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Diversity and distribution of lianas in a neotropical rain forest, Yasuní National Park, Ecuador

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ABSTRACT. Lianas (woody vines) contribute substantially to the diversity of woody plants in Yasuní National Park, Eastern Ecuador. In total 606 individuals, belonging to 138 species, were found in two 20-m × 100-m plots. The liana diversity was higher than in any comparable study, but the density was relatively low. Sapindaceae and Leguminosae were the most species-rich families, whereas Leguminosae and Celastraceae were the most abundant families. The number of liana individuals as well as the number of liana species was partially explained by forest structure, but 92% of the variation in number of liana species depended on the number of liana individuals. Areas with high density of small trees had high liana density, and areas with a high number of tree saplings had a relatively high diversity of climbing lianas. The probability of trees being colonized by lianas increased with tree diameter. The presence of one liana on a tree increased its risk of being colonized by additional lianas.

KEY WORDS: biodiversity, Ecuadorian Amazon, habitat specialization, host tree preference, woody vines

INTRODUCTION

The few studies undertaken on lianas (woody vines) in tropical forests suggest that they make a substantial contribution to the overall plant diversity, both in the neotropics (Duivenvoorden 1994, Gentry 1992, Grubb *et al.* 1964, Paz y Miño 1990) and in the Old World tropics (Appanah *et al.* 1993, Balfour & Bond 1993, Hegarty 1991, Putz & Chai 1987). In addition to being a conspicuous structural component of the rain forest, lianas play an important role as food plants for insects (Gentry 1985) and monkeys (Emmons & Gentry 1983), especially when other food sources are scarce (Sabatier 1985). Furthermore, it has

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been suggested that lianas influence forest dynamics by increasing the size of treefall gaps, and thereby increasing tree turnover rate (Phillips & Gentry 1994; Putz 1982, 1984a; Putz & Chai 1987).

Lianas are often associated with disturbed areas and high light intensities (Hegarty & Clifford 1991, Richards 1996), but some species prefer low-light environments (Chalmers & Turner 1994, Putz 1984b). Lianas use several different mechanisms for climbing, and various classification systems for these climbing modes have been proposed by e.g. Darwin (1867), Schenck (1893) and Putz (1984b). Putz (1984b) recognized the following climbing modes: stem twiners, branch twiners, root/adhesive tendril climbers, tendril climbers and scramblers. Stem twiners twine around their host as a result of the circular movements of the shoot tip that have been termed circumnutation. Branch twiners clasp their hosts by their, usually opposite, branches. Root climbers ascend with the aid of roots or adhesive tendrils, and tendril climbers climb with thin, sensitive tendrils modified from either leaves, inflorescences or branches (Gentry 1985). Scramblers, as defined by Putz, are here divided into hook/thorn climbers and scramblers. The hook/thorn climbers attach themselves to the vegetation with either backward-pointing spines or with hooks that may grow around their hosts. The scramblers, which represent the least specialized climbing mode, merely lean on their host plants. Although a liana may simultaneously utilize several of these climbing mechanisms, it is normally possible to recognize the prevalent climbing mode.

The primary goals of this paper are to estimate liana species richness and to describe liana distribution patterns on a site in the hitherto little studied upper Amazon Basin. The study comprises the second largest total enumeration of lianas in lowland Amazonia. Liana distribution and habitat requirements were studied at two different scales: (1) the community scale and (2 and 3) the individual scale. (1) It was hypothesized that liana density was positively correlated with trellis (support) availability, but negatively correlated with high densities of large trees, which are likely to increase shading effects. On the individual scale, it was tested (2) whether lianas with different climbing mechanisms were associated with hosts of different sizes and (3) whether lianas only were able to start climbing on small-diameter host plants.

Lianas with different climbing mechanisms were expected to use hosts with different diameters. The relatively shade-tolerant root climbers (Chalmers & Turner 1994) were predicted to climb the trunks of large host trees. The scramblers on the other hand were regarded as less specialized than the other types of lianas, and to be partly self-supporting. They were therefore expected to be thicker than the other lianas on host trees with a certain diameter. The difference in host-size preference was expected to be more subtle among the remaining types of climbers, that are only able to climb host trees of a certain size, although the tendril climbers have been shown to require thinner trellises than other climbers (DeWalt *et al.* 2000, Putz & Holbrook 1991).

STUDY SITE

The study was conducted in the Napo Province, Eastern Ecuador, at the northern end of Yasuní National Park, near Río Tiputini (00°40′S, 76°23′W). The plots were located in areas with relatively homogeneous, well-drained *terra firme* (never inundated) forest, *c.* 240 m asl. The forest is an old-growth tropical moist forest (*sensu* Holdridge *et al.* 1971) with a canopy height of 20–40 m. Only along the roads, and in areas that have been inhabited by Huaorani Indians, does the forest show signs of recent human disturbance.

At the Yasuní Scientific Research Station (YSRS), monthly precipitation in 1997–99 averaged 248 mm, ranging from 102 to 639 mm (Figure 1). No dry season is evident, but in Tiputini, *c.* 75 km further east, 5 mo with precipitation deficit were recorded during 8 y in the period 1972–78 (see Balslev *et al.* 1987). The average monthly temperature at the YSRS was 28.2 °C with average daily minimum and maximum temperatures of 21.5 °C and 34.7 °C, respectively.

The soil in the area is heavily weathered and nutrient-poor. It is classified as a Typic Paleudult derived from sedimentary tertiary clay conglomerates (Woodward 1995).

