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Dominance, diversity and distribution of lianas in Yasuní, Ecuador: who is on top?

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ABSTRACT. Lianas of Yasuní National Park and the Huaorani Ethnic Reserve, Ecuador were sampled using 0.2-ha subsamples from 12 1-ha plots. Using surveys and herbarium collections, the total species richness of lianas in the park and reserve is estimated to be close to 500 species. *Terra firme* habitats are significantly more species rich than floodplain habitats, but density of stems is not significantly different between habitats. The most abundant liana species is *Machaerium cuspidatum* Kuhlm. & Hoehne (Fabaceae) in both floodplain and *terra firme* habitats, representing more than 10% of all stems in census plots. Analysis of rarity indicates that none of the liana species encountered on the 12 plots is rare in terms of geographic range, and many species are not rare in terms of population size or habitat specificity. The rank order of abundance, combined with the coefficient of variability in species distribution among plots, is used to identify the 38 species (an oligarchy) that dominate forests in Yasuní.

KEY WORDS: Amazonia, climbers, endemism, oligarchy, rarity, species richness, tropical forest, vines

INTRODUCTION

Climbing plants are a characteristic life form in tropical rain forests the world over (Gentry 1991*a*, Richards 1996). Germinating on the ground and rooted permanently in the soil, woody climbers (lianas) use the support of trees to climb into the canopy where they can grow to be as old or older than host trees. Data on species richness and density of lianas over vast areas of the lowland neotropics were compiled by Gentry (1991*a*). His data, in combination with other studies of 1-ha plots (Faber-Langendoen & Gentry 1991, Laurance *et al*. 2001, Romero-S. 1999), provide a general picture of neotropical liana biogeography and richness. Primarily from Gentry's work, we have learned that lianas comprise about 20% of the woody species in moist, lowland neotropical

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forests (Gentry 1982, 1991*a*, Gentry & Dodson 1987, see Pérez-Salicrup *et al.* 2001 for particularly high species richness in 'liana forest').

In-depth studies of individual liana species or of specific 1-ha areas have contributed significantly to liana ecology. For example, apices of *Ipomoea phillomega* (Vell.) House creep up to 30 m without branching (Peñalosa 1984) in primary forest in Mexico. In central Panama, lianas contribute substantially to forest biomass in undisturbed forests where stem numbers of lianas are low (DeWalt *et al.* 2000) and yet, also in Panama, lianas contribute to the arrested development of successional pathways (Schnitzer *et al.* 2000). The allometric relationship between stem diameter and biomass of lianas was clarified in moist and in dry tropical forests by Putz (1983) and Bullock (1990). Yet, the gap between the continental-scale data of Gentry and investigations of individual sites and species leaves neotropical forest ecologists with little data on large-scale distribution of lianas, consistency of liana composition from site to site, dominance–diversity structure of liana communities, and habitat specificity of lianas over large areas. The research reported here aims to fill that gap for Yasuní National Park and the Huaorani Ethnic Reserve, Ecuador.

Some tree species are distributed widely in the Amazon lowlands of Ecuador and Peru and some occur at high population densities (Pitman *et al.* 1999, 2001). Many 1-ha plots are dominated by the same tree species – a palm – across large tracts of western Amazonia, a pattern that contrasts with a traditional view of tropical species occurring in clumped, isolated populations (Ashton 1976, Hubbell & Foster 1986, Richards 1996). Conversely, regionalism in tree composition at the family level in Amazonia has been demonstrated (ter Steege *et al.* 2000, Terborgh & Andresen 1998). Here I examine dominance within liana communities over a large area of western Amazonia.

This paper provides insight on liana communities over a large spatial scale, in an area sampled specifically for lianas. Two of the most abundant habitat types in eastern Ecuador (*terra firme* and floodplain) were sampled and compared. In addition to establishing baseline data on liana communities in Ecuador, the following questions about liana communities were addressed:

(1) Which are the ecologically dominant lianas in Yasuní?
(2) Are species of lianas in Yasuní, Ecuador, geographically widespread or restricted?
(3) Are species of lianas in Yasuní habitat generalists or habitat-specific?
(4) In spite of high species richness in Yasuní, is there a predictable rank order of species among lianas?
(5) Are the most important species in liana communities predictable from site to site across Yasuní?

SITE DESCRIPTION AND SAMPLING METHODS

Lianas were sampled from 1998 to 2000 within Yasuní National Park and the Huaorani Ethnic Reserve, an area of approximately 1.6 million ha at the western margin of the Amazon Basin. The park and reserve lie entirely within

Ecuador, forming its eastern boundary (Figure 1). Following Pitman (2000), the area referred to hereafter as 'Yasuní' includes both the park and ethnic reserve. The climate is warm and humid, with an estimated mean annual temperature of 26.5 °C and annual rainfall of ~2860 mm (Korning & Balslev 1994, Pitman 2000, Romero-S. *et al.* 2001). The area experiences little variation in rainfall throughout the year, with slightly drier seasons occurring in December–January and in August. There is no month in which rainfall is below 100 mm (Romoleroux *et al.* 1997).

