



## Landscape variation of liana communities in a Neotropical rain forest

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### Abstract

We studied local and landscape variation of liana communities across habitats differing in soil and topography in the Lacandon tropical rain forest, southeast Mexico. All liana stems  $\geq 1$  cm diameter breast height (DBH) were sampled within each one of eight 0.5 ha plots. Two plots were sampled in each of the following habitats: alluvial-terrace, flood plain, low-hill, and karst-range. In the whole sampled area, we recorded 2092 liana stems  $\text{ha}^{-1}$  representing a total basal area of  $1.95 \text{ m}^2 \text{ ha}^{-1}$  and 90 species within 34 families. Lianas showed a strong clumped spatial pattern and a high taxonomic diversity at the scale of  $50 \text{ m}^2$ . On average ( $\pm$  s.e.), we found  $10.4 \pm 0.6$  stems,  $4.4 \pm 0.2$  species and  $3.4 \pm 0.2$  families per  $50\text{-m}^2$  quadrat. Bignoniaceae (19 species), Malpighiaceae (9), and Fabaceae (8) comprised about 40% of total number of recorded species, and almost 50% of the total liana biomass, as expressed by an importance value index that combines species relative abundance, spatial frequency and basal area. Nineteen families (56%) were represented by just one species and *Cydista* (Bignoniaceae) and *Machaerium* (Fabaceae) were the most diverse genera with four species each. In the landscape, lianas showed a geometric diversity-dominance relationship with only three species (*Combretum argenteum*, *Hiraea fagifolia* and *Machaerium floribundum*) accounting for more than 50% of total biomass. More than 30% of the species were rare ( $< 15$  stems  $\text{ha}^{-1}$ ) and showed low spatial frequency (recorded in just one of the eight plots). Liana communities differed in structure and composition among sites and habitats. Among sites, lianas exhibited four-fold variation both in stem density and basal area and two-fold variation in species richness. Liana density was significantly and positively correlated with treefall disturbance. Ordination analysis indicated a strong habitat differentiation of lianas at the family and species levels. Most species with non-random distribution among habitats (69% from 25 species) were significantly most abundant in low-hill or flood plain sites, and some (12%) were preferentially found at the karst-range sites. The karst-range habitat was well differentiated from the others in species composition and structure, and shared only 50% of common species with other habitats.

Soil water availability, treefall dynamics, as well as tree host identity and abundance may play an important role in the organisation of the liana communities at the Lacandon forest.

**Nomenclature:** Ibarra-Manríquez & Sinaca (1995) and Martínez et al. (1994).

### Introduction

Tropical rain forests are one of the most species diverse plant communities (Gentry & Dodson 1987a). This assertion has been sustained for many years by studies focused on the tree component of the forest

(e.g., Richards 1996). Recently, the exploration of mechanically dependent plants, such as orchids, vines, and lianas has pinpointed the contribution of these elements to species diversity, structural complexity, and function of tropical rain forests (Gentry 1982, 1988, 1992; Gentry & Dodson 1987a, b; Putz 1984,

1995; Clark & Clark 1990; Hegarty & Caballé 1991; Campbell & Newbery 1993; Makana et al. 1998).

In neotropical rain forests, there are around 9216 liana species, representing 97 families of vascular plants (Gentry 1991a). At a local scale, lianas comprise between 12 and 24% of the total number of woody species (Gentry & Dodson 1987a, b; Ibarra-Manríquez & Sinaca 1995). In addition, lianas are structurally important in these forests. In moist and wet tropical forests, about 18–22% of understorey erect plants are juvenile lianas (Gentry 1982) and, on average, lianas comprise about 24% of total stems with  $DBH \geq 2.5$  cm (Gentry 1991a). Functionally, the liana community exhibits a diverse array of pollination, dispersal, and phenological systems, and provides several resources to the animal community (Emmons & Gentry 1983; Gentry 1982, 1983, 1985, 1991b; Putz & Windsor 1987; Hegarty 1990; Ibarra-Manríquez et al. 1991; Opler et al. 1991). Lianas influence forest regeneration dynamics; they produce weight loads that favour the occurrence of treefall gaps, and liana growth may inhibit tree regeneration in gaps and forest edges (Appanah & Putz 1984; Putz 1984, 1985; Putz et al. 1984; Clark & Clark 1990).

An increasing number of studies have documented the structure and composition of liana communities at the scale of a few dozen square meters (e.g., Gentry 1988; Putz & Mooney 1991). Some attempts have been made to document geographical relations between attributes of the liana communities and macro-environmental variables such as annual rainfall, climate seasonality, average temperature, and soil type (Clinebell et al. 1995). At present, however, few studies (Holdridge et al. 1971; Putz & Chai 1987; Molina-Freaner & Tinoco 1997) have explored how liana communities vary at a landscape scale where climate is virtually the same, but factors such as soil, topography, and arboreal vegetation are spatially heterogeneous. This type of analysis is necessary because the abundance and size of trellis and tree liana hosts, frequency and magnitude of forest disturbances, and soil-water availability are thought to affect local abundance and distribution of lianas (e.g., Putz 1984; Hegarty & Caballé 1991; Molina-Freaner & Tinoco 1997).

The present study was undertaken to explore structural and species composition trends of liana communities within and among contrasting soil-topographic habitats at the Lacandon forest in southeast Mexico. These habitats represent major environmental discontinuities within the Montes Azules Biosphere Reserve,

and sustain forests that vary in floristic composition and structure (Siebe et al. 1996). In addition to providing a detailed quantitative analysis of the structure and composition of the liana communities in the region, at a scale of about 100 km<sup>2</sup>, we addressed the following questions: what is the variation of the liana communities in the landscape in terms of abundance, spatial distribution, and species diversity? Are liana species segregated among habitats; if so, what factors are likely to promote such a differentiation? How comparable are the liana communities present at the Lacandon forest with that of other tropical rainforests?

### Study site

This study was conducted at the Chajul Tropical Biological Station, located to the south of the Montes Azules Biosphere Reserve (16°04' N; 90°45' W), within the Lacandon region, in southeast Mexico. This preserve covers an area of 331 200 ha, and an altitude range of 80 to 1750 m.a.s.l. At Chajul, average annual rainfall is about 3000 mm. Mean annual temperature is about 22 °C. There is a dry season from February to April (less than 100 mm per month) which accounts less than 10% total annual rainfall. In this area a mosaic of vegetation types is present including: lowland and mountain rain forests, savannah-like vegetation, elfin forest, and pine forest (Gómez-Pompa & Dirzo 1995). In the preserve, there are around 3400 species of vascular plants (Martínez et al. 1994) of which 573 are trees.

### Major landscape units

In the Chajul region there exist at least four different geo-morphological units (hereafter referred to as habitats) that were defined using soil and topographic criteria (Table 1). (i) Alluvial-terraces (altitude: 105–120 m.a.s.l.) are flat, fertile soil sites along margins of the Lacantún-river. (ii) Flood plains (altitude: 105–115 m.a.s.l.) are old meandric areas originated from the Lacantun-river and with hydromorphic soil characteristics; these areas remain flooded at least three months every year. (iii) Low-hills (altitude: 115–300 m.a.s.l.) are topographically irregular areas with small hills and valleys with sandy or limestone soils of low pH (< 5.5). (iv). Karst-range sites are topographically irregular mountain chain areas (300–700 m.a.s.l.), locally known as 'Cordon Chaquistero', where the soil is basically composed of a thin layer of organic matter,

*Table 1.* Characteristics of the four study habitats at the Lacandon rain forest in southeast Mexico. Where available, minimum and maximum values are shown. (a) Abiotic aspects based on soil and topography surveys in three to five 0.5-ha plots per habitat. Average available phosphorous (P, mg kg<sup>-1</sup>) and nitrogen (N, mg kg<sup>-1</sup>) are provided as soil nutrients; these values were estimated with samples taken from soil profiles of indicated depth\* (modified after Siebe et al. 1996). (b) Tree community attributes based on censuses of trees *DBH* ≥ 10.0 cm in three to five 0.5 ha plots in each habitat (Martínez-Ramos et al., unpubl. data). Forest canopy height is expressed as the among plots average maximum canopy height (± s.d.). Treefall disturbance is the percentage of forest canopy area in gaps (points where canopy height was less than 2 m).

(a)	Soil						Topography (Slope)	
	Habitat	Category (FAO, 1988)	Depth* (cm)	pH	Nutrients		Drainage	
					P	N		
Alluvial terrace	Haplic Luvisol	65–100	5.6–6.7	0.36–0.95	23.8–35.0	Moderate	Flat (< 10°)	
Flood plain	Eutric Planosol	45	4.9–6.0	0.22	12.2	Deficient	Flat (< 10°)	
Low-hill	Humic Acrisol	55–65	3.9–5.4	< 0.1	13.2–27.3	Moderate	Moderate-steep (15°–30°)	
Karst-range	Rendzic Leptosol	12–20	7.0	0.23	57.9	High	Very steep (30°–40°)	

(b) Tree community characteristics						
Habitat	Canopy height (m)	Tree density (ind ha <sup>-1</sup> )	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Tree species richness (in 0.5 ha)	% Area in gaps	
Alluvial terrace	40 ± 3	318–376	22.6–37.6	43–58	0.4–4.3	
Flood plain	40 ± 12	202–252	19.6–29.4	35–54	2.8–9.4	
Low-hill	35 ± 1	344–524	16.6–29.8	50–81	2.3–3.9	
Karst-range	35 ± 4	426–578	21.6–27.0	70–74	1.2–1.5	

with masses of limestone rocks exposes over a karst topography. Alluvial terraces have the most nutrient rich soils and low-hills have the poorest ones (Table 1).