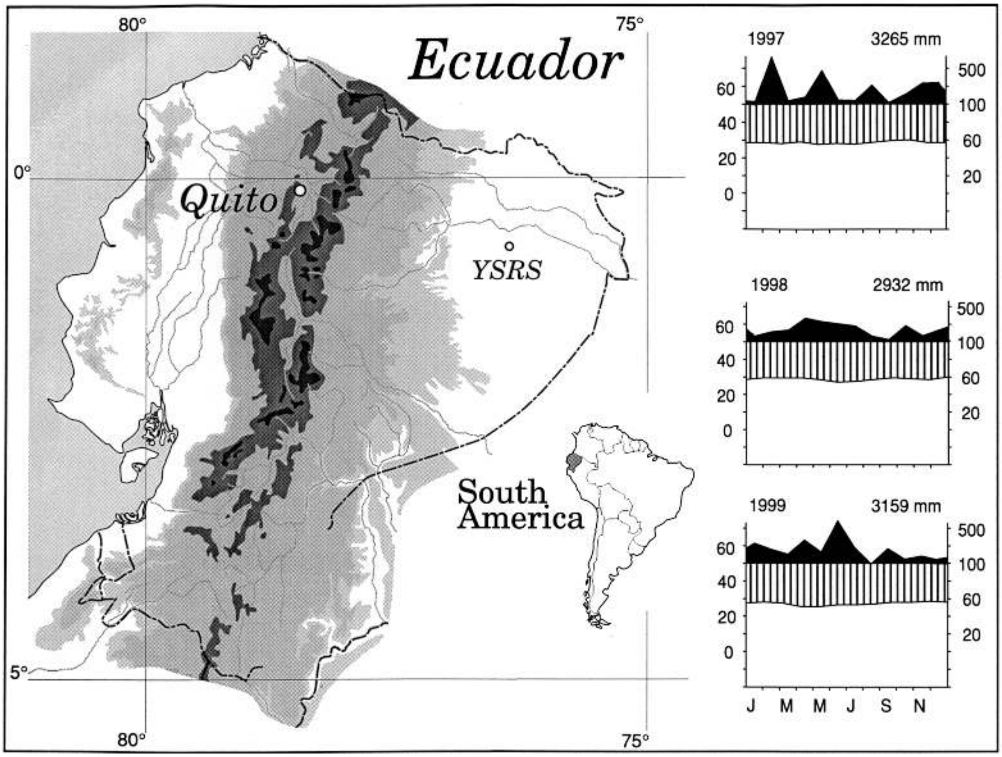

Figure 1. Location of the Yasuní Scientific Research Station (YSRS) in eastern Ecuador, and climate diagrams from the station from the years 1997 to 1999. The climate diagrams are based on unpublished records from YSRS.

METHODS

Data collecting

The field work was carried out from July to November 1996. Two 20-m × 100-m transects were established 1 km apart, close to the Yasuní Forest Dynamics Project plot. The first transect was located on a ridge side (inclination *c.* 10°) in a low canopy area, whilst the second transect was on a well-drained ridge top, characterized by a few large treefalls partly covered with *Duroia hirsuta* (Poepp. & Endl.) K. Schum. and *Aechmea* spp. Both transects were laid out in a north–south direction and divided into 10-m × 10-m subplots.

All climbing liana individuals in the transects were tagged and identified. Lianas were defined as woody climbing plants that were permanently rooted in the ground. All epiphytic and hemi-epiphytic climbers were excluded. Members of the family Araceae were also excluded, as most of the climbing species in the area were more or less succulent and hemi-epiphytic (Gentry 1993). An individual was defined as all the stems that were rooted in the same place, and all the shoots from a runner were therefore treated as belonging to the same individual as long as they were connected. Only individuals that were rooted within the transects were included. When specimens could not be identified in the field, vouchers were collected from the canopy, using single rope climbing techniques (Risley 1984) and crescent-shaped tree spurs. Upright (unsupported) lianas were excluded from the study due to potential confusion with tree saplings. The taxonomy followed Mabberley (1987). The diameter at breast height (dbh) was measured 130 cm above the ground, for both lianas and trees. Each time a liana started climbing a host from below 130 cm, both its dbh and the dbh of the host tree were measured. A host was classified as primary when it was evident that it was the initial support used to access the canopy. Trees that were climbed from the ground at a later stage were classified as secondary hosts (e.g. if they were climbed by a liana that had fallen down from its primary host), and trees that only had a liana infestation in the crown were classified as tertiary hosts. For multi-stemmed lianas, only the tree that supported the main stem was a primary host. In some cases it was not possible to determine which tree had served as host for a large liana. In that case, the tree it was attached to in the canopy was labelled a tertiary host.

To obtain a measure of the forest structure, dbh was recorded for all trees with dbh $\geq$ 1.0 cm. The trees in the 40 subplots were categorized as saplings ($\geq$ 50 cm high but $<$ 1 cm dbh), small trees (1 cm $\leq$ dbh $<$ 10 cm) and large trees (dbh $\geq$ 10 cm). The height of the saplings was measured instead of the dbh, and a theoretical dbh was calculated by extrapolating the linear regression line of $\log_{10}$ tree dbh on $\log_{10}$ tree height for trees with dbh 1–4 cm. Seedlings (plants $<$ 50 cm in height) were not measured. For liana-infested trees the tree height and the height to the first ramification was measured in addition to the dbh. This was done with a clinometer and/or measuring tape.

Data analyses

In the comparison of family distribution for lianas larger than 2.5 cm dbh with plants smaller than 2.5 cm dbh, the two rare families Verbenaceae and Apocynaceae were combined. The difference in relative abundance among lianas in different size classes was analysed with G-tests for the 10 most common families (Sokal & Rohlf 1995). The G-values were calculated using Williams's correction.

When making a species–area curve from a plot, the shape of the curve is affected by the order in which subplots are added to the cumulated area. As pointed out by Colwell & Coddington (1994), the samples can only be added in random order if the set of subplots is relatively homogeneous. To make the species–area curves applicable for species with a spatially autocorrelated distribution, I used a limited randomization procedure. Only adjacent subplots were added, each time the total area was increased to count the new total number of species. By doing so, each point on the species–area curve represents the number of species collected in a contiguous area. The species–area curves were fitted to the points representing the mean number of species in 100 iterations of this process, with a negative exponential function (He & Legendre 1996) using the Levenberg–Marquardt method (DeltaGraph for Macintosh; SPSS Inc. 1997).

I analysed how forest structure influenced liana diversity and density, by using two different multiple regressions. Either (i) the number of liana individuals per subplot, or (ii) the number of liana species per subplot were regressed on the number of trees per subplot. The trees were divided into three size classes, and tree density was nested by transect. A nearest-neighbour variable (average number of trees in neighbouring subplots) was included to compensate for spatial autocorrelation among the subplots.

In the regression of number of species, the number of liana individuals was included as a variable as well, since it was expected to be strongly correlated with number of species. The number of tree stems was used in the analysis rather than the number of individual trees, since it was judged that the number of potential trellises and the amount of competition for light, etc., was better correlated with number of stems than with number of individuals. All variables were normally distributed.

Mantel tests were used to determine whether the distribution of liana species and of trees in different size classes was spatially autocorrelated within the transects. The tests were performed with R-package for Macintosh (Legendre & Vaudor 1991). The confidence values in the Mantel tests were based on permutation tests with 9999 iterations.

The distribution of liana individuals on different-sized host trees was analysed in two different ways. First, the correlation between liana size and host tree size for lianas with different climbing mechanisms were investigated with analyses of covariance (ANCOVA). Next, a nominal logistic regression was used to examine the probability of liana presence on trees with respect to dbh of all potential host plants. Both the ANCOVAs and the logistic regression was made with JMP for Macintosh (SAS Inst. 1994).

In the ANCOVAs each liana individual was used only once. If a liana climbed more than one host, only the dbh of the primary host and the corresponding liana dbh were used. Only lianas with known host dbh were used. The family Urticaceae, which mainly consisted of small, subwoody plants, and the scrambling plants were excluded, as were the lianas with unknown climbing mechanism. It was determined which tree size measures were the best predictors of liana size for a given type of climbers using a backward elimination process, where both regressor variables and interaction terms were excluded if nonsignificant at $\alpha = 0.05$. Both liana dbh, and the variables tree dbh, tree height, and height to first ramification of the host trees were normally distributed after a $\log_{10}$ transformation, and it was checked that the relationship between $\log_{10}$ host tree dbh and $\log_{10}$ liana dbh was linear.