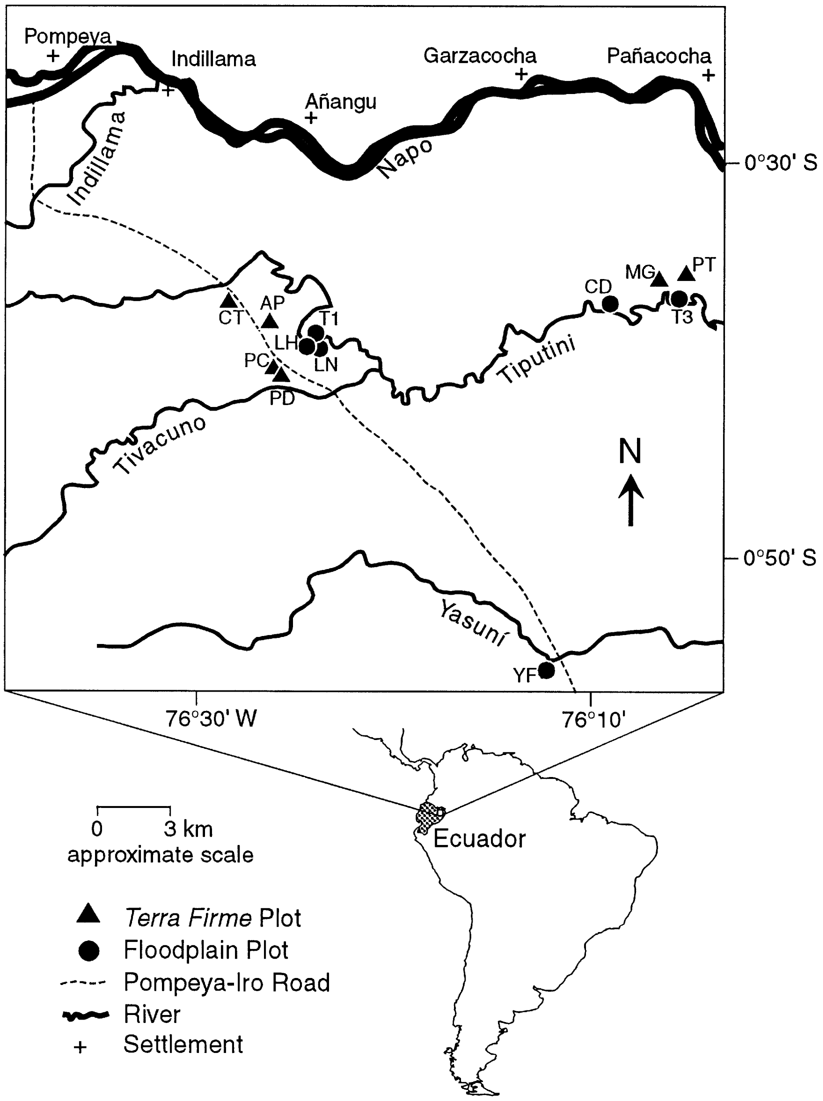

Figure 1. Location of 12 plots sampled for lianas in Yasuní National Park and the Huaorani Ethnic Reserve, Ecuador.

The area is vegetated in species-rich, dense tropical rain forest with canopy heights 30–35 m, and emergent trees to > 50 m (Neill *et al.* 1994). The most abundant tree species is a palm, *Iriartea deltoidea* Ruiz & Pav., representing ~7.5% of all stems ≥ 10 cm diameter at 1.3 m in a sample of 15 1-ha *terra firme* plots (Pitman *et al.* 1999, 2001). Tree species richness in 1-ha plots in *terra firme* or floodplain habitat ranges from 114 to 279 species (N. Pitman unpubl. data).

This study was conducted in the two most abundant habitat types in Yasuní: *terra firme* and floodplain. *Terra firme* habitat comprises as much as 80% of Yasuní, and is characterized by rolling hills and flat areas away from major river courses. *Terra firme* habitat is never flooded, and only following strong rainstorms does it maintain pools of standing water for longer than a few hours. Small creeks cross *terra firme* habitat and topographic relief can be as much as 35 m within a 1-ha plot. Floodplain habitat is more restricted in distribution, occurring close to the east-flowing rivers that cross Yasuní and ultimately join the Napo River. Floodplain habitat is inundated periodically when river levels rise following heavy rainfall. Flooding can last up to 2 wk and water stands as deep as 3 m above soil level during extreme flooding, which happens once or twice per year (*pers. obs.*).

Lianas were subsampled from 12 1-ha plots within Yasuní (Figure 1). Lianas are defined here to include only climbing plants originally and permanently rooted in the ground and climbing with support from another plant, thus excluding all members of the Clusiaceae, Cyclanthaceae, and Araceae, families that include hemi-epiphytes or 'nomads' (Moffett 2000). Excluding hemi-epiphytes is routine for liana surveys (Chalmers & Turner 1994, Nabe-Nielsen 2001, Pérez-Salicrup *et al.* 2001, Putz 1983, Putz & Chai 1987). Stems of the Marcgraviaceae are included in density measures, but are excluded from all species-level analyses because genera could not be reliably distinguished vegetatively. Species of Marcgraviaceae can be both hemi-ephiphytes and lianas, or woody vines (Jørgensen & León-Yánez 1999). Species of *Smilax* were not distinguished in this study below the generic level and '*Smilax* spp.' could represent up to four species (Jørgensen & León-Yánez 1999).

Sampling was designed to census liana species in 1-ha plots without counting all stems and to maximize species richness by covering a large non-contiguous area. Five parallel transects of 4 × 100 m were established within each 1-ha plot, each transect separated from the next by 16 m, thus completely sampling an area of 2000 m^2 (0.2 ha). Within each transect all climbing stems ≥ 1 cm diameter were measured and identified. Stems were measured at the thickest point above the ground, excluding nodal swelling or damage (DeWalt *et al.* 2000). Stems were included if they rooted in or grew into the transect ≤ 2 m above the ground from a rooted position outside of the transect. This method overestimated richness and density on a per-area basis. Multiple branches climbing to the canopy were not counted as multiple stems unless independent rooting for each branch was located (Putz & Chai 1987). In two plots (PC and PD, Table 1) tree sampling had been established previously in 10 × 1000-m areas. In these plots, the five transects were established end-to-end in the centre of the 10 × 1000-m area, thus sampling a rectangular area of 4 × 500 m (0.2 ha).