A preliminary study has documented the variation in the tree communities between these habitats (Siebe et al. 1996). Table 1 shows a summary of the main tree community attributes in the study habitats. It should be noted that karst-range and low-hill habitats sustain higher tree density and species richness while the alluvial-terrace habitat have the highest standing biomass (estimated from tree community basal area). Forest canopy disturbance, as measured by the percentage of forest area in gaps (localities with forest canopy height shorter than 2 m), is lowest in karst-range habitat and highest in the flood plain habitat (Table 1).

## Methods

### *The liana study system*

To enable comparison with other works (Gentry 1982, 1988, 1991a), in this study we included both lianas and those woody hemi-epiphytes that are liana-like. Lianas are woody vines that become established on the forest floor and grow upward, toward the forest canopy. Woody-liana-like hemi-epiphytes are climbing plants that germinate and establish themselves on trees and lianas, and their physiognomy and growth behaviour are similar to that of true lianas. As lianas, woody hemi-epiphytes may spread on more than one tree by producing a net of slender stems, some of which may root in the soil and grow upwards again (Gentry 1988, 1991a). Hemi-epiphyte strangler trees (e.g., several species of *Ficus*) and epiphyte trees (e.g., *Clusia* spp.), which are not liana-like, were not included. Hereafter we will refer to both true lianas and woody hemi-epiphytes that are liana-like as 'lianas'.

### *Liana surveys*

We conducted a census of lianas in each of the four habitats described above. Two different sites located at least 2 km apart represented each habitat. In each site, we established a permanent 0.5 ha ( $20 \times 250$ -m) plot that ensured a good representation of the forest regenerative mosaic, including gap, building and mature phases (*sensu* Whitmore 1978). The plot was grided with aluminium stakes (0.75 m height) in quadrats of  $5 \times 10$  m. For each plot we randomly selected 30 quadrats. All liana stems located within the quadrats and with a perimeter at breast height (*PBH*, 1.3 m above ground) larger or equal to 3.1 cm (or 1 cm *DBH*, assuming a circular cross-section stem area), were identified to species and measured for *PBH*. We used the perimeter rather than diameter to avoid errors associated with the irregular shapes of most liana stems. Later, *PBH* measures were converted to *DBH* values assuming a circular cross-section stem area (i.e.,  $DBH = PBH/\pi$ ).

We identified separate individual lianas when stems were clearly rooted; otherwise, we looked for possible underground stem connections. All non-rooted stems with a measurable *PBH* were assumed to belong to rooted lianas within the quadrats. Lianas were identified to species in the field using reproductive (flowers or fruits) and/or vegetative (leaves, trunks) characteristics and when necessary sterile material was collected for later identification at the MEXU Herbarium, where voucher specimens collected previously by others were deposited. Species nomenclature in this study follows that of Ibarra-Manríquez & Sinaca (1995) and Martínez et al. (1994).

### *Data analyses*

#### *Liana assemblage characterisation at the landscape level*

To describe average floristic and structural attributes of lianas at the landscape level, we combined data obtained from all plots. We used the frequency of species per family to characterise the floristic composition. To describe liana size structure, we obtained the frequency of stems in  $\log_{10}$  *DBH* classes. By dividing the total number of stems by the total number of rooted lianas, we roughly estimated the average number of stems with *DBH* > 1 cm per rooted liana. We also obtained the abundance (total number of individual lianas and stems), basal area (cross-sectional area of stems at 1.3 m above ground), and

frequency (number of quadrats or plots in which a species was recorded) per species, family, and for the whole liana assemblage. Basal area per stem was obtained as  $\pi(DBH/2)^2$ , assuming stem cross-section area as a circle. To quantify the structural importance of families and species, we used an Importance Value Index ( $IV_i$ ). Following Müller-Dumbois & Ellenberg (1974), this index was calculated as  $IV_i = A_i + F_i + BA_i$ , where  $A_i$ ,  $F_i$  and  $BA_i$  are, respectively, the percentages of abundance, quadrat frequency, and basal area of the  $i$ th family or species.

The coefficient of dispersion ( $CD = \text{variance}/\text{mean}$ ) of the number of stems per  $5 \times 10$  m quadrat was used to assess local spatial pattern of the liana stem community. A  $CD$  value statistically equal to 1 indicates a random pattern,  $CD > 1$  indicates an aggregated pattern, and  $CD < 1$  an uniform one. We used a  $t$ -test to assess significant deviation from  $CD = 1.0$  (Pielou 1969).

Following Magurran (1988), we used the total number of species recorded in the eight plots (species richness), as well as Shannon ( $H'$ ) and Simpson ( $D$ ) diversity indices to quantify species diversity. Shannon index emphasises the contribution of rare species to species diversity, while Simpson index emphasise the contribution of the most abundant (dominant) species. We also obtained the evenness index  $J$  associated with  $H'$  and the evenness index  $E$  associated with  $D$  (Magurran 1988). In all these indices we used  $IV_i$  as a criterion of species biomass. Additionally, following Gotelli & Graves (1996), we used species  $IV_i$  to construct a dominance-diversity curve for the whole liana assemblage.

Variation in abundance among species was expressed as the frequency of species in  $\log_2$  abundance categories. The spatial distribution of species in the landscape was defined by the frequency of quadrats and plots in which each species was recorded. Finally, to explore abundance-distribution relationships and to assess the relative contribution of abundance, basal area, and frequency to species importance value, we explored pair-wise linear relationships among these structural variables.

#### *Community variation among sites and habitats*

We quantified the same parameters described above for each site and habitat. These values were calculated at the scale of the total area sampled per site (or habitat), and at the scale of the  $5 \times 10$ -m quadrats. To assess structural and composition changes among habitats, we performed ordination by correspondence analysis

(CA). In this analysis, we assumed that taxa (families or species) have optimum performance (e.g., abundance) in one particular habitat (Jongman et al. 1987). We constructed matrixes with  $h$  (habitats) columns, and  $t$  (families or species) rows. The number of rows corresponded to the total number of taxa recorded in the eight study plots. Matrix cells corresponded to the taxa importance value in each habitat. We used the program Orden V.2.0 (Ezcurra 1992) to perform the CAs. Additionally, the Sørensen index (Magurran 1988) was used to quantify the floristic similarity among habitats. Simple correlation analysis was used to explore relationships between inter-site variation in liana abundance, basal area and species diversity with canopy disturbance (as measured by natural logarithm of percentage of forest area in gaps) and tree ( $DBH \geq 10$  cm) density (data from Table 1).

To assess statistical differences in abundance, basal area, and floristic (species and family) diversity among sites and habitats, we used Analyses of Deviance (ANDEVA) procedures (Crawley 1993). We performed one-way ANDEVAs using the two plot values per habitat as habitat replicates. We performed a second series of ANDEVAs to test the effects of habitat and site on structural variables by using data from individual quadrats. For count variables, we used a Poisson error and a log-link function and, when required, over-dispersion problems were corrected by rescaling dependent variables (Crawley 1993). The effect of site and habitat type was assessed by the amount of explained deviance from total deviance, which approximates to  $\chi^2$  values (Crawley 1993). For continuous variables, we used a normal error and a linear link function, in which case ANDEVA becomes equivalent to one-way Analysis of Variance. To avoid violation of ANOVA normality requirements, we used logarithmic transformation (Sokal and Rohlf 1995) for basal area and species diversity values (both  $H'$  and  $D$ ). Also, we used analyses of deviance to test association analyses between species abundance and habitats, and to assess correlations between liana species diversity or abundance and canopy disturbance (assessed as percentage of forest area in gaps) and the abundance of trees with  $DBH > 10$  cm. All statistical tests were run using the statistical package GLIM 3.77 (1985).

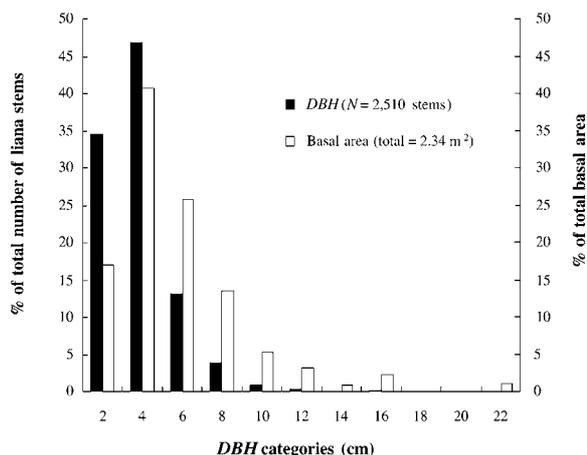


Figure 1. Size distribution ( $DBH$  classes and their relative contribution to total basal area) of lianas at the Lacandon forest in southeast Mexico. Along the X's axis, the upper limit of each category is showed.

## Results

### *Liana community composition and structure at the landscape level*

In the eight study plots (total area = 1.2 ha), we recorded a total of 1252 rooted lianas (1043 lianas  $ha^{-1}$ ), and 2510 liana stems (2092 stems  $ha^{-1}$ ). These stems represented a total basal area of 2.34  $m^2$  (1.95  $m^2 ha^{-1}$ ). Lianas were widely distributed in the study area as we recorded liana stems in 93.3% of total sampled quadrats ( $N = 240$ ). On average ( $\pm$  s.e.), an individual rooted liana had  $2.0 \pm 0.1$  stems at the forest floor level. Eighty one percent of total stems had between 1 and 4 cm- $DBH$  and only 1.6% had a  $DBH > 9.9$ -cm  $DBH$ . These big lianas, however, represented 16% of the total basal area (Figure 1). The biggest stem measured 21.0-cm- $DBH$  (*Souroubea loczyi*, Marcgraviaceae) and on average stems measured  $2.7 \pm 0.1$  cm in  $DBH$ .