In the logistic regression, all trees ≥ 50 cm tall were used. For trees with dbh < 1.0 cm, the dbh was estimated as mentioned earlier. A tree was recognized as having a liana, if it was either primary or secondary host to a liana. Each liana could be included more than once in the analysis, if it fell to the ground and climbed another tree later. The data from the two transects were lumped.

To test whether trees with at least one liana had a greater probability of having more than one liana, the observed number of trees hosting different number of lianas was compared with the numbers expected from the Poisson distribution. All trees taller than 50 cm were included in the analysis. The expected and the observed values were compared with a G-test. Trees hosting 3–9 lianas were grouped to avoid expected values smaller than one.

RESULTS

Diversity of lianas

The number of lianas in transect 1 was 318, representing 96 species in 36 different plant families. In transect 2, the 288 individuals belonged to 86 species in 33 families. In total there were 606 liana individuals in the two transects, distributed among 138 species in 43 families (Table 1). Of the 606 individuals, 82.0% were identified to species (see species list, Appendix 1). When the transects were split up in four 20-m × 50-m transects (the plot size used by others, e.g. Duivenvoorden (1994) and Putz & Chai (1987)), the number of lianas per 0.1 ha was 151.5 ± 33.2 (mean ± SD), the number ≥ 1.0 cm was 94.5 ± 28.0 and the number ≥ 2.5 cm dbh was 33.0 ± 15.2. The number of species of lianas per 0.1 ha in the same size classes was 61.8 ± 3.6, 44.3 ± 6.8, and 20.5 ± 6.2, respectively, with ranges 57–65, 35–51 and 12–27.

The relative importance of the families depended on the diameter cutoff-limit. The family Sapindaceae had the highest species richness when all size classes were considered, with a total of 16 species in the two transects. The

Table 1. The total number of liana individuals per family in two, 0.2-ha plots in Yasuní National Park in Ecuadorian Amazonas. The families are listed in descending order of density.

Family	All size classes		dbh ≥ 1.0 cm		dbh ≥ 2.5 cm	
	N	%	N	%	N	%
Leguminosae	93	15.3	71	18.5	37	26.4
Celastraceae	70	11.6	38	9.9	11	7.9
Sapindaceae	55	8.9	34	8.9	4	2.9
Dilleniaceae	46	7.6	32	8.4	21	15.0
Menispermaceae	45	7.4	22	5.7	4	2.9
Bignoniaceae	36	5.9	23	6.0	12	8.6
Malpighiaceae	25	4.1	16	4.2	3	2.1
Asteraceae	24	4.0	11	2.9	4	2.9
Verbenaceae	18	3.0	11	2.9	0	0.0
Apocynaceae	17	2.8	6	1.6	2	1.4
Convolvulaceae	17	2.8	6	1.6	4	2.9
Hydrangeaceae	17	2.8	13	3.4	3	2.1
Polygalaceae	10	1.7	7	1.8	3	2.1
Icacinaceae	9	1.5	7	1.8	2	1.4
Loganiaceae	9	1.5	9	2.3	3	2.1
Connaraceae	8	1.3	7	1.8	3	2.1
Euphorbiaceae	7	1.2	6	1.6	3	2.1
Melastomataceae	7	1.2	2	0.5	1	0.7
Smilacaceae	7	1.2	2	0.5	2	1.4
Dichapetalaceae	6	1.0	3	0.8	1	0.7
Urticaceae	5	0.8	4	1.0	3	2.1
Mendonciaceae	5	0.8	4	1.0	0	0.0
Arecaceae	4	0.7	3	0.8	0	0.0
Malvaceae	4	0.7	4	1.0	0	0.0
Polygonaceae	4	0.7	3	0.8	0	0.0
Cucurbitaceae	4	0.7	3	0.8	0	0.0
Combretaceae	3	0.5	3	0.8	0	0.0
Marcgraviaceae	3	0.5	2	0.5	1	0.7
Annonaceae	2	0.3	1	0.3	0	0.0
Aristolochiaceae	2	0.3	0	0.0	0	0.0
Rubiaceae	2	0.3	2	0.5	1	0.7
Solanaceae	2	0.3	2	0.5	0	0.0
Ulmaceae	2	0.3	2	0.5	0	0.0
Passifloraceae	2	0.3	2	0.5	0	0.0
Vitaceae	2	0.3	1	0.3	0	0.0
Boraginaceae	1	0.2	1	0.3	1	0.7
Gesneriaceae	1	0.2	1	0.3	1	0.7
Moraceae	1	0.2	1	0.3	0	0.0
Amaranthaceae	1	0.2	1	0.3	1	0.7
Piperaceae	1	0.2	1	0.3	0	0.0
Rhamnaceae	1	0.2	0	0.0	0	0.0
Sapotaceae	1	0.2	0	0.0	0	0.0
Asclepiadaceae	1	0.2	1	0.3	0	0.0
Indetermined	26	4.3	15	3.9	9	6.4
Total	606	100.0	383	100.0	140	100.0

ten most species-rich families comprised 85 species, or 62% of the species recorded in the two transects. If only individuals larger than 1.0 cm dbh were considered, Leguminosae had as many species as Sapindaceae, and when only individuals larger than 2.5 cm dbh were considered Leguminosae had the most species, followed by Bignoniaceae and Dilleniaceae (Figure 2).

