and forest following dynamics in seasonally dry tropical forests of the southern Yucatan peninsula. *Land Use Policy* 21:71-84.
- Achard, F., H. Eva, A. Glienni, P. Mayaux, T. Richards, and H. J. Stibig. 1998. Identification of deforestation hot spot areas in the humid tropics. European Commission, Luxembourg, Luxembourg.
- Anderson, M. J. 2004a. PERMANOVA_2factor: a FORTRAN computer program for permutational multivariate analysis of variance (for any two-factor ANOVA design) using permutation tests. Department of Statistics, University of Auckland, Auckland, New Zealand.
- Anderson, M. J. 2004b. PERMDISP: a FORTRAN computer program for permutational analysis of multivariate dispersions (for any two-factor ANOVA design) using permutation tests. Department of Statistics, University of Auckland, Auckland, New Zealand.
- Boose, E. R., D. R. Foster, A. Barker Plotkin, and B. Hall. 2003. Geographical and historical variation in hurricanes across the Yucatán Peninsula. Pages 193-213 in A. Gómez-Pompa, M. F. Allen, S. Fedick, and J. J. Jiménez-Osornio, editors. *Lowland Maya area: three millennia at the human-wildland interface*. Haworth Press, New York, New York, USA.
- Carey, A. B., and M. L. Johnson. 1995. Small mammals in managed, naturally young, and old-growth forests. *Ecological Applications* 5:336-352.
- Carr, A., III. 1999. Monitoring in the Selva Maya. Pages 6-9 in A. Carr III and A. C. D. Stoll, editors. *Biological monitoring in the Selva Maya*. U.S. Man and the Biosphere Program/Tropical Ecosystem Directorate, Wildlife Conservation Society, Gainesville, Florida, USA.
- Ceballos, G., C. Chávez, A. Rivera, C. Manterola, and B. Wall. 2002. Tamaño poblacional y conservación del jaguar en la reserva de la biosfera Calakmul, Campeche, México. Pages 403-417 in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, Jr., A. Rabinowitz, K. H. Redford, J. G.