At the scale of the  $5 \times 10$  m quadrats, we obtained an average stem density of  $10.4 \pm 0.6$ . This mean density showed a great variance: 50% of total quadrats included less than 15% of total stems while fifteen percent of quadrats contained more than 50% of total stems. Maximum liana stem density per quadrat was 51. The coefficient of dispersion ( $CD = 8.9$ ) indicated that lianas had a strongly clumped spatial pattern ( $t = 13.5$ ,  $DF = 238$ ,  $P < 0.0001$ ).

A total of 90 liana species, representing 34 angiosperm families, were recorded. Appendix I shows the list of taxa recorded in each one of the eight study

Table 2. Structural contribution of the ten most important families with liana species in the Lacandon forest, southeast, Mexico. Percentage values (in parenthesis) were obtained by pooling all plots (1.2 ha).

Family	Species richness	Stem abundance	Basal area (m <sup>2</sup> )	Importance value
1. Bignoniaceae	18 (20)	628 (25)	60.1 (26)	75.9 (25)
2. Fabaceae	8 (9)	301 (12)	37.8 (16)	40.7 (14)
3. Combretaceae	2 (2)	251 (10)	34.0 (15)	33.2 (11)
4. Sapindaceae	6 (7)	326 (13)	21.2 (9)	32.8 (11)
5. Malpighiaceae	9 (10)	226 (9)	15.1 (7)	25.1 (8)
6. Compositae	5 (6)	176 (7)	15.7 (7)	19.9 (7)
7. Apocynaceae	4 (4)	108 (4)	7.7 (3)	12.6 (4)
8. Hippocrateaceae	1 (1)	93 (4)	9.8 (4)	10.9 (4)
9. Marcgraviaceae*	2 (2)	75 (3)	8.2 (4)	7.3 (2)
10. Dilleniaceae	2 (2)	50 (2)	3.9 (2)	5.9 (2)
Subtotal	57 (63)	2234 (89)	273.9 (93)	264.1 (87)
Other families	24 (37)	276 (11)	39.5 (7)	35.9 (13)
Total	90 (100)	2510 (100)	234.4 (100)	300.0 (100)

\*Marcgraviaceae was represented by one liana and one woody hemi-epiphyte species.

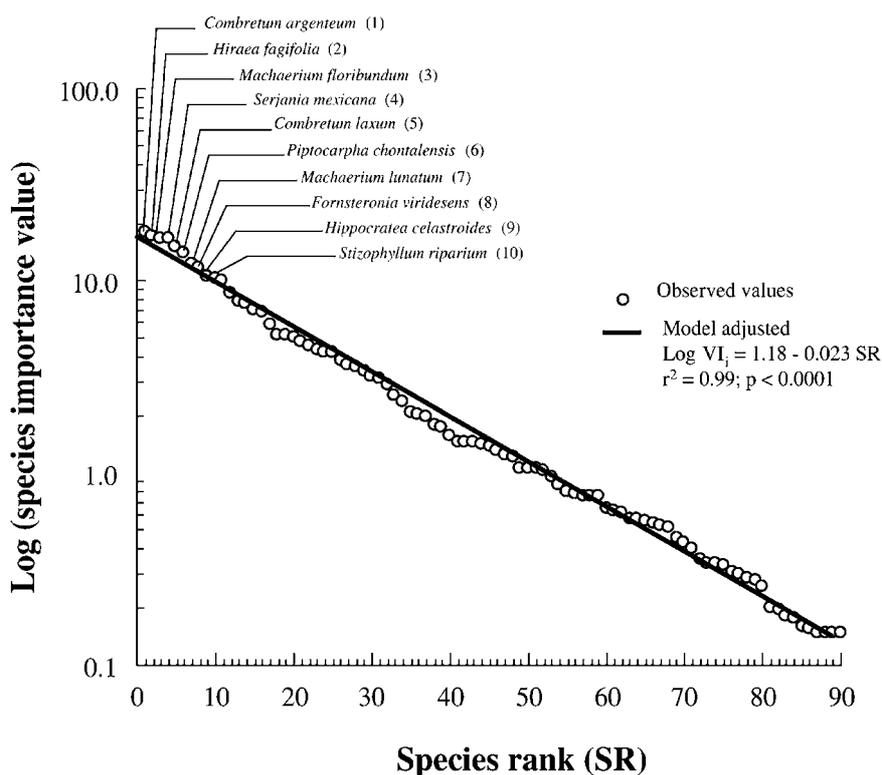


Figure 2. Species-dominance relationship for the study liana communities at the Lacandon forest, southeast Mexico. The latin names of the ten most important species and parameter values of the adjusted regression model are given.

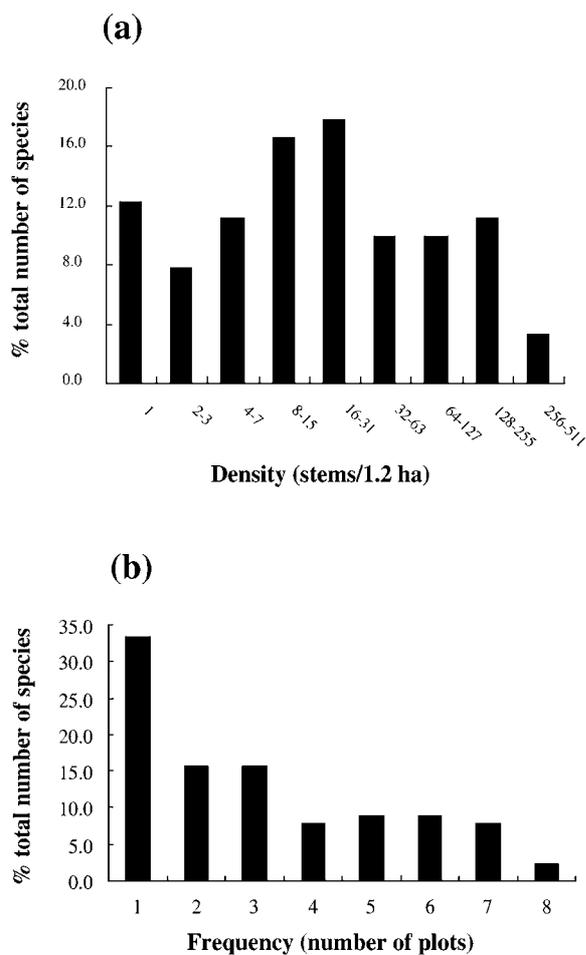


Figure 3. Structural components of the liana community at the Lacandon forest, southeast Mexico. (a) Frequency distribution of species in log<sub>2</sub> categories of stem density, (b) frequency distribution of species categorised by the number of plots in which they appeared.

plots. On average, a  $5 \times 10$  m quadrat had  $4.4 \pm 0.2$  species and  $3.4 \pm 0.2$  families. There was strong taxonomic dominance as only five families contributed about 50% of total number of recorded species (Table 2), and nineteen families were represented by only one species (Appendix I). The most diverse genera were *Cydista* and *Machaerium*, each one with four species, whereas *Arrabidaea*, *Paullinia*, and *Stigmaphylum* had three species each (Appendix I).

Just one Bignoniaceae (*Schlegelia parviflora*), two Marcgraviaceae (*Marcgravia mexicana* and *Souroubea loczyi*) species and *Drymonia serrulata* (Gesneriaceae) were liana-like hemi-epiphytes and the rest were true lianas. These hemi-epiphyte species accounted for less than 5% of total abundance, basal

area, and importance value, and each species was recorded in less than 5% of total sampled quadrats.

The most species rich families were also the most structurally important, as only five families represented 69% of total abundance, 73% of total basal area, and 69% of total community importance value (Table 2). Bignoniaceae and Fabaceae were the most structurally important families. Combretaceae was the third in importance but was represented by only two species.

The Shannon index of diversity for the whole liana community was 1.65, with relatively high evenness index ( $J = 0.85$ ). However, Simpson diversity index ( $D = 32.5$ ) indicates that only a third of total species ( $E = 0.36$ ) were the most structurally important. Among dominant species, eleven species accounted for 50% of total community importance value. The observed community dominance-diversity curve fitted tightly to a geometric model; *Combretum argenteum*, *Hiraea fagifolia*, and *Machaerium floribundum* were the species with the highest importance values (Figure 2).

Most of the recorded species were rare, but several were very abundant (Figure 3a). About 30% of total species had less than seven stems in the eight study plots (*i.e.*, less than  $5.8 \text{ stems ha}^{-1}$ ), and about 15% of total species had more than 127 stems (*i.e.*, more than  $106 \text{ stems ha}^{-1}$ ). Most species were spatially restricted. About 35% of total species were found in just one of the eight studied plots (Figure 3b). Only *Combretum laxum* and *Hiraea fagifolia* were recorded in all plots (Appendix I). *Combretum argenteum*, *Cydista potosina*, *Forsteronia viridescens*, *Machaerium kegelii*, *Paragonia pyramidata*, *Paullinia venosa*, and *Serjania mexicana* were also widely distributed, as they were recorded in seven of the eight study plots.