Climbers were identified to species or morphospecies using vegetative characteristics of sterile specimens collected or observed in the field. Fertile specimens were encountered very rarely. Sterile specimens were compared with fertile reference material collected by the author and others throughout Yasuní, housed at Field Museum (F), University of Michigan Herbarium (MICH), Missouri Botanical Garden (MO) and the National Herbarium of Ecuador (QCNE). Some specimens were identified using characteristics of wood slash and stem odour, characters recently highlighted in a field key for Brazilian forests (Ribeiro *et al*. 1999).

DATA ANALYSIS

Species richness and density

Total species richness ha^{-1} in Yasuní (Table 1) is underestimated by the data presented here for two reasons. First, only 0.2 ha was directly sampled. Because sampling was consistent from site to site, and because random surveys in unsampled areas of each 1-ha plot only occasionally revealed species not counted in transects, the species richness values are considered a consistent minimum number of the liana species richness ha^{-1}. Second, because stems

Table 1. Site names, acronyms, habitat type, stem density, species richness, Fisher's α, family richness and dominant liana species on 12 ha in Yasuní National Park, Ecuador. Fisher's α values are based only on stems identified to species or morphospecies, while species richness values include all distinct species for a plot, even if not identifiable to genus or species. Number of stems represents all stems, regardless of whether they were identified to any taxonomic level.

Site name (acronym)	Habitat type	Number species	Number stems	Fisher's α	Number families	Most abundant species
Monkey PC (PC)	TF	88	302	41.3	32	*Machaerium cuspidatum*
Capiron (CT)	TF	104	344	54.0	32	*Machaerium cuspidatum*
Puente TBS (PT)	TF	105	347	53.5	30	*Machaerium cuspidatum*
Aulestia Pirana (AP)	TF	100	433	41.0	31	*Petrea maynensis*
Monkey PD (PD)	TF	109	314	61.9	31	*Petrea maynensis*
Maquisapa-Guacamayo (MG)	TF	86	313	39.5	29	*Machaerium cuspidatum*
TBS Floodplain (T3)	FP	71	360	27.0	22	*Tetracera volubilis*
Yasuní Floodplain (YF)	FP	87	292	40.0	32	*Machaerium cuspidatum*
ECY Floodplain (T1)	FP	82	435	30.6	26	*Machaerium cuspidatum*
Laguna Nutria (LN)	FP	89	441	33.1	28	*Machaerium cuspidatum*
Laguna Hoatzin (LH)	FP	62	337	22.6	22	*Doliocarpus guianensis*
Caiman Durmiente (CD)	FP	72	430	24.5	29	*Machaerium cuspidatum*
Mean		87.9	362	39.1	29	
±SD		± 14.8	± 56.9	± 12.4	± 3.4	

Habitat types: TF = *terra firme*, FP = Floodplain.

not assigned to species or morphospecies were excluded from richness values, richness represents the minimum number of species ha^{-1}. When a single representative of a family or genus was encountered in a plot, the morphospecies was included in the species richness values in Table 1, even if not identifiable to species. Fisher's α (Hayek & Buzas 1997, Leigh 1999) is presented in Table 1 for each plot, calculated based only on stems identified to species or morphospecies. All stems censused were included in the density values reported here, regardless of whether or not they had been assigned to a species or morphospecies.

Stepwise elimination of plots from total species richness allows evaluation of the relative importance of single sites in contributing to total richness, with two possible scenarios. One-by-one elimination, starting with the most species-poor plots, gives an indication of a best-case scenario with forest destruction (least species removal), while elimination starting with the most species-rich sites gives an indication of a worst-case scenario during forest destruction.

Rarity analysis

A modification of rarity analysis (Pitman *et al.* 1999, Rabinowitz *et al.* 1986) addressed the question of endemism and habitat specificity. Rarity was classified as due to (1) limited geographic distribution (2) small population sizes or (3) habitat specificity. Geographic distribution was defined as 'small' if the species in question was reported only from Amazonian Ecuador. If the species inhabited areas beyond Amazonian Ecuador the geographic distribution was defined as 'large'. Geographic distribution was based on comparison of species in Brako & Zarucchi (1993), Jørgensen & León Yánez (1999) and the Missouri Botanical Garden Tropicos VAST database. Population size was defined as 'small' if the number of stems was $\leq$ 1 stem ha^{-1} everywhere within the 12 plots, otherwise population size was defined as 'large'. Habitat specialization was defined as 'narrow' if the species was found in only one of the two habitat types, otherwise habitat specialization was defined as 'broad'. Species evaluated included only 191 of the 311 species from the plots because each species must occur in at least two of the 12 plots sampled to be evaluated for habitat specificity and because morphospecies were not comparable to published species lists for range size determination.

Rank order and heterogeneity of species among samples

Dominants of the liana community are defined here as those species, ranked in decreasing order of abundance, that comprise 50% of the cumulative distribution of all stems (*sensu* Campbell 1994). Composition of a dominant group of liana species from each habitat (based on six plots each) was defined in an analogous manner. A parallel criterion for defining dominant species, based on species contributing $\geqslant$ 1% of all liana stems to a particular habitat, also was evaluated.

A measure of heterogeneity among plots, coefficient of variation (CV), identified those species that were most consistent in their contribution to all stems from the plots sampled. CV is the standard deviation of the proportional dominance divided by the mean proportional dominance, represented as 100 × (standard deviation/mean). The CV highlights differences between species that were very common at one or a few sites versus those that were only moderately common at all sites. Species with a low CV, regardless of absolute abundance, were equitably distributed, while those with a high CV showed a high degree of variability in their distribution. A CV of less than 150 was used to subdivide the continuum represented by the liana species in Yasuní and was used in combination with rank order to identify an oligarchy among the liana species across both habitats. This single objective method for designating dominance subdivided an obvious continuum of relative abundance for practical purposes.