When considering lianas of all size classes, the most abundant type of

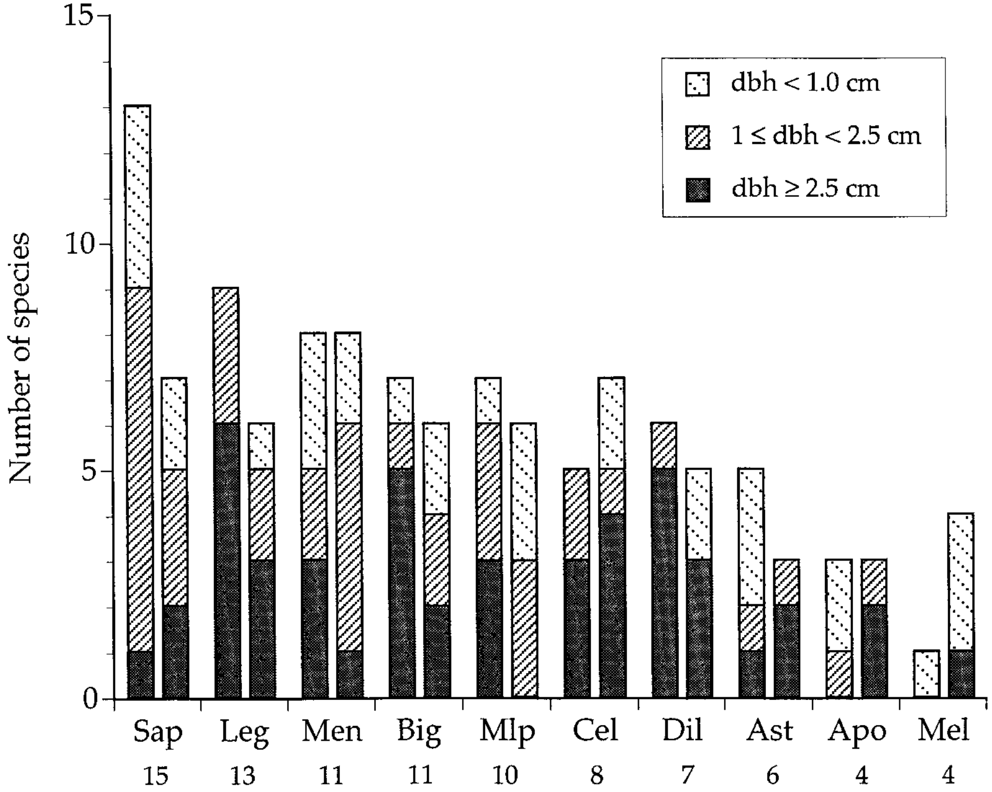

Figure 2. Number of different liana species per 0.2 ha in the 10 most species-rich families. The columns to the left are for transect 1, the ones to the right are for transect 2. The total number of species is shown below the family labels. Sap: Sapindaceae, Leg: Leguminosae, Men: Menispermaceae, Big: Bignoniaceae, Mlp: Malpighiaceae, Cel: Celastraceae, Dil: Dilleniaceae, Ast: Asteraceae, Apo: Apocynaceae, Mel: Melastomataceae.

climbers was the stem twiners, followed by the tendril climbers and branch twiners (Figure 3). The prevalence of stem twiners was mostly due to the abundance of stem twining legumes.

The relative number of individuals of the 10 most abundant families varied among the size classes. The relative dominance of the families was significantly different for lianas with dbh $\geq$ 1.0 cm as compared to lianas with dbh $<$ 1.0 cm ($G = 22.3$, $df = 9$, $P < 0.01$). The difference in the relative abundance of families was even larger for lianas above and below 2.5 cm dbh ($G = 54.9$, $df = 8$, $P < 0.001$).

The species–area curves (Figure 4) were used to estimate the total number of species (S_{max}). In transect 1 S_{max} was 134 and for transect 2 it was 112. These estimates should probably be regarded as lower bounds for the true total number of species, since empirical results often show that the calculated maximum is higher if the total area sampled is larger (Colwell & Coddington 1994).

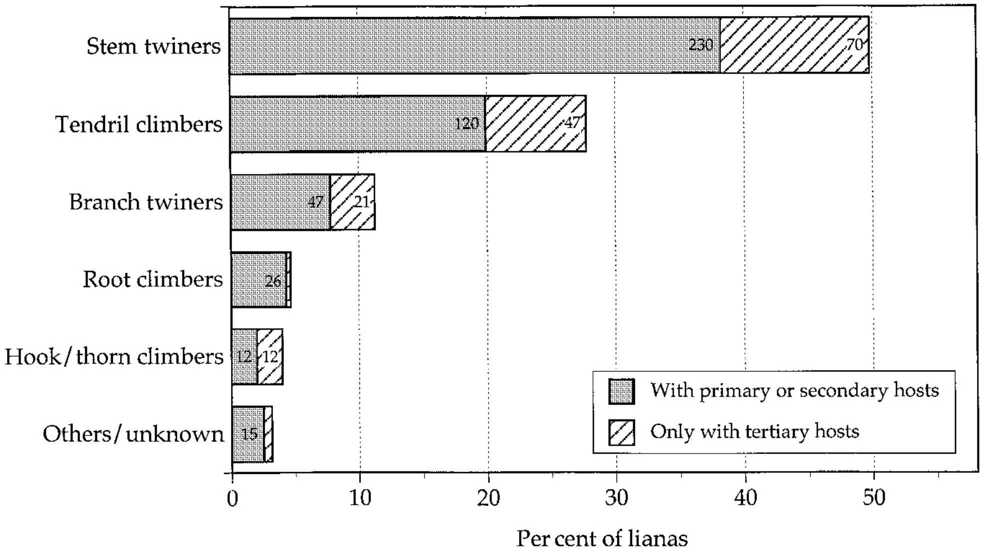

Figure 3. Number of liana individuals possessing different climbing mechanisms. The number of individuals in the subgroups is indicated. The group 'Others' include five scramblers, five individuals from the family Urticaceae (loosely twining or scrambling, subwoody plants), and nine lianas with unknown climbing methods.

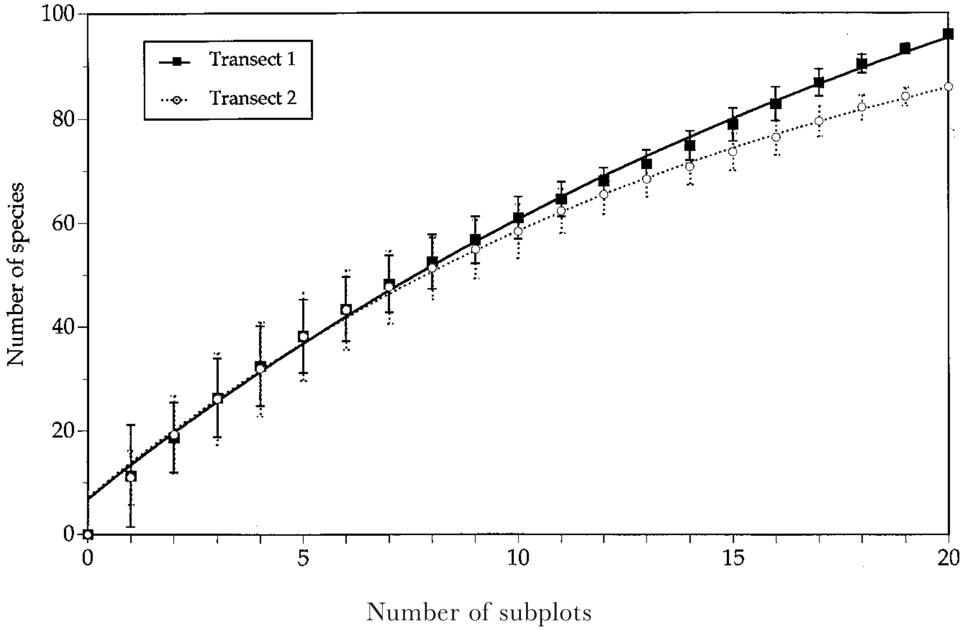

Figure 4. Species-accumulation curves for the two 0.2-ha transects. Each point on the curves represents the average of 100 restricted permutations of the sampling order (see text), and the error bars indicate the SD. The curves were fitted to the points using a negative exponential curve fit. $S(n) = S_{max}(1-e^{-Kn})$, where $S(n)$ is the number of species, n is the number of subplots, and S_{max} is the estimated total number of species. For transect 1: $S_{max} = 134.2$, $K = 0.0605$, $\chi^2 = 107.5$. For transect 2: $S_{max} = 112.3$, $K = 0.0638$, $\chi^2 = 169.0$.