- Robinson, E. W. Sanderson, and A. B. Taber, editors. El jaguar en el nuevo milenio. Fondo de Cultura Económica, Universidad Nacional Autónoma de México and Wildlife Conservation Society, México and New York, New York, USA.
- Chao, A., and S. M. Lee. 1992. Estimating the number of classes via sample coverage. *Journal of the American Statistical Association* 87:210–217.
- Chazdon, R. L., R. K. Colwell, J. S. Denslow, and M. R. Guariguata. 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. Pages 285–309 in F. Dallmeier and J. A. Comiskey, editors. *Forest biodiversity research, monitoring and modeling: conceptual background and old world case studies*. Parthenon Publishing, Paris, France.
- Colwell, R. K. 2005. EstimateS. Statistical estimation of species richness and shared species from samples. Version 7.5. (<http://www.viceroy.eeb.uconn.edu/estimates>)
- Cuarón, A. D. 2000. Effects of land-cover changes on mammals in a neotropical region: a modeling approach. *Conservation Biology* 14:1676–1692.
- Curran, L. M., S. N. Trigg, A. K. McDonald, D. Astiani, Y. M. Hardiono, P. Siregar, I. Caniango, and E. Kasischke. 2004. Lowland forest loss in protected areas on Indonesian Borneo. *Science* 303:1000–1003.
- DeFries, R., A. Hansen, B. L. Turner, R. Reid, and J. Liu. 2007. Land use change around protected areas: management to balance human needs and ecological function. *Ecological Applications* 17:1031–1038.
- Eastman, J. R., J. Toledano, S. Crema, H. Zhu, and H. Jiang. 2005. In-process classification assessment of remotely sensed imagery. *GeoCarto International* 20:33–44.
- Escamilla, A., M. Sanvicente, M. Sosa, and C. Galindo-Leal. 2000. Habitat mosaic, wildlife availability, and hunting in the tropical forest of Calakmul, Mexico. *Conservation Biology* 14:1592–1601.
- Espadas Manríquez, C., R. Durán, and J. Atgáez. 2003. Phytogeographic analysis of taxa endemic to the Yucatán Peninsula using geographic information systems, the domain heuristic method and parsimony of endemism. *Diversity and Distribution* 9:313–330.
- Gómez-Pompa, A. 1987. On Maya silviculture. *Mexican Studies* 3:1–17.
- Hansen, A. J., and R. DeFries. 2007. Ecological mechanisms linking protected areas to surrounding lands. *Ecological Applications* 17:974–988.
- INEGI (Instituto Nacional de Estadística, Geografía e Informática). 2000. XII census general de población y vivienda. Principales resultados por localidad estados Unidos Mexicanos. Aguascaliente, Mexico.
- James, F. C., and N. O. Wamer. 1982. Relationship between temperate forest bird communities and vegetation structure. *Ecology* 63:159–171.
- Keys, E. 2004. Commercial agriculture as creative destruction or destructive creation: a case study of chili cultivation and plant–pest disease in the southern Yucatán region. *Land Degradation and Development* 15:397–409.
- Klepeis, P. 2004. Forest extraction to theme parks: the modern history of land change. Pages 39–62 in B. L. Turner II, J. Geoghegan, and D. Foster, editors. *Integrated land-change science and tropical deforestation in the southern Yucatán: Final frontiers*. Clarendon Press of Oxford University Press, Oxford, UK.
- Klepeis, P., and C. Vance. 2003. Neoliberal policy and deforestation in southeastern Mexico: an assessment of the PROCAMPO program. *Economic Geography* 73:221–240.
- Lambert, J. D. H., and T. Arnason. 1981. *Ramón* and Maya ruins: an ecological, not economic, relation. *Science* 216: 298–299.
- Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241:1455–1460.
- Lawrence, D. 2004. Erosion of tree diversity during 200 years of shifting cultivation in Bornean rain forest. *Ecological Applications* 14:1855–1869.
- Lawrence, D. 2005. Regional-scale variation in litter production and seasonality in the tropical dry forests of southern Mexico. *Biotropica* 37:561–570.
- Lawrence, D., H. Vester, D. Pérez-Salicrup, J. R. Eastman, B. L. Turner II, and J. Geoghegan. 2004. Integrated analysis of ecosystem interactions with land-use change: the southern Yucatán peninsular region. Pages 277–292 in R. DeFries, G. Asner, and R. Houghton, editors. *Ecosystem interactions with land use change*. American Geophysical Union, Washington, D.C., USA.
- Legendre, P., and L. Legendre. 1998. *Numerical ecology*. Elsevier Science, Amsterdam, The Netherlands.
- Lundell, C. L. 1934. Preliminary sketch of the phytogeography of the Yucatan Peninsula. *Contribution to American Archaeology* 12(436). Carnegie Institute of Washington, Washington, D.C., USA.
- Magurran, A. 2004. *Measuring biological diversity*. Blackwell, Malden, Massachusetts, USA.
- Malizia, N. R. 2006. Examining inter-annual variation of deciduousness in the seasonally dry tropical forests of the southern Yucatan. Thesis. Clark University, Worcester, Massachusetts, USA.
- Martínez, E., and C. Galindo-Leal. 2002. La vegetación de Calakmul, Campeche, México: clasificación, descripción y distribución. *Boletín de la Sociedad Botánica de México* 71: 7–32.
- Maya Martínez, A., C. Pozo, and E. May Uc. 2005. Las mariposas (Rhopalocera: Papilionidae, Pieridae y Nymphalidae) de la selva alta subperennifolia de la región de Calakmul, México, con nuevos registros. *Folia Entomologica Mexicana* 44:123–143.
- Mayfield, M. M., and G. C. Daily. 2005. Countryside biogeography of neotropical herbaceous and shrubby plants. *Ecological Applications* 15:423–439.
- McArdle, B. H., and M. J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 81:290–297.
- Miranda, F., and E. Hernández X. 1963. Los tipos de vegetación de México y su clasificación. *Boletín de la Sociedad Botánica de México* 28:29–179.
- Morales Rosas, J., and S. Magaña Rueda. 2001. Fuentes de impacto, Necesidades de Investigación Científica y Monitoreo en Calakmul, Campeche. Pronatura Peninsula de Yucatán, A. C. and The Nature Conservancy, Merida, Mexico.
- Moran, E. F., and E. Ostrom. 2005. Seeing the forest and the trees: human–environment interactions in forest ecosystems. MIT Press, Cambridge, Massachusetts, USA.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
- Naughton-Treves, L., J. Luis Mena, A. Treves, and V. Christian Radeloff. 2003. Wildlife survival beyond park boundaries: the impact of slash-and-burn agriculture and hunting on mammals in Tambopata, Peru. *Conservation Biology* 17:1106–1117.
- O'Hara, R. B. 2005. Species richness estimators: how many species can dance on the head of a pin? *Journal of Animal Ecology* 74:375–386.
- Pennington, T. D., and J. Sarukhán. 1968. Manual para la identificación de campo se los principales árboles tropicales de México. Instituto Nacional de Investigaciones Forestales, Secretaría de Agricultura y Ganadería, Mexico, D.F., Mexico.
- Pérez-Salicrup, D. 2004. Forest types and their implications. Pages 63–80 in B. L. Turner II, J. Geoghegan, and D. Foster,