RESULTS

Species richness and density

Lianas were represented by 311 species among the 4348 stems sampled in 12 plots. Of the total 4348 stems, 7% remain unidentified to species or morphospecies. The total number of liana species in Yasuní is not known, however 175 additional species (never encountered in the 12 plots) have been collected in the park and ethnic reserve by the author and other collectors (e.g. D. Neill, H. Romero-S., M. Aulestia, N. C. A. Pitman, R. B. Foster) over the past 10 y (species list in Burnham 2002), yielding species richness of lianas in Yasuní of about 450–500. The most abundant species was *Machaerium cuspidatum* (Fabaceae), representing 10.9% of all stems censused (3.9–19.5% of stems on individual plots).

Species richness ranged from 62 to 109 species per plot (mean = 88, Table 1). *Terra firme* plots were significantly more species-rich (mean = 98, range = 86–109) than floodplain plots (mean = 77, range = 62–89), t-test, $P < 0.002$. Fisher's α (Table 1) is also significantly larger in *terra firme* plots (t-test, $P < 0.001$). In calculating Fisher's α, the number of stems ranged from 269 to 424 per plot (90–98% of stems in each plot) after removal of unidentified stems.

Density of stems sampled ranged from 292 to 441 stems per plot (Table 1). Density in floodplain plots averaged 382 stems (range: 292–441) while density in *terra firme* plots averaged 342 stems (range: 302–433). Density was not statistically different between habitats (t-test, $P > 0.11$).

Rarity

Among all species analysed for rarity due to geographic range restriction, none was restricted to Amazonian Ecuador (Table 2). Most species were also found in Amazonian Peru, but many extend to Colombia, Venezuela or Bolivia. Thus, of the three aspects of rarity, no species was characterized by all three,

Table 2. Proportion of species showing combinations of rarity traits as defined by Rabinowitz *et al.* (1986). Each percentage value is the number of species in each category represented divided by 191. Number of species is in parentheses.

	Geographic range large		Geographic range small	
	Habitat specificity wide	Habitat specificity narrow	Habitat specificity wide	Habitat specificity narrow
Population size large	62.9 (120)	25.7 (49)	0	0
Population size small	3.66 (7)	7.85 (15)	0	0

while only 15 species of the 191 analysed were characterized by two types of rarity and 56 species were characterized by one type of rarity.

Of the 191 species analysed for rarity due to habitat restriction (Table 2), the majority (127 species) were found in both habitats. Three-quarters of the habitat-restricted species (49 of 64 species) had large population sizes in at least one plot (> 1 stem ha^{-1}). Just over 10% of the species evaluated (22 of 191) were always found at low population densities.

Heterogeneity of species composition in liana communities of Yasuní

Of the 311 species encountered, only 26 occurred in > 9 plots (Figure 2), indicating a high degree of heterogeneity in distribution. Plots sampled share an average of 37.3 species with other plots (range: 22–54), with the largest number of species shared between pairs of *terra firme* plots (mean = 43), and the fewest species shared between floodplain and *terra firme* plots (mean = 34). Similar comparisons using Sørenson's Coefficient (Magurran 1988), which normalizes for variable numbers of stems compared, reveals that same-habitat

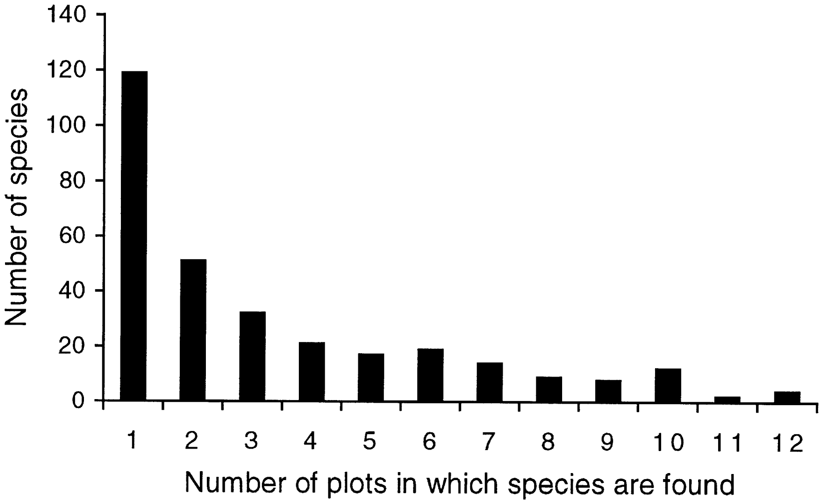

Figure 2. Species presence per 1-ha plot. Bars show the number of species found in increasing numbers of plots sampled.

comparisons are significantly more similar than cross-habitat comparisons (t-test; $P < 0.001$).

Stepwise elimination of plots gives insight into the degree of heterogeneity among sites (Figure 3). Eliminating six plots results in a list with 60–80% of all species, depending on the order in which plots are removed. Eliminating ten plots can reduce total species richness to 31–52% of all species.

Dominance among species in Yasuní

Machaerium cuspidatum was the dominant across Yasuní in both habitats. Although not the dominant on every plot, *M. cuspidatum* was always present and abundant. Twenty-eight species contributed to the combined-habitats dominance group (Figure 4). Only one of these species, *Doliocarpus major* J.F. Gmel., was found exclusively in floodplain habitats (but it is found in other habitats elsewhere: DeWalt *et al.* 2000). All other dominant species were present in both habitats, even if at low frequencies. In spite of this indication of habitat breadth, most species were more abundant in either floodplain or in *terra firme* habitats. Therefore, dominance among the liana community in Yasuní is more adequately represented by two distinct lists, one from each habitat (Figure 5).