Species abundance, basal area, and quadrat frequency showed a positive association across the whole sampled area. Species abundance and spatial distribution were closely related (Figure 4a). No species covered the entire sample area, and the most abundant species were recorded in less than 30% of total sampled quadrats (Figure 4a). The relationships between species basal area and species abundance or distribution were more variable (Figures 4b and 4c). Species with similar levels of abundance and distribution differed strongly in basal area (Figures 4b and 4c), indicating that the average individual stem basal area varied greatly among species. For example, the abundant and widely distributed species, *Combretum argenteum*, *Machaerium floribundum*, *C. laxum*, and

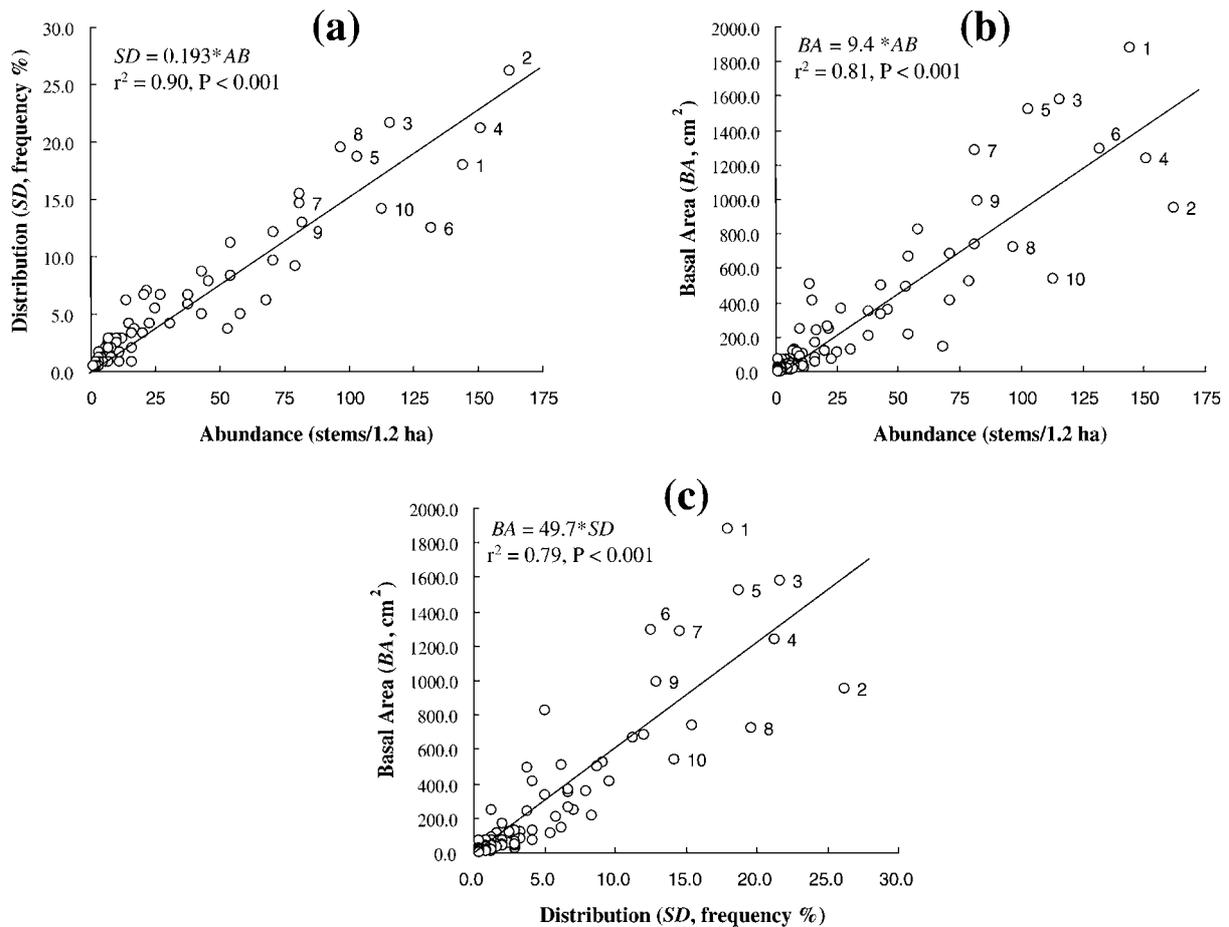


Figure 4. Relationships between variables related to species importance of the liana community at the Lacandon forest, Southeast Mexico: (a) Abundances spatial distribution; (b) abundance vs basal area, (c) distribution vs basal area. Distribution values are expressed as the percentage of quadrats in which a species was recorded. In each case, parameter values of the adjusted linear regression and their statistical significance are indicated. The numbers inside the graphs indicate the ten species with the highest importance value as indicated in Figure 2.

*M. lunatum*, had basal area stems between 40 to 60% higher than the community average ( $9.4 \text{ cm}^2 \text{ stem}^{-1}$ ; Figure 4). On the contrary, *Hiraea fagifolia*, *Stizolobium riparium*, and *Fornsteronia viridescens* had basal area stems 20 to 50% lower than the community average.

#### Liana community variation among sites and habitats

At the family level, CA analysis segregated flood plain and karst-range from low-hill and alluvial-terrace habitats (Figure 5). Among the ten most important families, Marcgraviaceae, Hippocrataceae and, to a lesser degree, Sapindaceae and Vitaceae, were associated with the karst-range habitat, while Bignoniaceae, Fabaceae, Combretaceae, Malpighiaceae, Compositae, and Apocynaceae were associated with the low-

land habitats (Figure 5). Some families with medium importance value were also associated with particular habitats: Acanthaceae with low-hill and alluvial-terrace, and Malvaceae with the flood plain habitat.

At the species level, CA analysis again segregated alluvial-terrace and low-hill from karst-range and flooded plain habitats (Figure 6). The two first axes explained 77% of total variation. Several species that were found exclusively in one habitat had very low importance values. Although dominant species were mostly found in lowland habitats (Figure 6), some were clearly associated with one or two particular habitats: *Hippocratea celastroides* in karst-range, *Piptocarpha chontalensis* in low-hill and alluvial-terrace, and *Stizophyllum riparium* in the flood plain sites.

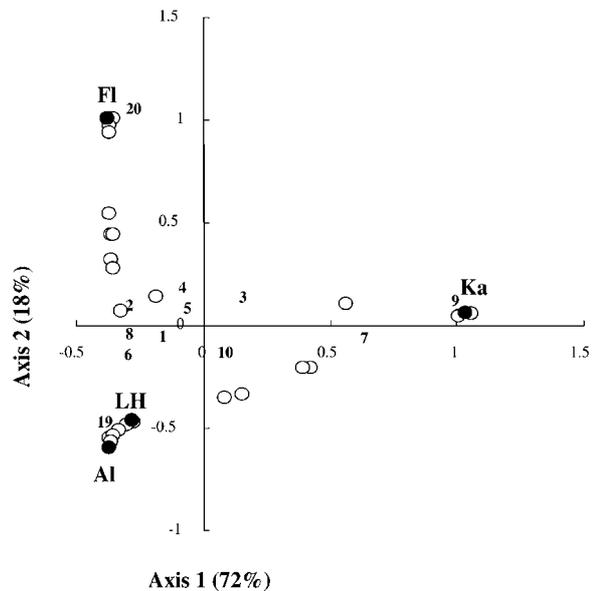
**Table 3.** Variation of liana community attributes among sites and habitats at the Lacandon forest, southeast Mexico. AT = alluvial-terrace, FP = flood plain, KR = karst-range, LH = low-hill sites. Values for habitats are in italics. Abundance is the total number of rooted lianas (or stems indicated in parenthesis) per site (0.15 ha) or habitat (0.30 ha). Frequency is the percentage of total sampled quadrats occupied by lianas. Maximum stem *DBH* recorded in each site is indicated in parenthesis (minimum *DBH* in all cases was 1.0 cm). Sites and habitats not sharing same letter are statistically different ( $P < 0.025$ ).

Attribute	Sites							
	AT-1	AT-2	FP-1	FP-2	KR-1	KR-2	LH-1	LH-2
Abundance	240 (387)	138 (210)	232 (522)	74 (151)	73 (159)	98 (261)	262 (548)	135 (274)
Lianas (stems)	<i>378<sup>c</sup> (597)<sup>b</sup></i>		<i>304<sup>b</sup> (673)<sup>b</sup></i>		<i>181<sup>a</sup> (422)<sup>a</sup></i>		<i>397<sup>c</sup> (820)<sup>c</sup></i>	
Stems liana <sup>-1</sup> (mean $\pm$ s.e)	1.6 $\pm$ 0.1 <sup>b</sup> <i>1.6 <math>\pm</math> 0.1<sup>a</sup></i>	1.5 $\pm$ 0.1 <sup>b</sup>	2.3 $\pm$ 0.1 <sup>a</sup> <i>2.2 <math>\pm</math> 0.1<sup>b</sup></i>	2.0 $\pm$ 0.3 <sup>a</sup>	2.2 $\pm$ 0.2 <sup>a</sup> <i>2.5 <math>\pm</math> 0.2<sup>b</sup></i>	2.7 $\pm$ 0.3 <sup>a</sup>	2.1 $\pm$ 0.1 <sup>a</sup> <i>2.1 <math>\pm</math> 0.1<sup>b</sup></i>	2.0 $\pm$ 0.2 <sup>a</sup>
Frequency (%)	96.7 <i>96.7</i>	96.7	93.3 <i>91.7</i>	90.0	93.3 <i>93.3</i>	93.3	96.7 <i>91.7</i>	86.7
Basal area (m <sup>2</sup> )	0.35 <i>0.59<sup>a</sup></i>	0.24	0.36 <i>0.54<sup>a</sup></i>	0.18	0.17 <i>0.38<sup>a</sup></i>	0.21	0.51 <i>0.83<sup>a</sup></i>	0.32
Stem <i>DBH</i> mean $\pm$ s.e. (max)	2.6 $\pm$ 0.1 (14.5)	2.7 $\pm$ 0.1 (16.0)	2.3 $\pm$ 0.1 (11.6)	2.9 $\pm$ 0.1 (13.0)	2.6 $\pm$ 0.1 (21.0)	2.7 $\pm$ 0.1 (9.5)	2.7 $\pm$ 0.1 (10.5)	2.9 $\pm$ 0.1 (12.5)
	2.6 $\pm$ 0.1 <sup>a</sup>		2.5 $\pm$ 0.1 <sup>a</sup>		2.5 $\pm$ 0.1 <sup>a</sup>		2.8 $\pm$ 0.1 <sup>b</sup>	