- editors. Integrated land-change science and tropical deforestation in the southern Yucatán: Final frontiers. Oxford University Press, Oxford, UK.
- Pozo de la Tijera, C., C. Galindo Leal, J. R. Cedeño, R. R. Calderón, S. Uc, and A. Maya. 2000. Inventario y monitoreo de anfibios, reptiles y mariposas de la reserva de Calakmul. Campeche. Fase II. Final Report. ECOSUR-CONABIO. Chetumal, Quintana Roo, Mexico.
- Raman, T. R. S., G. S. Rawat, and A. J. T. Johnsingh. 1998. Recovery of tropical rainforest avifauna in relation to vegetation succession following shifting cultivation in Mizoram, north-east India. *Journal of Applied Ecology* 35: 214–231.
- Read, L., and D. Lawrence. 2003. Recovery of biomass following shifting cultivation in dry tropical forests of the Yucatan. *Ecological Applications* 13:85–97.
- Reyna-Hurtado, R. A. 2002. Hunting effects on the ungulate species in Calakmul forest, Mexico. Thesis. University of Florida, Gainesville, Florida, USA.
- Roy Chowdhury, R., and L. Schneider. 2004. Land cover and land use in the region: classification and change analysis. Pages 105–144 in B. L. Turner II, J. Geoghegan, and D. Foster, editors. Integrated land-change science and tropical deforestation in the southern Yucatán: Final frontiers. Oxford University Press, Oxford, UK.
- Roy Chowdhury, R., and B. L. Turner II. 2006. Reconciling agency and structure in empirical analysis: smallholder land use in southern Yucatán, Mexico. *Annals of the Association of American Geographers* 36:302–322.
- Schneider, L. C. 2004. Bracken fern invasion in southern Yucatán: a case for land-change science. *Geographical Review* 94:229–241.
- Schneider, L. C. 2006. Invasive species and land-use: the effect of land management practices on bracken fern invasion in the region of Calakmul, Mexico. *Journal of Latin American Geography* 5:91–107.
- Schulze, C. H., K. E. Linsenmair, and K. Fiedler. 2001. Understorey versus canopy: patterns of vertical stratification and diversity among Lepidoptera in a Bornean rain forest. *Plant Ecology* 153:133–152.
- Smith, T. M., and H. H. Shugart. 1987. Territory size variation in the ovenbird: the role of habitat structure. *Ecology* 68: 695–704.
- Snook, L. K. 1998. Sustaining harvests of mahogany (*Swietenia macrophylla* King) from Mexico's Yucatán forests: past, present, and future. Pages 62–80 in R. B. Primack, D. Bray, H. A. Galletti, and I. Ponciano, editors. Timber, tourists, and temples: conservation and development in the Maya forest of Belize, Guatemala, and Mexico. Island Press, Washington, D.C., USA.
- Standley, P. C. 1930. Flora of Yucatan. Field Museum of Natural History Botanical Series 3:157–189.
- Turner, B. L., II et al. 2001. Deforestation in the southern Yucatán peninsular region: an integrative approach. *Forest Ecology and Management* 154:343–370.
- Turner, B. L., II, P. Klepeis, and L. Schneider. 2003. Three millennia in the southern Yucatán peninsular region: implications for occupancy, use, and “carrying capacity.” Pages 361–387 in A. Gómez-Pompa, M. Allen, S. Fedick, and J. Jimenez-Osornio, editors. The lowland Maya area: three millennia at the human-wildland interface. Halworth Press, New York, New York, USA.
- van der Maarel, E. 1990. Ecotones and ecoclines are different. *Journal of Vegetation Science* 1:135–138.
- Vester, H. F. M., and S. Calmé. 2003. Los ecosistemas terrestres de la península de Yucatán: Estado actual de los paisajes, vegetación, flora y fauna. Pages 159–173 in P. Colunga GarciaMarin and A. Larque Saavedra, editors. Naturaleza y sociedad en el area Maya, pasado presente y futuro. Academia Mexicana de Ciencias y Centro de Investigaciones Científicas de Yucatán, Mexico, DF, Mexico.
- Vester, H. F. M., and A. M. Cleef. 1998. Tree architecture and secondary tropical rain forest development: a case study in Araracuara, Colombian Amazonia. *Flora* 193:75–97.
- Weber, M. 2000. Effects of hunting on tropical deer populations in Southeastern Mexico. Thesis. Royal Veterinary College, University of London, London, UK.
- Whigham, D. F., I. Olmsted, E. Cabrera Cano, and M. E. Harmon. 1991. The impact of hurricane Gilbert on trees, litterfall, and woody debris in a tropical forest in the northeastern Yucatan Peninsula. *Biotropica* 23:434–441.
- Wilcove, D. S., and R. M. May. 1986. National park boundaries and ecological realities. *Nature* 324:206–207.
- Zimmerer, K. 2000. The reworking of conservation geographies: nonequilibrium landscapes and nature-society hybrids. *Annals of the Association of American Geographers* 90:356–369.

APPENDIX A

Dominant species in forests of the southern Yucatán (*Ecological Archives* A017-036-A1).

APPENDIX B

Numbers of individuals trapped and netted during 1997 in two forest types and their derived secondary forest of two age classes (*Ecological Archives* A017-036-A2).