The floodplain dominance group included 15 species while the *terra firme* dominance group included 35 species (Figure 5). Only eight species were shared between the two dominance groups, in spite of the indication from the rarity analysis of minimal habitat restriction. In the plots from Yasuní, only *D. major* was restricted to floodplains, while the following species were restricted to *terra firme: Arrabidaea affinis* A.H. Gentry, *A. nicotianiflora* Kraenzl., *Petrea blanchetiana* Schauer, *Mezia includens* (Benth.) Cuatrec., *Stizophyllum inaequilaterum* Bureau & K. Schum. and *S. riparium* (Kunth) Sandwith.

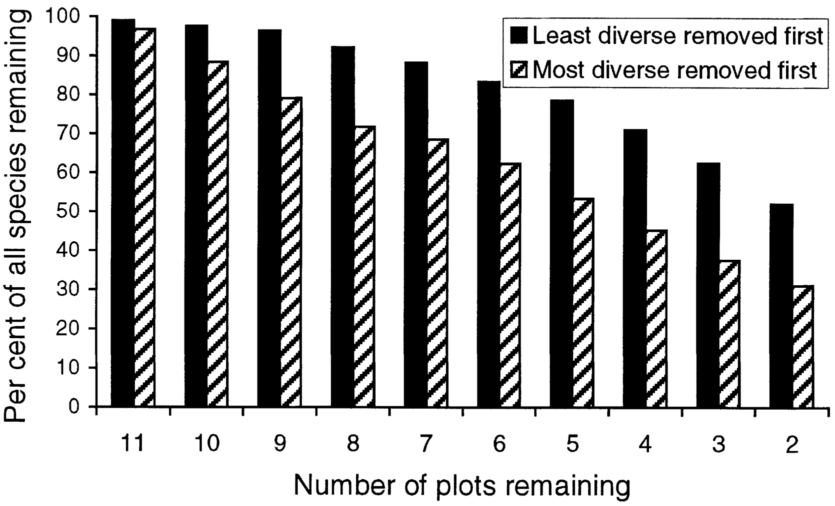

Figure 3. Proportion of total species richness remaining after one-by-one plot elimination starting with most diverse (diagonal shading) and least diverse (solid shading) plots.

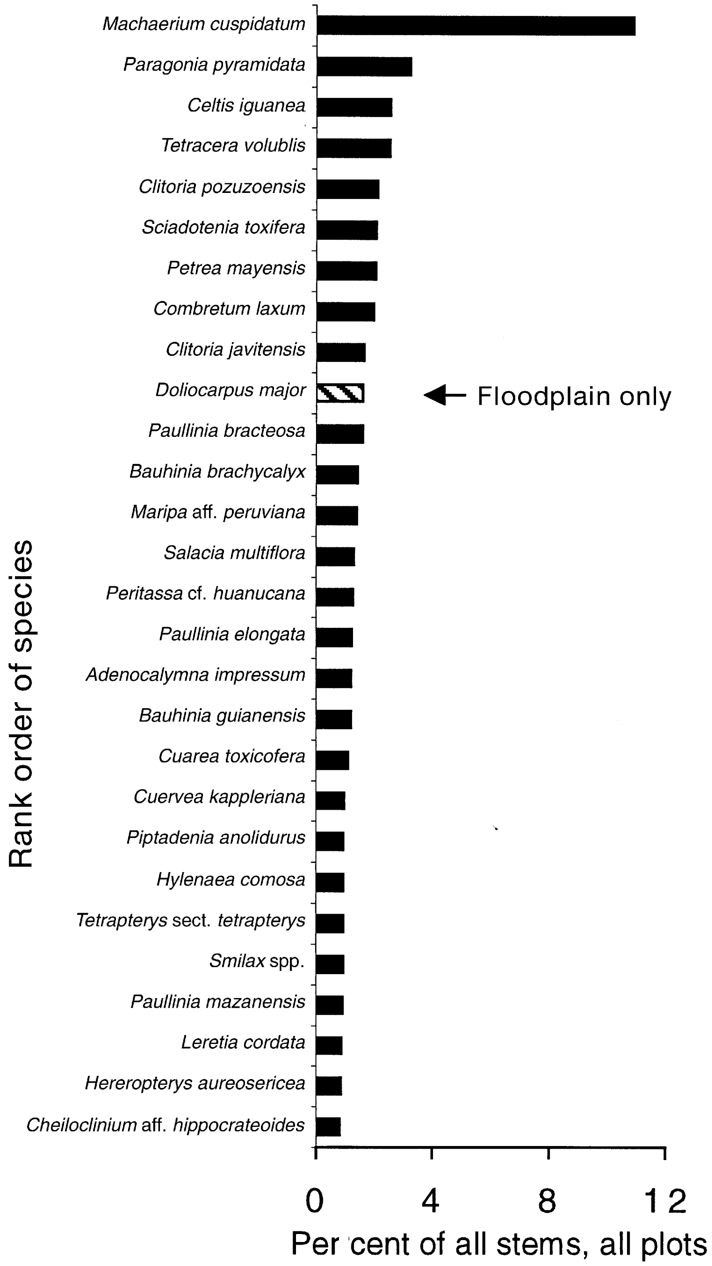

Figure 4. Dominant liana species in 12 plots combined. Species included here contribute to 50% of all stems on all plots combined. Only *Doliocarpus major* is found exclusively in floodplain plots, all other dominant species are found in both plot types (at low frequency in some plots).