Broadness of distribution among habitats did not necessarily reflect the lack of habitat preference of the species. Considering only species with more than 20 stems in 1.2 ha, we found 25 of them with a preference for a particular habitat, with respect to a random (uniform) distribution among habitats. Four (16.0%) of these species were significantly more abundant in the alluvial-terrace, eight (32.0%) in the flood plain, three (12%) in the karst-range, and ten (40%) in the low-hill (Figure 7). Another four species were equally abundant among habitats except in the karst-range sites where they showed a significantly lower abundance (*Acacia hayesii*, *Cydista potosina*) or were absent (*Tetracera volubilis*, *Mikania leiostachya*). Finally, *Abuta panamensis* exhibited equal abundance in the karst-range and low-hill habitats but was virtually absent from alluvial-terrace and flood plain sites. Only *Machaerium kegelii* ( $n = 21$ ) had a statistically equal abundance in all habitats ( $\chi^2 = 6.2$ ,  $DF = 3$ , N.S.).

Classification analysis, using Sørensen similarity index, showed a very high  $\beta$ -species diversity. The karst-range was the most floristically dissimilar habitat, sharing less than 50% of common species with the other habitats. Alluvial-terrace and low-hill were the most floristically similar habitats, sharing about 75% of common species.

Liana abundance, basal area, and species richness varied two to four-fold among sites (Tables 3, 4 and 5). The frequency with which lianas were recorded in



**Figure 5.** Correspondence Analysis by habitat for the liana community represented by 36 families recorded in 1.2 ha at the Lacandon forest, southeast Mexico. The black dots indicate the habitat position: AL = alluvial sites, LH = low hill sites, FP = flood plain sites, KR = karst-range sites. The numbers indicate position of the ten most important families as listed in Table 2, except 19 (Acanthaceae), and 20 (Malvaceae).

the sampled quadrats was consistently high in all sites (>86%). Inter-site variation in liana abundance was the only community liana parameter significantly cor-

Table 4. Structural liana community variation among sites and habitats at the scale of 50 m<sup>2</sup> (10 × 5 m quadrats) at the Lacandon forest, southeast Mexico. Values for habitats are in italics. Sites or habitats not sharing same letter are statistically different ( $P < 0.025$ ). Dispersion index values with one \* are significantly different from randomness at  $P < 0.001$ , those with \*\* at  $P < 0.0001$ .

Attribute	Site							
	AT-1	AT-2	FP-1	FP-2	KR-1	KR-2	LH-1	LH-2
Stems quadrat <sup>-1</sup> (mean, ± s.e.)	12.9 ± 1.8 <sup>c</sup> <i>10.0 ± 1.2<sup>b</sup></i>	7.2 ± 1.3 <sup>b</sup>	17.4 ± 2.2 <sup>c</sup> <i>10.9 ± 1.4<sup>bc</sup></i>	5.0 ± 0.8 <sup>a</sup>	5.3 ± 0.8 <sup>ab</sup> <i>7.0 ± 0.9<sup>a</sup></i>	8.7 ± 1.5 <sup>b</sup>	18.3 ± 1.8 <sup>c</sup> <i>13.0 ± 1.3<sup>c</sup></i>	9.1 ± 1.6 <sup>b</sup>
Dispersion index (s <sup>2</sup> mean <sup>-1</sup> )	8.0** <i>8.3**</i>	6.9**	8.5** <i>10.9**</i>	4.0**	3.4** <i>6.5**</i>	7.8**	5.1** <i>7.5**</i>	8.0**
Number of families quadrat <sup>-1</sup> (mean ± s.e.)	4.5 ± 0.4 <sup>b</sup> <i>3.8 ± 0.3<sup>bc</sup></i>	3.0 ± 0.4 <sup>a</sup>	5.1 ± 0.5 <sup>b</sup> <i>3.4 ± 0.3<sup>b</sup></i>	1.8 ± 0.2 <sup>a</sup>	2.0 ± 0.2 <sup>a</sup> <i>2.2 ± 0.2<sup>a</sup></i>	2.3 ± 0.3 <sup>a</sup>	5.2 ± 0.4 <sup>b</sup> <i>4.2 ± 0.4<sup>c</sup></i>	3.0 ± 0.4 <sup>a</sup>
Number of species quadrat <sup>-1</sup> (mean ± e.e.)	5.8 ± 0.6 <sup>b</sup> <i>4.8 ± 0.4<sup>bc</sup></i>	3.8 ± 0.6 <sup>a</sup>	6.2 ± 0.7 <sup>b</sup> <i>4.1 ± 0.5<sup>b</sup></i>	2.0 ± 0.3 <sup>a</sup>	2.2 ± 0.3 <sup>a</sup> <i>3.3 ± 0.3<sup>a</sup></i>	2.7 ± 0.4 <sup>a</sup>	6.7 ± 0.5 <sup>b</sup> <i>5.4 ± 0.6<sup>c</sup></i>	4.0 ± 0.6 <sup>a</sup>

Table 5. Components of liana species diversity and their spatial variation at the Lacandon forest, southeast Mexico. Values based on samples taken in 0.15 ha per site.  $H'$  = Shannon diversity index,  $J$  = evenness index for  $H'$ ,  $D$  = Simpson diversity index,  $E$  = evenness index for  $D$ . Values in italics correspond to averages (± s.e.) per habitat and those in parenthesis were obtained mixing the two plots per habitat. Habitats not sharing same letter are statistically different ( $P < 0.05$ ).

Attribute	Sites							
	AT-1	AT-2	FP-1	FP-2	KR-1	KR-2	LH-1	LH-2
Species richness	45	41	41	23	24	28	47	42
	<i>43.0 ± 2.0 (58)<sup>b</sup></i>		<i>32.0 ± 9.0 = (48)<sup>ab</sup></i>		<i>26.0 ± 2.0 (40)<sup>a</sup></i>		<i>44.5 ± 2.5 = (56)<sup>b</sup></i>	
Diversity ( $H'$ )	1.48	1.47	1.39	1.16	1.23	1.09	1.43	1.36
	<i>1.48 ± 0.00 = (1.56)<sup>a</sup></i>		<i>1.28 ± 0.11 (1.45)<sup>a</sup></i>		<i>1.16 ± 0.07 (1.31)<sup>a</sup></i>		<i>1.40 ± 0.03 (1.47)<sup>a</sup></i>	
Equitability ( $J$ )	0.89	0.90	0.86	0.85	0.85	0.79	0.88	0.87
	<i>(0.89)</i>		<i>(0.86)</i>		<i>(0.82)</i>		<i>(0.84)</i>	
Diversity ( $D$ )	23.7	21.8	17.7	9.0	11.5	7.6	20.5	17.2
	<i>22.8 ± 1.0 (27.6)<sup>a</sup></i>		<i>13.4 ± 4.4 (19.3)<sup>a</sup></i>		<i>9.6 ± 2.0 (13.0)<sup>a</sup></i>		<i>18.9 ± 1.7 (18.6)<sup>a</sup></i>	
Equitability ( $E$ )	0.53	0.53	0.43	0.39	0.41	0.32	0.49	0.46
	<i>(0.48)</i>		<i>(0.40)</i>		<i>(0.33)</i>		<i>(0.33)</i>	

related with canopy disturbance ( $r = 0.73$ ,  $DF = 6$ ,  $P < 0.05$ ). The variation among sites in abundance, basal area, and species richness were not correlated with inter-site variation in tree density ( $P > 0.10$ ). The number of stems per liana differed significantly among habitats ( $\chi^2 = 33.7$ ,  $DF = 3$ ,  $P < 0.001$ ); the number of stems with  $DBH \geq 1$  cm per rooted liana in the alluvial-terrace was about half as much as in the other habitats (Table 3). Average liana size, as measured by stem  $DBH$ , was significantly ( $F_{3, 1247} =$

$3.08$ ,  $P < 0.05$ ) larger in the low-hill than in the other habitats. The biggest liana, however, was found in one of the karst-sierra sites (Table 3).