Effect of forest structure on liana distribution

The density of tree saplings (57.4 ± 37.4, mean per subplot, ± SD) and small trees (51.3 ± 16.8) correlated with liana density and diversity in different ways. The number of large trees (7.0 ± 3.0) per subplot was not correlated with liana density or species richness.

The liana density was correlated with the number of small trees (Table 2). Liana density was not correlated with the number of trees in the other size classes. The number of liana species, on the other hand, was strongly dependent on the number of liana individuals in the squares, and this variable alone explained 92% of the variation in number of species among subplots. Also, the number of liana species was higher in subplots with more tree saplings, but this variable alone only described 2% of the variation in number of liana species.

The liana species were significantly autocorrelated in transect 1 (Hubert's standardized $r = 0.69$, $P < 0.004$), but not in transect 2 ($r = 0.05$, $P = 0.40$). The distribution of trees with respect to size classes was significantly autocorrelated in transect 1 ($r = 0.18$, $P < 0.04$), but not so in transect 2 ($r = 0.08$, $P = 0.22$).

Table 2. Results of two multiple regressions of the number of liana individuals or number of liana species on number of trees in three dbh classes per 10-m × 10-m subplot. Both regressions were done on both individuals in the same subplot and on the average number of individuals in the neighbouring subplots. The number of either tree stems or liana individuals is shown in the column labelled n. The number of liana individuals per subplot was included as a variable in the regression for number of liana species. The number of trees was nested on transect in both analyses.

Individuals per subplot					
	n	F	df	r^2	P
Same subplot					
dbh < 1 cm	2294	1.60	2	0.01	0.22
1 ≤ dbh < 10 cm	2050	5.03	2	0.31	0.01
dbh ≥ 10 cm	280	2.14	2	0.06	0.14
Neighbouring subplot					
dbh < 1 cm	2279	0.50	2	–0.01	0.61
1 ≤ dbh < 10 cm	2048	1.36	2	0.02	0.27
dbh ≥ 10 cm	281	2.51	2	0.10	0.10
Whole model		3.63	13	0.47	0.003
Species per subplot					
	n	F	df	r^2	P
Same subplot					
Individuals	606	54.00	2	0.92	<0.001
dbh < 1 cm	2294	3.76	2	0.02	0.04
1 ≤ dbh < 10 cm	2050	0.45	2	<0.01	0.64
dbh ≥ 10 cm	280	0.36	2	<0.01	0.70
Neighbouring subplot					
Individuals	615	0.26	2	<0.01	0.78
dbh < 1 cm	2279	2.82	2	0.02	0.08
1 ≤ dbh < 10 cm	2048	0.98	2	<0.01	0.39
dbh ≥ 10 cm	281	0.89	2	<0.01	0.42
Whole model		32.15	17	0.93	<0.001

Differences in trellis requirements

Lianas using different climbing mechanisms preferred host trees with different diameters. The hook/thorn climbers were climbing on thinner host plants than were the tendril climbers, branch- and stem twiners (ANCOVA: n = 409, F = 11.4, df = 1, $P < 0.001$) whereas the root climbers climbed on larger host trees (n = 423, F = 17.0, df = 1, $P < 0.0001$) (Figure 5). There was no significant difference among stem twiners, branch twiners and tendril climbers.

The size of lianas was strongly dependent on the diameter of their host trees, when all five climbing methods were considered together (n = 435, F = 133.3, df = 4, $P < 0.0001$, $r^2_{adj.} = 0.50$). The regressions of $\log_{10}$ liana dbh on $\log_{10}$ host dbh had the same slope for lianas with different climbing mechanisms (the interaction between host dbh and climbing mechanism was non-significant), and liana dbh was not correlated with height to the first ramification of the trees. Tree height had a borderline significance (F = 3.24, df = 1, P = 0.07), but it was highly correlated to tree dbh, and was therefore of minor importance as a predictor of liana dbh.

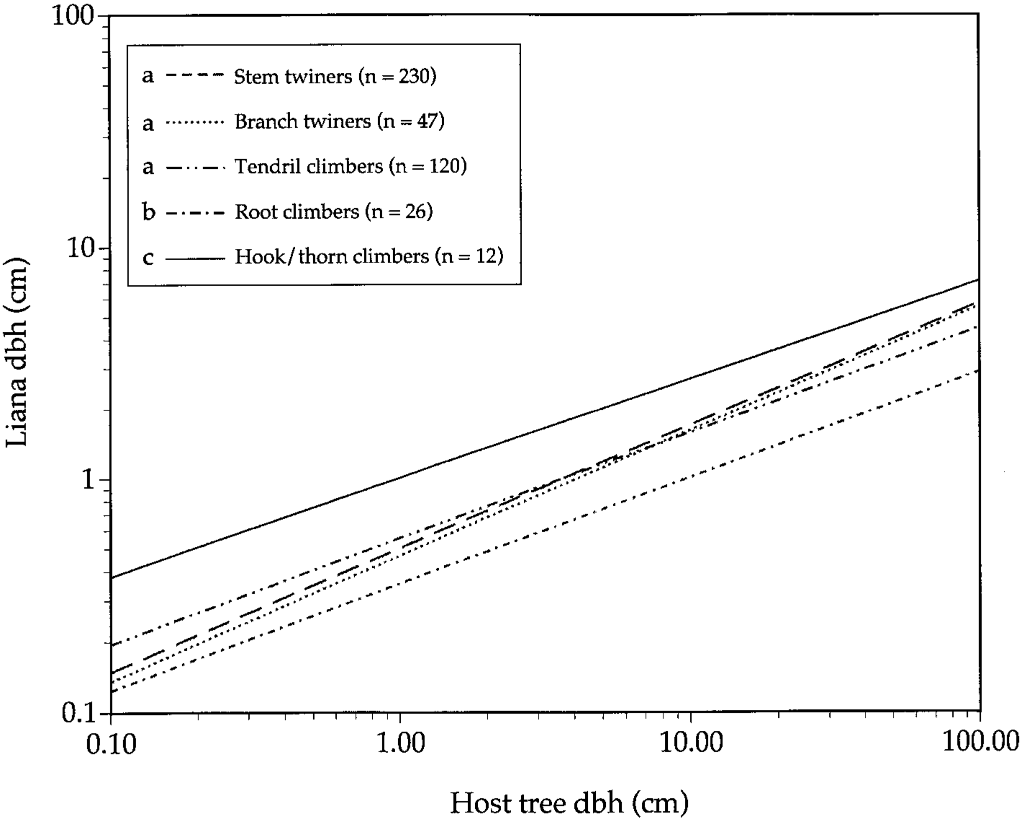

Figure 5. Relationship between liana- and host dbh for the lianas with different climbing mechanisms. The lines are predicted from the ANCOVA analyses. Significantly different climbing mechanisms are marked with different letters. Slopes are not significantly different.