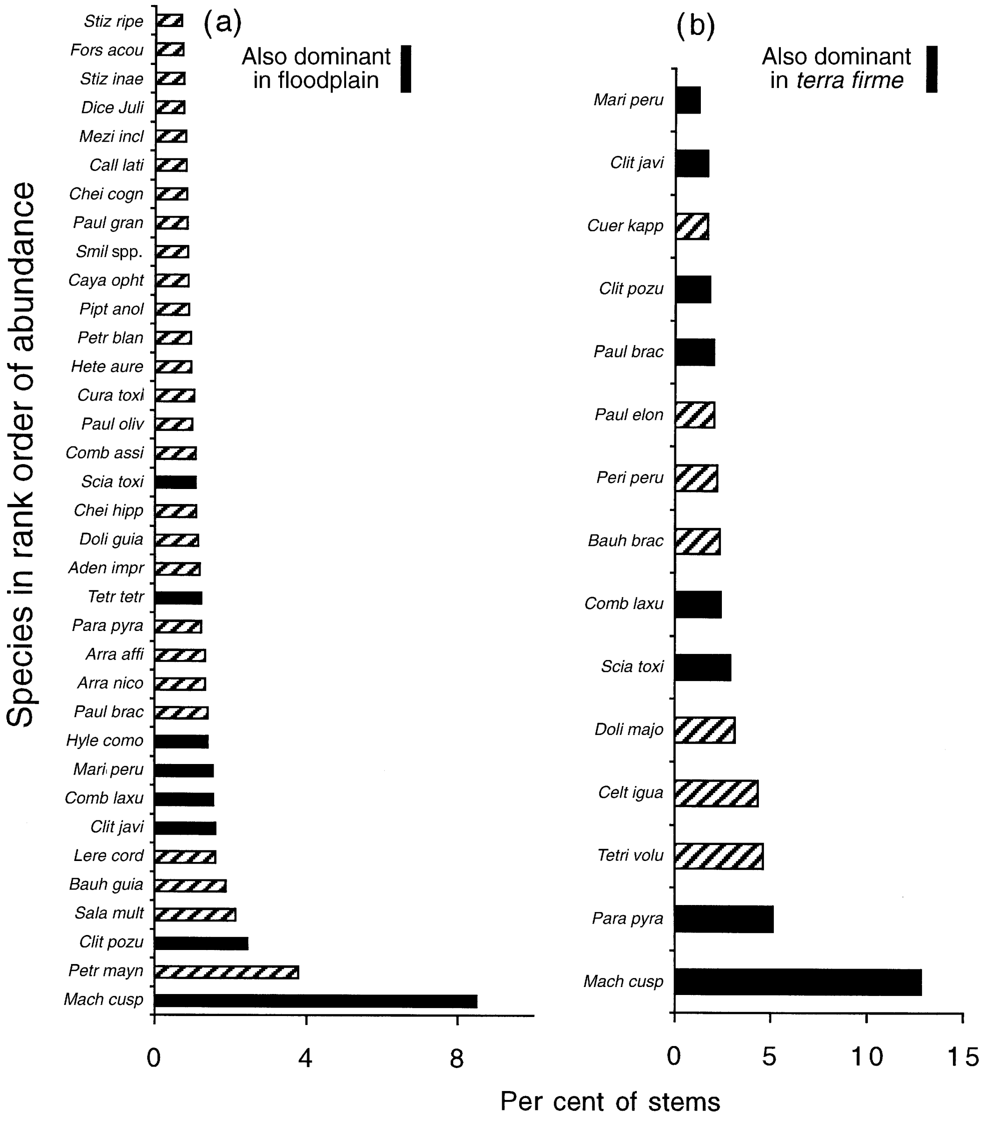

Figure 5. Dominant liana species in *terra firme* and floodplain habitats, each represented by six plots. Species included in each dominance group contribute to 50% of all stems on six combined plots. (a) *Terra firme* habitat dominants include 34 species; eight also are present in the floodplain dominance group. (b) Floodplain habitat dominants include 15 species, eight also are present in the *terra firme* dominants. Genus and species have been abbreviated here to the first four letters of each name. Refer to Table 3 for full names. Species not listed in Table 3 are: Bignoniaceae: *Adenocalymna impressum*, *Arrabidaea nicotianiflora*, *Arrabidaea affinis*, *Callichlamys latifolia*; Sapindaceae: *Paullinia olivacea-paulliniodes*; Malpighiaceae: *Mezia includens*, *Dicella julianii*; Hippocrateaceae: *Cheiloclinium hippocrateoides*; Verbenaceae: *Petrea blanchetiana*.

Floodplain habitats in Yasuní have fewer species contributing to the top 50% of stems than do *terra firme* habitats (Figure 5). Any species with ≥ 14 stems among the six *terra firme* plots were included in the *terra firme* dominants while only species with ≥ 29 stems among the six floodplain plots were included in the floodplain dominants. Twice as many species are included in the *terra firme* dominants as in the floodplain dominants. However, using a criterion by which only species representing ≥ 1% of all stems of a habitat as a dominance group results in similar-sized groups: *terra firme* has 22 species and floodplain has 21. The significant drawback to this latter definition of a dominance group was that floodplain dominants include 500 stems more than the *terra firme* dominants. That these two measures differed underscores the strong influence of the few species that dominated floodplains. The dominance group was larger in *terra firme* habitats, and individual species exerted less influence over rank order. Thus, predictability of dominant species from plot to plot was lower in *terra firme* habitats than in floodplains.

Using coefficient of variation and rank order to define an oligarchy

The 'oligarchy' is defined here as that group of species with consistent influence over the species rank order within a single habitat across a large tract of forest. Coefficient of variation (CV) of species abundance (Figure 6) varied from 42 to 245 in both *terra firme* and floodplain habitats, but the dominant species (Figure 6: dots to the left of the vertical lines) showed a different pattern between the two habitats. The CV of the floodplain dominants was always < 150, indicating relatively consistent contributions to the proportion of stems within each of the six plots. In *terra firme* plots, five or nine of the dominant species (depending on whether 1% or 50% criterion is used) showed a CV > 150. Species with high rank order and high CV were those with high variation from plot to plot in *terra firme* habitats (locally important, regionally less important). The predictability of their contribution to the regional dominants was low. Still, there are many *terra firme* species whose representation was both predictable from plot to plot and abundant enough to contribute to a dominance group. Species with both low CV and high rank order (using the 1% or 50% criterion) were included in the Yasuní liana oligarchy (Table 3). These 38 species collectively represent 54.6% of all liana stems in this study.