Liana abundance and basal area tended to be high in the low-hills and low in the karst-range sites in the 20 × 250 m plots. ANDEVA, however, did not detect significant differences ( $P > 0.10$ ) for these variables. Considering the 5 × 10 m quadrats, stem abundance differed among sites ( $\chi^2 = 81.3$ ,  $DF = 7$ ,  $P < 0.01$ ) and habitats ( $\chi^2 = 16.6$ ,  $DF = 3$ ,

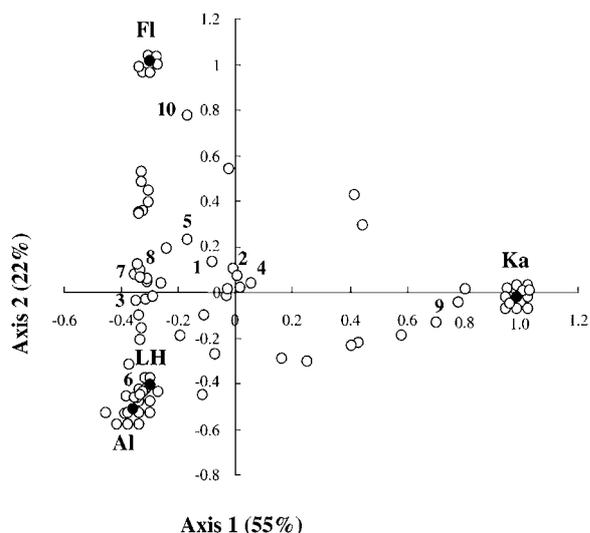


Figure 6. Correspondence analysis of the liana community ordering 90 species among habitats at the Lacandon forest, southeast Mexico. The black dots indicate habitat position: AL = alluvial sites, LH = low hill sites, Fl = flooded sites, Ka = karstic sites. The numbers indicate position of the ten most important species as in Figure 2.

$P < 0.01$ ; Table 4). The karst-range had a significantly lower abundance of liana stems than the other habitats, and the low-hill showed the highest abundance. In all sites and habitats liana stems were strong clumped, especially in the flood plain sites (Table 4).

At the 0.5 ha plot scale, species richness ( $\chi^2 = 10.1$ ,  $DF = 3$ ,  $P < 0.01$ ) was significantly lower in the karst-range than in the alluvial-terrace and low-hill, but was similar to that of the flood plain habitat (Table 4). Although species diversity (measured either with the Shannon or Simpson indices) showed same trend, ANDEVA did not detect significant differences in species diversity among habitats ( $P > 0.10$ ; Table 5). On the basis of the evenness indices, the alluvial-terrace showed the maximum diversity (Table 5).

The number of species ( $\chi^2 = 38.3$ ,  $DF = 3$ ,  $P < 0.01$ ) or families ( $\chi^2 = 28.8$ ,  $DF = 3$ ,  $P < 0.001$ ) per 50 m<sup>2</sup> quadrat was significantly higher at the alluvial-terrace and low-hill habitats and lower at the karst-range. On average, we recorded an inter-site variation of 5 to 18 stems representing two to five families, and two to seven species per quadrat (Table 4). Roughly, we found different taxa every two to three liana stems. Maximum values for species and family richness per quadrat ranged among sites from six to fifteen and from four to nine, respectively.

## Discussion

### *Liana communities at Chajul compared to other tropical rain forests*

#### *Taxonomic attributes*

We found that Bignoniaceae, Fabaceae (Leguminosae), Malpighiaceae, and Sapindaceae were the most species rich families; this is also the case for most neotropical rainforests studied to date (Gentry 1990, 1991a; Dewalt et al. 2000). In addition, the most speciose genera in our study (e.g., *Machaerium* and *Paullinia*) are among the most speciose in other neotropical rain forests (Gentry 1991a). Our finding that only ten families comprised 69% of liana species is very close to Gentry's (1991a) conclusion that about 64% of the estimated 9216 climbing species in the Neotropics belong to only twelve families. Similar observations were made at Los Tuxtlas, Mexico, where 69% of total number of species of climbing plants belongs to eleven families (Ibarra-Manríquez et al. 1997). Perhaps, this pattern is related to the ecological advantages conferred by specialised climbing structures and mechanisms evolved in certain families, as is the case of tendrils (e.g., Bignoniaceae) and sensitive young branch lets (e.g., Malpighiaceae; Gentry 1991a; Hegarty 1990; Dewalt et al. 2000).

The families with high species richness were also the most structurally important. Bignoniaceae and Fabaceae were the dominant families (Table 2), as has been reported for most neotropical rain forests (Gentry 1991a). The dominance of a few speciose families has been also noted in tree communities of tropical rain and deciduous forests (Lott et al. 1987; Balée & Campbell 1990; Valencia et al. 1994). An exception to this trend was the Combretaceae, third in community importance value in our study, which was represented by only two species (Table 2).

#### *Structural attributes*

Compared with the density values for lianas ( $DBH > 1$  cm) at other locations around the world (Gentry 1991a), liana density at Chajul (116 stems 0.1 ha<sup>-1</sup>) was above the average value for the Neotropics (69–78 0.1 ha<sup>-1</sup>). It was similar to the maximum value recorded for the Neotropics in Jauneche, Ecuador, and to the values found in some rain forests in Africa (106–122 0.1 ha<sup>-1</sup>). The ratio between liana ( $DBH > 2.5$  cm) density to tree ( $DBH > 10$  cm) density, claimed by Gentry (1991a) to be around 1 in neotropical rain forests, was 2.8 at Chajul. This high ratio

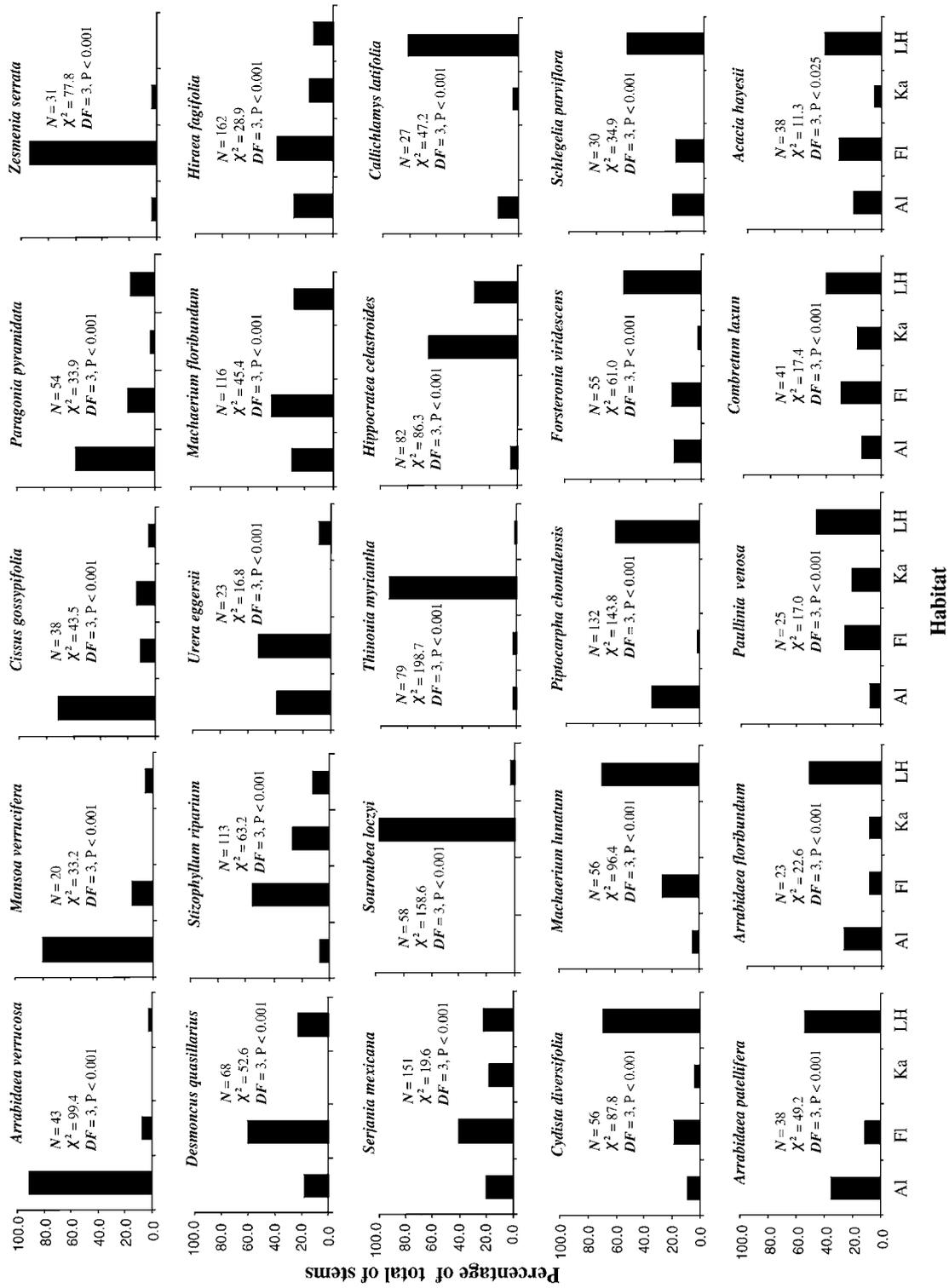


Figure 7. Relative abundance (%) for the most abundant species among four contrasting soil-topographic habitats at the Lacandon forest, southeast Mexico. In all cases, the distribution was significantly different from a uniform (random) one as indicated by the  $\chi^2$  values inset each graph.

may result from a relative low tree density at Chajul. However, we can estimate for Chajul (from Tables 1 and 5) an average of 2.0 trees  $\geq 10$  cm *DBH* per  $5 \times 10$  m quadrat, and an average of four liana stems per tree. This liana abundance per tree is higher than that recorded at other rain forest localities (e.g., Campbell & Newbery 1993).