The probability that trees were either primary or secondary hosts to at least one liana depended on dbh of the trees (Figure 6). In total 417 of the 4624 tree and liana stems were either primary or secondary hosts to at least one liana. The probability that trees were hosts to lianas increased from about 10% for trees with a dbh of 1 cm to more than 60% for large trees (logistic regression; $\chi^2 = 240.5$, df = 1, n = 4621, $P < 0.0001$). Fifty-two per cent of the trees with dbh > 40 cm were hosts to lianas.

The majority of the lianas that had recently climbed their hosts were growing on small diameter host trees. For tendril climbers, stem- and branch-twiners, 90% of the individuals ≤ 1.0 cm grew on trees with dbh less than 15, 8 and 8 cm, respectively.

Large-diameter trees had a higher probability of being infested with at least one liana, and in addition the number of lianas per tree was higher (Table 3). The difference between observed and expected number of lianas per tree was significant (G = 8.1, df = 2, P = 0.02, likelihood ratio).

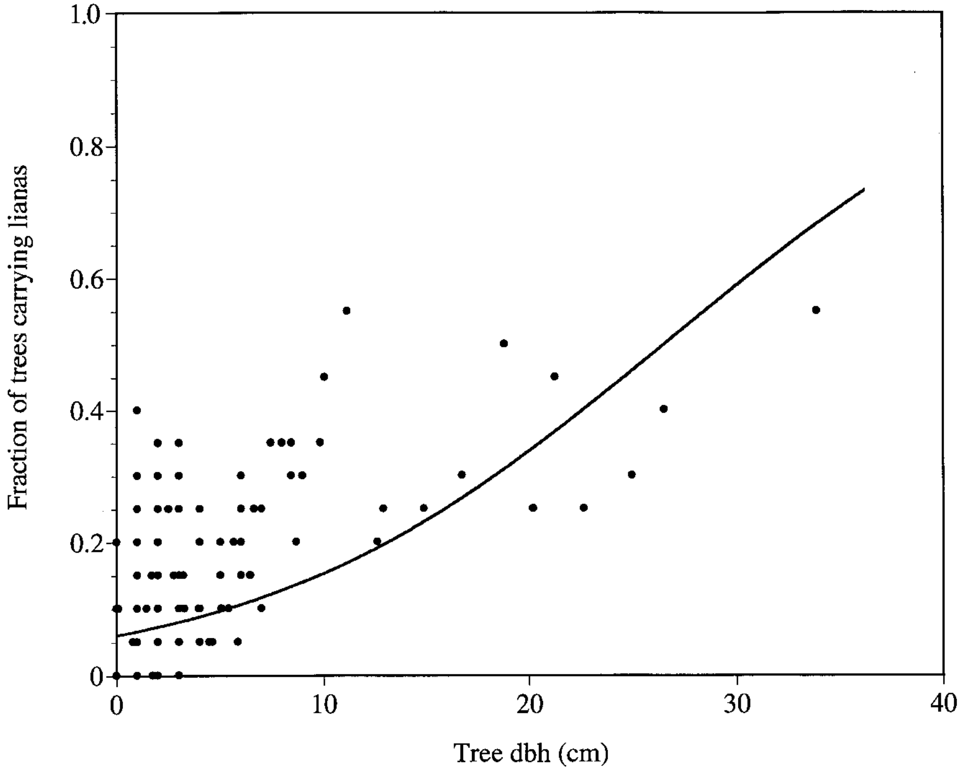

Figure 6. Logistic regression of probability of liana infestation on tree dbh. Trees in all size classes with known dbh were used (n = 4621). The line shows the probability of liana infestation as predicted by the logistic regression. The points illustrate the observed probability of liana infestation, and they were not used for fitting the line. The trees were sorted by dbh, and each point indicates the fraction of consecutive groups of 20 trees that was infested with lianas vs. the average dbh for the 20 trees.

Table 3. Number of trees with varying number of lianas. The expected number of trees with lianas is calculated from the Poisson distribution.

No. of lianas per tree	No. of trees	Expected no. of trees	Mean tree dbh (cm)
0	4205	4089	2.4
1	332	503	7.0
2	55	31	11.1
3	19	1	17.8
4	5	0	17.9
5	3	0	26.4
6	3	0	19.4
7	0	0	—
8	1	0	25.1
9	1	0	28.5

DISCUSSION

Diversity of lianas

The liana species richness in the studied transects was higher than in any comparable study. Ninety-six species of lianas (all dbh classes) were present in a 0.2-ha plot, corresponding to 27 species with dbh ≥ 2.5 cm in the most diverse 0.1-ha subplot. In comparison Duivenvoorden (1994) found a maximum of 17 species with dbh ≥ 2.5 cm per 0.1 ha in a series of plots on Ultisol in middle Caquetá, Colombia. Appanah *et al.* (1993) found a total of 59 liana species with dbh ≥ 2.5 cm in a 0.1 ha plot in Jatun Sacha, some 130 km west of Yasuní (this included 12 species of hemi-epiphytes and one strangler; see appendix 1 in Gentry 1991). This is the highest number of liana species ever recorded, but the plot was composed of several small transects (the Exploded Quadrat method; Gentry 1982, 1986). Because of the clumped distribution of conspecific lianas mentioned earlier, and because the risk of covering several habitat types is higher when large areas are investigated, the result is not strictly comparable to the one from Yasuní. Few studies of lianas include lianas of all sizes (cf. table 11.1 in Hegarty & Caballé 1991). Putz & Chai (1987) found 53 species in a 0.1-ha plot at Lambir, Malaysia, which is the study that reports the highest diversity, as far as I am aware. This is less than the maximum of 65 per 0.1 ha found in Yasuní.

Both the relative dominance of the families and the relative number of species per family were highly dependent on the size class studied. The families Leguminosae, Dilleniaceae and Bignoniaceae constituted a higher fraction of the individuals when a larger dbh cut-off limit was used. Gentry (1991) found the same trend in a series of 21 lowland Amazonian plots (liana diameter ≥ 2.5 cm) where either Bignoniaceae or Leguminosae nearly always were the most species-rich liana family, whereas Dilleniaceae were of minor importance. Most species of both Sapindaceae, Menispermaceae, and to some extent the Malpighiaceae, were only represented in the plots as small individuals in the transects in Yasuní, indicating either that they mainly consisted of subcanopy species, or that they had a lower diameter to length ratio, and therefore reach the canopy despite their small diameters.

The shape of the species–area curves suggested that the total number of species would continue to increase with plot size, even though the plots were located in apparently homogeneous forest. This pattern has two possible causes. The main reason is that the majority of species are rare, and therefore the probability of encountering them increases with plot size. The second, and often overlooked reason is that liana species are positively spatially autocorrelated. This may be a result of the lianas' well-documented tendency to reproduce clonally (Appanah & Putz 1984, Caballé 1994), or it may be caused by species-specific habitat requirements.