DISCUSSION

Species richness

Yasuní and Cuyabeno Reserve to the north are often cited among the richest sites in the world in tree species (Ashton & LaFrankie 1999, de Oliveira & Mori 1999, Romoleroux *et al.* 1997, ter Steege *et al.* 2000, Valencia *et al.* 1994, Vasquez-M. & Phillips 2000). One plot in Cuyabeno (Paz y Miño 1990, reanalysed by Romero-S. 1999) contained 90 liana species ha^{-1} but there are few other sampled plots with which to compare the results. The mean richness here (87.9 ha^{-1}) is in line with the Cuyabeno data, although the Yasuní liana richness ha^{-1} is certainly underestimated (see above).

Gentry (1991*a*) reported a mean species richness of hemi-epiphytes *and* lianas in lowland neotropical sites of 69 species ≥ 2.5 cm diameter in 0.1-ha

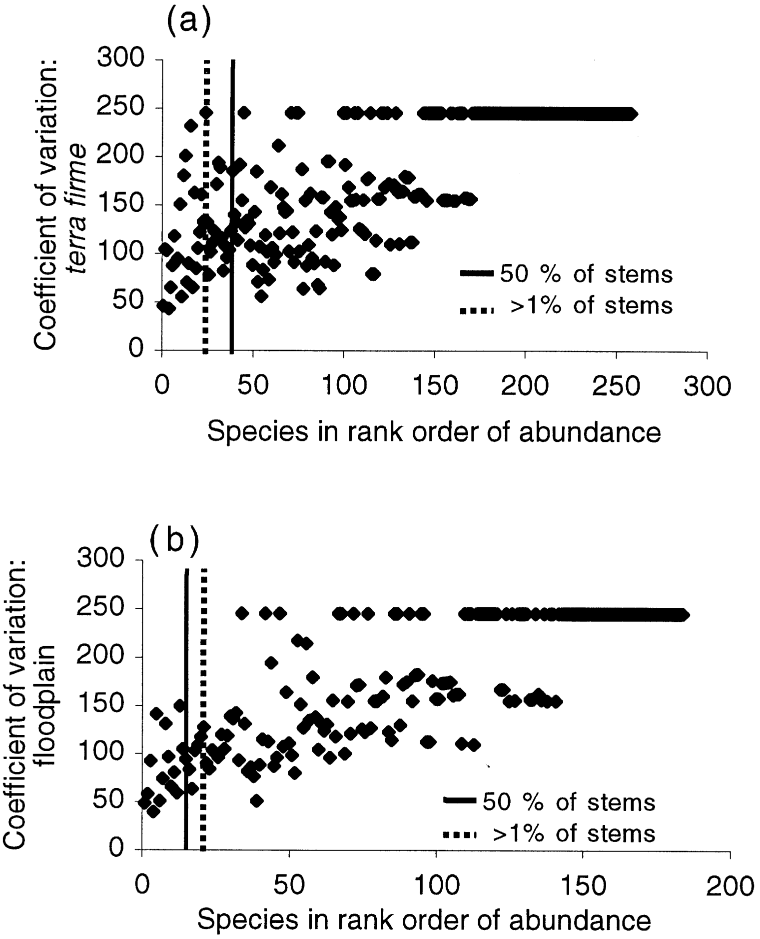

Figure 6. Rank order of all species within each habitat, scored by coefficient of variation (CV). Two dominance groups are indicated: species comprising the top 50% of all stems in the six habitat plots (solid vertical line) and species with a minimum of 1% total abundance in the six habitat plots (dashed vertical line). (a) Dominant *terra firme* species show a wide range of CV; 5–9 species have CV > 150. (b) Dominant floodplain species show a narrower range of CV; all dominant species showing CV ≤ 150.

plots. He estimated that hemi-epiphytes make up one-third of those species. From this estimate, a lianas-only mean for Gentry's 0.1-ha plots was estimated as 46 species, including only stems ≥ 2.5 cm diameter. However, his data for five plots within lowland Ecuador (< 1200 m), have a range of 23–50 lianas per 0.1 ha, with only Jatun Sacha, Ecuador including > 35 species of lianas per 0.1 ha (taxonomic data updated and verified by the author on vouchered specimens). Restricting Yasuní liana data to stems ≥ 2.5 cm diameter and 0.1 ha plots results in 31–50 species of lianas ha^{-1}. Yasuní plots show a higher minimum diversity than the sites sampled by Gentry and, on average, comparable 0.1-ha plots in Yasuní are more diverse than 0.1-ha plots sampled by Gentry in lowland Ecuador. In two 20 × 100-m *terra firme* transects in Yasuní,

Table 3. Oligarchy in floodplain and *terra firme* habitats in Yasuní. A species is listed only if it has a coefficient of variation ≤ 150 *and* it contributes either to the top 50% of all stems for the habitat *or* it contributes an average of ≥1% of stems for plots of the sampled habitat. Species are listed in order of decreasing total abundance within each habitat. Species preceded by * are present in both lists.