The abundance of big lianas (*DBH* > 10 cm) may indicate the regenerative status of a tropical rain forest. As a general trend, as forest successional age increases the abundance and basal area of big lianas also tend to increase (Schnitzler 1995, Dewalt et al. 200). In mature neotropical forests, big lianas represent between 1 and 2% of the total basal area of woody plants with  $\geq 10$  cm *DBH* (Hegarty & Caballé 1991). These values are higher than that we found at Chajul. Considering that the community of trees and lianas  $\geq 10$  cm *DBH* at Chajul has an average basal area of  $25.2 \text{ m}^2 \text{ ha}^{-1}$  (Martínez-Ramos et al., unpubl. data), we calculate that big lianas represent only 0.7% of the liana and tree community basal area. This value was several times lower than the relative abundance (4.1%) accounted by big lianas among tree and liana stems with *DBH*  $\geq 10$  cm (416 stems  $\text{ha}^{-1}$ ; Martínez-Ramos et al., unpubl. data). Such a difference may reflect the great vegetative growth capacity of lianas, which prolifically produce slender stems and branches as they grow from host tree to another. Such a capacity is also illustrated by our finding that, on average, a rooted liana has two stems detectable near the forest floor level (Table 3). Future studies need to compare forest dynamics to determine whether the relatively low frequency of big lianas at Chajul results from a higher frequency of disturbance in this locality than in forests with higher basal area of big lianas.

#### *Spatial pattern of the liana community*

The strongly clumped spatial pattern exhibited by the lianas at Chajul resembles that described in Sabah, East Malaysia (Campbell & Newbery 1993). A clumped pattern has been also documented for lianas in other forests (e.g., Putz 1984; Putz & Chai 1987). Trellis and light have been proposed as factors that promote clumped liana distribution: once an individual liana successfully climbs a tree, it becomes a trellis itself, allowing other lianas to climb. This process may be more active near light gap edges where lianas grow faster (Campbell & Newbery 1993; Putz 1984). A clumped pattern may also result when several liana stems are deposited on the forest floor as a consequence of a treefall. Also, new liana shoots may grow

from these stems, stimulated by the rich light environment of the gap (Putz 1985; Putz & Chai 1987; Hegarty & Caballé 1991).

The above observations may help to explain why we found a significant correlation of liana abundance and canopy disturbance. Appanah & Putz (1984) also found in Malaysia that climbers tend to be more abundant in places with more frequent natural treefalls. In our study sites, liana aggregation was strongest in the most disturbed site, the flood plain site FP-1, which had the highest percentage of gap area, a high liana abundance, and the minimum average liana *DBH* (an indicator of high recruitment; Tables 1, 3 and 4). It is possible, however, that the abundant growth of lianas in gaps may lower canopy turnover rates by inhibiting tree regeneration. In addition to canopy disturbance, poor seed dispersal (i.e., limited spatial recruitment), prolific vegetative growth, and spatial pattern of host trees are factors that may be involved in the clumped behaviour of lianas.

#### *Dominance-diversity relationship*

The geometric dominance-diversity curve fitted to the studied liana communities contrasts with the log-normal and 'broken-stick' curve types, which is commonly found for tropical rain forest tree communities (e.g., Bongers et al. 1988; Hubbell 1979). The geometric curve presumably expresses a colonisation process where each species arrives at open habitats at random intervals pre-empting a constant proportion of available resources (Gotelli & Graves 1996). Log-normal and broken-stick curves, on the other hand, suggest situations where species populations are near a numerical equilibrium in different environmental patches, presumably as a result of species competitive interactions (but see Hubbell 1979).

A geometric curve type has often been found for pioneer, early successional plant communities (e.g., Whittaker 1972; Bazzaz 1975; May 1975). From this perspective, the liana communities we studied are structurally similar to assemblages of pioneer species. Although not all liana species are light demanding, several may need open spaces to recruit, grow and reproduce (Putz 1984; Hegarty & Caballé 1991; Dewalt et al. 2000). As with some pioneer and light demanding species (e.g., Brokaw 1987), different species of lianas may differ in their ability to disperse or survive as seeds, seedling or saplings under shaded conditions and pre-empt forest gaps. However, in contrast to pioneer trees, lianas may rely relatively more on vegetative growth than on seed dispersal to colonise gaps.

Also, a geometric curve may result from a species' differential use of gaps of different sizes, as gap frequency itself declines geometrically with increased size (Hubbell & Foster 1986a).

#### *Abundance-distribution relationship*

The tight relationship we found between liana species abundance and distribution (Figure 4a) suggests that widespread species are locally more abundant than spatially restricted ones. At least four hypotheses have been proposed to explain this general pattern (Gotelli & Graves 1996). First, this may result from a sampling artefact as species abundance may depend upon what part of the species distribution range is included in the sampled area. This possibility apparently does not apply to our case as we widely spaced our samples of liana communities across habitats and sites. Also, we detected that species tended to be restricted to particular habitats (Table 7) where they have a higher density.

Second, the abundance-distribution relationship may be obtained purely by chance when a Poisson process defines species local density across the landscape. Under this scenario, a null linear relation with a slope of  $-1$  and an intercept of  $0$  is expected between the natural logarithm of the species frequency of absences ( $\ln f$ ) and species average local density ( $D$ ; Gotelli & Graves 1996). Regressing  $\ln f$  (estimated as  $\ln$  of  $1 -$  relative frequency of quadrats in which a species was recorded) on  $D$  (stems per  $50\text{-m}^2$  quadrat) we obtained a slope  $\pm$  s.e.) of  $-0.402 \pm 0.022$  ( $F = 723.5$ ,  $DF = 89$ ,  $r^2 = 0.88$ ,  $P < 0.0001$ ). This slope value was significantly less steep than that expected by random. A slope value lower than  $-1.0$  indicates that abundant species tend to be spatially aggregated, as was the case for the lianas we studied at the landscape and site levels (Table 5).

A third possibility is that species abundances and distributions reflect niche breadth, and those factors favouring (or limiting) abundance also determine the wideness of species distributions (Brown 1984). This may imply that in our liana study system there were some species with broad niches (generalist species), such as *Combretum laxum* and *Hiraea fagifolia*, which were recorded in all plots and were among the most abundant and frequent species in all studied soil-topographic habitats. Rarity in this context may result from the low availability of habitat of required for habitat-specialist species.

As in trees, liana species niche breadth may be determined by dispersal capacity and the spatial fre-

quency of habitats where successful seed germination and growth occurs. However, unlike trees, liana niche breadth may also depend on the abundance and spatial frequency of host-tree species where liana maturation takes place. In the same study sites, it was found that the most abundant tree species showed a strong segregation among the habitats here studied; for example, Sapotaceae species (e.g., *Manilkara sapota*, *Pouteria* spp.) were very abundant in the karst-range sites and almost absent from the other habitats, while Legume trees (e.g., *Dialium guianense*) that were abundant in low-hill sites were rare in the karst-range sites (Martínez-Ramos et al., unpubl. data). In this study we found that some liana species were restricted to the karst-range (e.g., *Thinouia myriantha*) and others to the low-hill habitat (e.g., *Zesmenia serrata*; Figure 7).

Finally, the abundance-distribution relationship may result from species metapopulation dynamics. Hanski (1982) and Hanski & Gyllenberg (1993) predicted that local population density and the fraction of an area occupied by a species depends on stochastic or deterministic variation in local extinction and colonisation rates across the landscape. This is the so-called 'core-satellite hypothesis'. Most frequent species are those restricted to a small fraction of available sites ('satellite', rare, prone to extinction species), and those occurring in most sites ('core', abundant, demographically growing species). Local populations of satellite species may persist through migration ('rescue effect') from other sympatric host populations (Hanski & Gyllenberg 1993). To test this idea, assuming that species are ecologically similar and have comparable metapopulation dynamics, a bimodal distribution in the species frequency of occurrence must be observed in the community (Gotelli & Graves 1996). This certainly was not the case at Chajul. We found a single modal distribution skewed towards less frequent species, for both plots (Figure 3b) and quadrats (50% of species were present in only 2.5% of total sampled quadrats). It has been theoretically argued that when low colonisation rates, a small amount of variation in environmental patch sizes, and a small rescue effect operate on the species in a community, one should expect a single modal distribution skewed towards a low occurrence frequency (Hanski & Gyllenberg 1993).

*Variation of liana community structure across the landscape*

Our four-fold range of liana abundance variation among study habitats compares with that found by Gentry (1991a) for a large set of neotropical forest localities. In a dipterocarp forest at Pahang, Malaysia, Appanah & Putz (1984) showed that liana ( $\geq 2$  cm *DBH*) abundance changed as much as two-fold among hectares. The same result was obtained in Sarawak, Malaysia where liana density (*DBH* > 2 cm) was twice as high in a valley as on a hilltop (Putz & Chai 1987).

High liana density has been recorded in localities with a marked dry season where a transition from moist to dry forest is present (Holdridge et al. 1971, Gentry 1991a). At Chajul, a clear dry season occurs from January to March, when precipitation accounts for less than 10% of total annual rainfall. Also, at Chajul there is a clear distinction between evergreen tall forests (along river edges) and semi-deciduous medium sized forests (in karst-range and low-hill sites). Among other things, such a vegetation change is related to changes in soil drainage capacity (Table 1) and soil water availability that, in general, decrease as the distance to the Lacantún-river edge increases. Although we found maximum liana abundance in low-hills, some alluvial terrace and flood plain sites have also high liana density (Tables 3 and 4), which resembles other seasonally inundated forest (Appanah & Putz 1984; Putz & Chai 1987; Gentry 1991a), especially if the soil is not hydromorphic (Schnitzler 1995).