The high number of species in Yasuní is even more striking when it is compared with the relatively low number of individuals. In 31 neotropical sites, Appanah *et al.* (1993), and Gentry (1983, 1986) found 64.1 ± 21.1 lianas (mean ± SD) with diameter $\geq$ 2.5 cm per 0.1-ha, which is twice the 33.0 ± 15.2 individuals found in the four 0.1 ha subplots in this study. Lianas are generally dependent on treefall disturbances (Putz 1983, Webb 1958), so the low density of lianas in the studied areas in Yasuní may be a sign that the tree-fall rate was low in the investigated areas.

Liana distribution on a community scale

The large trees, which were predicted to have a negative impact on the liana density, both through direct competition with the lianas for light and nutrients, and through their indirect effect as competitors to the lianas' host trees, had no influence on the density of lianas, or on the number of liana species per subplot. This may suggest that any negative impacts on the lianas through shading are counterbalanced by the large trees' ability to support lianas, although it is more likely that the lack of correlation is caused by the low number of large trees.

The number of liana individuals was highly correlated with the number of small trees, probably due to their importance as trellises. Because of the strong correlation between number of liana species and number of liana individuals, the areas with a high density of small trees also had more species of lianas.

The tree saplings were expected to be of some importance to the lianas as potential trellises, but they were also expected to compete with the lianas for resources. The number of saplings per subplot was correlated with number of liana species, but not with liana density. This may indicate that when the forest is more open, which is probably the case in areas with a high number of small trees, it becomes possible for light- or small-trellis requiring liana species to become established, while the more shade-tolerant species are still able to survive in the area.

In general, the large lianas were growing on large-diameter host trees, irrespective of the climbing method they used. The correlation between liana dbh and host tree dbh is probably due to the lianas growing up together with their host trees, but in addition, some of the smaller lianas, that are adapted to growth in the low-light understorey environment, may only grow on small size supports.

Relation between climbing mechanism and host size

For a given host diameter, the hook/thorn climbers were larger than tendril climbers, branch- and stem twiners. This is probably due to the hook/thorn climbers' ability to remain self-supporting longer than the other types of climbers. Some species of *Strychnos* (Loganiaceae), for example, are able to grow several m tall before they have to rely on trees for support (Nabe-Nielsen, *pers. obs.*; Caballé 1993). Hook/thorn climbers may therefore be seen as an ecological intermediate between trees and the other lianas. The relatively high mean diameter of the root climbers' host trees, as compared with hosts of equal-sized lianas with other climbing modes, is caused by their ability to climb very big trees. In particular the small individuals of *Hydrangea tarapotensis*, which represented 17 of the 27 root climbers, were often found appressed to trunks of large trees. The results above are not directly comparable to earlier studies (Putz 1984b, Putz & Chai 1987), where only the upper diameter limit for the supports was recorded.

Probability of liana infestation vs. tree diameter

In spite of the fact that nearly all the lianas that recently climbed host trees had small diameter hosts, in both this study and others (Putz 1984b, Putz & Chai 1987), the fraction of trees that supported at least one liana steadily increased with host diameter. The proportion of the trees that hosted lianas would have been even higher for large trees if the lianas that entered trees from the crown of a neighbouring tree had been included. The increase in the number of liana-infested trees was partly caused by lianas that were initially attached to small branches on the large host trees, and to irregularities in their bark. The root climbers' ability to climb large trees also contributed to the increase in the number of liana-infested trees. The increase in the proportion of trees that supported lianas illustrates an important point, namely that the rare event that lianas climb large trees may be more important for their regeneration than the case of lianas climbing small-diameter trees. This is particularly so when lianas that climb small-diameter trees are unable to span the gap to adjacent trees, and are forced to wait until their hosts reach the canopy.

The presence of one liana increased the probability that a tree carried more than one liana, which is consistent with the findings of Putz (1984b) on Barro Colorado Island, and of Campbell & Newbery (1993) in Sabah, Malaysia. That lianas are aggregated on a few host trees may either be due to an increased susceptibility of the trees once a liana is present, or simply that some trees are growing in places with a high density of lianas. Different tree species also have different probabilities of being infested by lianas (Campbell & Newbery 1993).

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APPENDIX

List of liana species collected in the two 0.2-ha transects in Yasuní National Park. Vouchers are stored in the herbarium AAU; their numbers are given in parentheses (Jacob Nabe-Nielsen is abbreviated JN). The specimens were matched with collections in the herbaria MO, NY and AAU or identified by specialists.