Maximum liana abundance in the low-hill habitat could be associated with high host tree availability (Table 1). The fact that the inter-site variation in liana abundance was not significantly related to the abundance of trees with *DBH* > 10 cm weakens this idea. However, the abundance of saplings and small trees, which can act as trellis for lianas, was 30 to 60% higher in low-hills than in other habitats (Martínez-Ramos et al., unpubl. data). This high trellis abundance and relatively high canopy disturbance levels (Table 1) may favour high abundance of lianas in the low-hill sites. Also, the availability of soil resources seems to be involved in the variation of liana abundance among habitats. For example, lianas were less abundant in the karst-range sites where soil water availability seems to be an important limiting factor (Table 1). The water conducting system of lianas is composed of large and wide vessels, which are very

sensitive to low water availability (Ewers et al. 1990; Gartner et al. 1990). After a severe drought, the xylem may become dysfunctional due to vessel embolism, detrimentally affecting individual liana fitness. In a seasonal dry forest at Chamela, Mexico (Lott et al. 1987), and in a xeric system, at Sonora, Mexico (Molina-Freaner & Tinoco, 1997), liana abundance also decreased in areas with low soil water availability.

As discussed above, the variation of liana abundance among sites may also result from differences in forest gap dynamics. Liana abundance may change with gap size and frequency as well as with the type and persistence of disturbance (Appanah & Putz 1984; Hegarty & Caballé 1991). In the alluvial-terrace, flood plain, and low-hill sites, where liana abundance tends to be high, most fallen trees are uprooted creating large gaps (> 200 m<sup>2</sup>; Martínez-Ramos et al., unpubl. data). The low liana abundance recorded in the karst-range sites, on the other hand, may be associated with low treefall disturbance (Table 1b). Although the tree sizes at the karst-range are similar to those at the low-hills (Table 1), the gaps at the karst-range are smaller. This is because at the karst-range most gaps are produced by the fall of tree branches and snapped-off trees, not by entire trees being uprooted (Martínez-Ramos et al., unpubl. data). It is possible that roots of the large trees in the karst-range sites are strongly anchored to limestone rocks, reducing the probability of uprooting.

Gentry (1991a) observed that in the Neotropics liana species diversity declines from pluvial to drier forests. At Chajul, liana species diversity seems to decline with soil water availability, as discussed above for the case of liana abundance. Gentry's observation that liana diversity declines with the altitude can be applied marginally to our study system, since karst-range sites are 200–500 m higher in altitude than the other study habitats. In contrast, liana species diversity did not decline with decreasing soil fertility as noted by Gentry (1982, 1988, 1991a), and Appanah & Putz (1984) for other tropical localities. Thus, our data support the affirmation of Clinebell et al. (1995) that species richness of lianas in tropical forests is independent of soil quality. Liana diversity was not lower at the low-hills where soils have the poorest nutrient availability, especially of phosphorous (Table 1).

Liana species composition and density greatly varied among habitats. Species differentiation related to soil-topographic habitats has also been reported for liana species in a desert-scrub community (Molina-Freaner & Tinoco 1997), and for tree species in neotropical (Gentry 1986, 1988; Baillie et al. 1987;

Hubbell & Foster 1986b) and Malaysian rain forests (Asthon & Hall 1992). The fact that species of the same family or same genera tended to dominate different habitats suggests that evolutionary niche differentiation has occurred within some liana phylogenetic lineages (Figures 5 and 6). For example, different genera of Bignoniaceae tended to dominate different habitats: *Mansoa* and *Paragonia* at alluvial-terraces; *Stizophyllum* at flooded sites; and, *Callichlamys*, *Cydistia* and *Arrabidaea* at low-hill sites (Figure 7). A similar pattern occurred within genera. For example, the Bignoniaceae *Arrabidaea verrucosa* was mostly present in the alluvial-terrace while *A. patellifera* and *A. floribundum* were more abundant at the low-hill sites; within Fabaceae, *Machaerium floribundum* was over-represented in the flood plain habitat while *M. lunatum* was dominant in the low-hills (Figure 7).

At Chajul, similar patterns of taxonomic differentiation among closely related tree species are also apparent. For example, within the Leguminosae, *Dialium guianense* is significantly more abundant in the low-hills, *Platymiscium yucatanum* in the flood plains and *Inga pavoniana* in the alluvial terraces; within the Meliaceae, *Trichillia acuntanthera* is restricted to karst-range sites while *Guarea* species are mostly found at the lowland sites. Also, species of the same genera show strong habitat differentiation. Examples include *Cymbopetalum*, *Guarea*, *Protium*, and *Quararibea* species (Martínez-Ramos et al., unpubl. data). These observations suggest that in the studied region a purported evolutionary niche differentiation has operated as a general phenomenon in the woody communities.

## Conclusions

Liana communities vary strongly in their structural characteristics and taxonomic composition across a 100 km<sup>2</sup> landscape in the Lacandon rain forest. The variation in some community attributes was comparable to that reported for other forests at much larger geographical scales. Liana abundance at Chajul is among the highest recorded in tropical rain forests. The dominance-diversity relationship suggests that a pre-emptive colonisation process may be driving the organisation of the liana community, in a manner similar to that suggested for early successional plant communities. Several liana species were segregated along environmental gradients, producing an important level of  $\beta$ -species diversity. Soil water availability,

soil fertility, treefall disturbance regime, as well as the abundance and identity of trellis and tree hosts, may influence the responses of the liana community to environmental heterogeneity present at Chajul. We along with others (e.g., Gentry 1988, 1991a) propose several hypotheses about factors influencing the community structure and composition of liana assemblages and also about the population properties of lianas. Now, we urgently need to develop an experimental approach testing these hypotheses.

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## Appendix I. Continued.

Family/species	AT1	AT2	FP1	FP2	KR1	KR2	LH1	LH2	Total
Hippocrateaceae									
<i>Hippocratea celastroides</i> Kunth	*	*			*	*	*	*	6
Loganiaceae									
<i>Strichnos tabascana</i> Sprague & Sandw.	*	*			*	*	*		5
Malpighiaceae									
<i>Heteropterys laurifolia</i> (L.) Adr. Juss.		*	*				*	*	4
<i>Hiraea fagifolia</i> (DC.) Adr. Juss.	*	*	*	*	*	*	*	*	8
<i>H. smilacina</i> Standl.	*					*	*		3
<i>Mascagnia rivularis</i> C.V. Morton & Standl.		*				*			2
<i>Stigmaphyllon dentatus</i>					*				1
<i>S. ellipticum</i> (Kunth) Adr. Juss.				*					1
<i>S. lindenianum</i> Adr. Juss.	*	*					*		3
<i>Tetrapteryx schiedeana</i> Schlttdl.					*				1
<i>Tetrapteryx</i> sp.					*				1
Malvaceae									
<i>Hibiscus</i> sp.			*						1
Marcgraviaceae									
<i>Marcgravia mexicana</i> Gilg				*					1
<i>Souroubea loczyi</i> (Al. Richter) de Roon					*	*		*	3
Menispermaceae									
<i>Abuta panamensis</i> (Standl.) Krukoff & Barneby	*	*			*	*	*	*	6
Nyctaginaceae									
<i>Pisonia aculeata</i> L.	*	*	*	*					4
Passifloraceae									
<i>Passiflora</i> spp.						*			1
Phytolaccaceae									
<i>Trichostigma octandrum</i> (L.) H. Walt.		*	*						2
Rhamnaceae									
<i>Gouania lupuloides</i> (L.) Urb.	*				*				2
<i>G. polygama</i> (Jacq.) Urb.	*				*				2
Rubiaceae									
<i>Chione</i> sp.						*			1
<i>Randia</i> sp.			*		*				2
<i>Rubiaceae</i> 1		*							1

**Appendix I.** Continued.

Family/species	AT1	AT2	FP1	FP2	KR1	KR2	LH1	LH2	Total
<b>Sapindaceae</b>									
<i>Paullinia clavigera</i> Schlttdl.	*	*		*			*		4
<i>P. fuscescens</i> Kunth	*	*		*					3
<i>P. venosa</i> Radlk.	*	*	*	*		*	*	*	7
<i>Serjania goniocarpa</i> Radlk.			*				*	*	3
<i>S. mexicana</i> (L.) Willd.	*	*	*		*	*	*	*	7
<i>Thinouia myriantha</i> Triana & Planchón	*	*		*	*	*		*	6
<b>Sterculiaceae</b>									
<i>Byttneria aculeata</i> Jacq.	*								1
<i>B. catalpifolia</i> Jacq.					*				1
<b>Ulmaceae</b>									
<i>Celtis iguanaea</i> (Jacq.) Sarg.								*	1
<b>Urticaceae</b>									
<i>Urea eggersii</i> Hieron.	*	*	*					*	4
<b>Verbenaceae</b>									
<i>Aegiphila elata</i> Sw.			*						1
<b>Vitaceae</b>									
<i>Cissus gossypifolia</i> Standl.	*	*	*			*	*		5
<i>C. sicyoides</i> L.		*							1
<i>Vitis tiliifolia</i> Kunth						*			1