AMARANTHACEAE: *Chamissoa altissima* (Jacq.) Kunth (JN 177); ANNONACEAE: cf. *Anaxagorea* sp. 1 (JN 250); APOCYNACEAE: *Forsteronia acouci* (Aubl.) A. DC. (JN 203); *F. amblybasis* S.F. Blake ssp. *decipiens* (Woods) Hansen (JN 528); *Odontadenia cognata* (Stadelm.) Woodson (JN 433); ARECACEAE: *Desmoncus giganteus* An. Hend. (JN 278); ARISTOLOCHIACEAE: *Aristolochia klugii* O.C. Schmidt (JN 231); *A. sprucei* Mast. (JN 71); ASCLEPIADACEAE Indet. sp. 1 (JN 614); ASTERACEAE: *Mikania* cf. *chagalensis* Hieron. (JN 296); *M.* cf. *decora* Poepp. & Endl. (JN 60); *M. hookeriana* DC. (JN 481); *M.* cf. *houstoniana* (L.) B.L. Rob. (JN 295); *M.* cf. *mathewsii* B.L. Rob. (JN 559); *M. nigropunctulata* Hieron. (JN 483); BIGNONIACEAE: *Adenocalymna impressum* (Rusby) Sandwith (JN 545); *Callichlamys latifolia* (Rich) K. Schum. (JN 604); *Clytostoma binatum* (Thunb.) Sandwith (JN 417); *Cydista aequinoctialis* (L.) Miers (JN 306); *Lundia corymbifera* (Vahl) Sandwith (JN 346); *Paragonia pyramidata* (Rich.) Bureau (JN 562); *Stizophyllum riparium* (Kunth) Sandwith (JN 520); *Tynanthus panurensis* (Bureau) Sandwith (JN 549); Indet. sp. 1 (JN 82); BORAGINACEAE: *Tournefortia angustiflora* Ruiz & Pav. (JN 569); CELASTRACEAE: *Cheiloclinium hippocrateoides* (Peyr.) A.C. Sm. (JN 500); *Hylenaea comosa* (Sw.) Miers (JN 240); *Peritassa* sp. 1 (JN 383); *Salacia multiflora* (Lam.) DC. (JN 479); S. sp. 2-3 (JN 16, 246); *Tontelea corymbosa* (Huber) A.C. Sm. (JN 206); Indet. sp. 1 (JN 384); COMBRETACEAE: *Combretum* sp. 1 (JN 601); CONNARACEAE: *Rourea camptoneura* Radlk. (JN 321); Indet. sp. 1 (JN 51); CONVOLVULACEAE: *Dicranostyles holostyla* Ducke (JN 230); *Maripa pauciflora* D.F. Austin (JN 216); *Turbina* sp. 1 (JN 290); CUCURBITACEAE: *Cayaponia ophthalmica* R.E. Schult. (JN 374); *Siolmatra pentaphylla* Harms (JN 464); DICHAPETALACEAE: *Dichapetalum* cf. *amazonicum* K. Krause (JN 373); *D. odoratum* Baill. (JN 324); *D. rugosum* (Vahl) Prance (JN 401); DILLENIACEAE: *Doliocarpus* cf. *dentatus* (Aubl.) Standl. (JN 392); *D. dasyanthus* Kubitzki ssp. *robustus* Aymard (JN 285); *D.* cf. *major* J.F. Gmel. ssp. *major* (JN 196); *Neodillenia coussapoana* Aymard (JN 86); *Pinzona coriacea* Mart. & Zucc. (JN 89); *Tetracera* cf. *volubilis* L. (JN 12); Indet. sp. 1 (JN 532); EUPHORBIACEAE: *Omphalea diandra* L. (JN 277); Indet. sp. 1 (JN 573); GESNERIACEAE: *Drymonia coccinea* (Aubl.) Wiehler (JN 186); HYDRANGEACEAE: *Hydrangea tarapotensis* Briq. (JN 148); ICACINACEAE: *Leretia cordata* Vell. (JN 150); LEGUMINOSAE – CAESALPINIOIDEAE: *Bauhinia guianensis* Aubl. (JN 178); *B. microstachya* (Raddi) J.F. Macbr. (JN 279); LEGUMINOSAE – MIMOSOIDEAE: *Acacia multipinnata* Ducke (JN 591); *Piptadenia uaupensis* Spruce ex Benth. (JN 53); LEGUMINOSAE – PAPILIONOIDEAE: *Clitoria javitensis* (Kunth) Benth. (JN 587); *Dioclea ucayalina* Harms (JN 488); *D.* sp. 2 (JN 578); *Machaerium cuspidatum* Kuhlm. & Hoehne (JN 22); *M. quinata* (Aubl.) Sandwith (JN 96); *Mucuna* sp. 1 (JN 225); Indet. sp. 1-2 (JN 502, 390); LOGANIACEAE: *Strychnos jobertiana* Baill. (JN 114); *S. ramitifera* Ducke (JN 438); MALPIGHIACEAE: *Hiraea fagifolia* (DC.) A. Juss. (JN 308); *H.* sp. 2 (JN 336); *Jubelina uleana* (Nied.) Cuatrec (JN 579); *Mascagnia* sp. 1-2 (JN 130, 227); *Stigmaphyllon sinuatum* (DC.) A. Juss. (JN 366); Indet. sp. 1-3 (JN 548, 35, 271); MALVACEAE: *Malvaviscus* cf. *concinnus* Kunth (JN 291); MARCGRAVIACEAE: *Marcgravia coriacea* Vahl (JN 219); *M. eichleriana* Wittmack (JN 415); MELASTOMATACEAE:

Adelobotrys adscendens (Sw.) Triana (JN 212); *Blakea caudata* Triana (JN 267); *Clidemia epifitica* (Triana) Cogn. (JN 209); C. sp. 2 (JN 224); MENDONCIACEAE: *Mendoncia* cf. *bivalvis* (L. f.) Merr. (JN 280); *M.* cf. *cardonae* Leonard (JN 577); *M. velloziana* (Mart.) Nees (JN 355); *M.* sp. 4 (JN 553); MENISPERMACEAE: *Abuta solimoesensis* Krukoff & Barneby (JN 480); *A.* cf. *pahni* (Mart.) Krukoff & Barneby (JN 313); *A. velutina* Gleason (JN 426); *A.* sp. 4 (JN 616); *Borismene japurensis* (Mart.) Barneby (JN 120); *Curarea* sp. 1 (JN 17); *Odontocarya* cf. *emarginatus* Barneby (JN 615); *O.* cf. *rusby* Barneby (JN 115); *Sciadotenia toxifera* Krukoff & A.C. Sm. (JN 94); *Telitoxicum* cf. *krukovii* Moldenke (JN 478); *T. minutiflorum* (Diels) Moldenke (JN 468); MORACEAE: *Trymatococcus amazonicus* Poepp. & Endl. (JN 493); PASSIFLORACEAE: *Passiflora auriculata* Kunth (JN 205); *P. spinosa* (Poepp. & Endl.) Mast. (JN 552); *P.* sp. 3 (JN 197); PIPERACEAE: *Piper* sp. 1 (JN 126); POLYGALACEAE: *Moutabea* cf. *guianensis* Aubl. (JN 158); POLYGONACEAE: *Coccoloba* sp. (JN 222); RHAMNACEAE: *Gouania colombiana* Suess. (JN 287); RUBIACEAE: *Randia altiscandens* (Ducke) C.M. Taylor (JN 249); SAPINDACEAE: *Paullinia alata* (Ruiz & Pav.) G. Don (JN 154); *P. caloptera* Radlk. (JN 410); *P. clathrata* Radlk. (JN 484); *P. elegans* Cambess. ssp. *neglecta* (Radlk.) D.R. Simpson (JN 168); *P. eriocarpa* Triana & Planch. (JN 63); *P. faginea* (Triana & Planch.) Radlk. (JN 272); *P. fissistipula* J.F. Macbr. (JN 544); *P. granatensis* (Planch. & Linden) Radlk. (JN 88); *P. laeta* Radlk. (JN 606); *P. mazanensis* J.F. Macbr. (JN 18); *P. nobilis* Radlk. (JN 166); *P. pachycarpa* Benth. (JN 330); *P. serjaniifolia* Triana & Planch. (JN 50); *P. simulans* J.F. Macbr. (JN 508); *Serjania glabrata* Kunth (JN 52); *Thinouia obliqua* Radlk. (JN 159); SAPOTACEAE: *Micropholis venulosa* (Mart. & Eichler) Pierre (JN 377); SMILACACEAE: *Smilax cumanensis* Humb. & Bonpl. ex Willd. (JN 8); *S.* cf. *poeppigii* Kunth (JN 594); *S. siphilitica* Humb. & Bonpl. ex Willd. (JN 248); SOLANACEAE: *Solanum barbeyanum* Huber (JN 19); *S. leucopogon* Huber (JN 620); ULMACEAE: *Celtis iguanaea* (Jacq.) Sarg. (JN 581); URTICACEAE: *Urera eggersii* Hieron. (JN 25); VERBENACEAE: *Petrea maynensis* Huber (JN 376); VITACEAE: *Cissus* sp. 1 (JN 33); INDET.: Indet. sp. 1-2 (JN 339, 276).