Floodplain oligarchy		Terra firme oligarchy	
Fabaceae	*_Machaerium cuspidatum_ Kuhlm. & Hoehne	Fabaceae	*_Machaerium cuspidatum_ Kuhlm. & Hoehne
Bignoniaceae	*_Paragonia pyramidata_ (Rich.) Bureau	Verbenaceae	_Petrea maynensis_ Huber
Dilleniaceae	_Tetracera volubilis_ L.	Fabaceae	*_Clitoria pozuzoensis_ J.F. Macbr.
Ulmaceae	_Celtis iguanaea_ (Jacq.) Sarg.	Hippocrateaceae	_Salacia multiflora_ (Lam.) DC.
Dilleniaceae	_Doliocarpus major_ J.F. Gmel.	Fabaceae	_Bauhinia guianensis_ Aubl.
Menispermaceae	*_Sciadotenia toxifera_ Krukoff & A.C. Sm.	Icacinaceae	_Leretia cordata_
Fabaceae	_Bauhinia brachycalyx_ Ducke	Convolvulaceae	*_Maripa_ aff. _peruviana_ Ooststr.
Combretaceae	*_Combretum laxum_ Jacq.	Fabaceae	*_Clitoria javitensis_ (Kunth) Benth.
Hippocrateaceae	_Peritassa_ aff. _peruviana_ (Miers) A.C. Sm.	Combretaceae	*_Combretum laxum_ Jacq.
Sapindaceae	_Paullinia elongata_ Radlk.	Hippocrateaceae	_Hylenaea comosa_ (Sw.) Miers
Fabaceae	*_Clitoria pozuzoensis_ J.F. Macbr.	Sapindaceae	*_Paullinia bracteosa_ Radlk.
Sapindaceae	*_Paullinia bracteosa_ Radlk.	Bignoniaceae	*_Paragonia pyramidata_ (Rich.) Bureau
Fabaceae	*_Clitoria javitensis_ (Kunth) Benth.	Malpighiaceae	_Tetrapterys_ 'sect. Tetrapterys'
Hippocrateaceae	_Cuervea kappleriana_ (Miq.) A.C. Sm.	Combretaceae	_Combretum assimile/fruticosum_
Convolvulaceae	*_Maripa_ aff. _peruviana_ Ooststr.	Dilleniaceae	_Doliocarpus_ cf. _guianensis_
Rubiaceae	_Uncaria guianensis_ (Aubl.) J.F. Gmel.	Menispermaceae	*_Sciadotenia toxifera_ Krukoff & A.C. Sm.
Menispermaceae	_Chondrodendron tomentosum_ Ruiz & Pav.	Menispermaceae	*_Curarea toxicofera_ (Wedd.) Barneby & Krukoff
Sterculiaceae	_Byttneria catalpifolia_ Jacq.	Hippocrateaceae	_Cheiloclinium cognatum_ (Miers) A.C. Sm.
Menispermaceae	*_Curarea toxicofera_ (Wedd.) Barneby & Krukoff	Smilacaceae	_Smilax_ spp.
Sapindaceae	_Paullinia mazanensis_ J.F. Macbr.	Malpighiaceae	_Heteropterys aureosericea_ Cuatrec.
Fabaceae	*_Piptadenia anolidurus_ Barneby	Fabaceae	*_Piptadenia anolidurus_ Barneby
Sterculiaceae	_Byttneria ancistrodonta_ Mildbr.	Cucurbitaceae	_Cayaponia ophthalmica_ R.E. Schult.
		Sapindaceae	_Paullinia grandifolia_ Benth. ex Radlk.
		Apocynaceae	_Forsteronia acouci_ (Aubl.) A. DC.
		Bignoniaceae	_Stizophyllum inaequilaterum_ Bureau & K. Schum.
		Bignoniaceae	_Stizophyllum riparium_ (Kunth) Sandwith

Nabe-Nielsen reported 12–27 liana species ≥ 2.5 cm diameter per 0.1-ha (Nabe-Nielsen 2001), a lower range than reported here for Yasuní. These differences may be due to contiguous sampling by Nabe-Nielsen versus non-contiguous sampling here. *Terra firme* tree species richness ranges from 188 to 295 species ha^{-1} among plots in Yasuní (Pitman *et al.* 2001). Although some sites in Yasuní may be among the richest known in lianas, not every *terra firme* site in Yasuní is equally species-rich. Yasuní *terra firme* habitats are richer in lianas than most floodplain habitats, in line with surveys of trees and other life-forms in these two habitat types in Amazonia (Campbell 1994, Duque *et al.* 2001, Pitman *et al.* 1999, Romero-S. *et al.* 2001, ter Steege *et al.* 2000).

Machaerium cuspidatum was always among the five most important species in all sampled plots. The demonstration of one liana species with consistent dominance across a large spatial scale invites an analysis of both the biological characteristics of this species and liana surveys in other areas of high species richness to identify other dominants. Preliminary analysis of this dominant (Nabe-Nielsen 2000) suggested that the ability to use both sexual and vegetative reproduction was present in the species and that vegetative reproduction may contribute to its persistence in floodplain habitats. However, the geographic extent of the dominance, the viability of its seeds and seedlings in Yasuní, pollination mechanisms and population genetic differentiation remain unknown for the species.

Machaerium cuspidatum is not the dominant climber in other moist forests in the neotropics. Romero-S. (1999), working at 850 m in the Amazon Basin of Ecuador, reports that *Adelobotrys adscendens* (Sw.) Triana is the most abundant of 137 species among 1085 climber stems in 0.5 ha. In Cuyabeno, Ecuador, the most abundant liana was *Cydista aequinoctialis* (L.) Miers (Paz y Miño 1990 in Romero-S. 1999). Preliminary surveys (3 ha) in Manu National Park, Peru, indicated that *M. cuspidatum* was neither a dominant nor abundant liana on any of the plots sampled (R. Burnham unpubl. data). In Panama, DeWalt *et al.* (2000) found *Maripa panamensis* Hemsl. to be the most abundant species in almost 2000 liana stems (11% of all stems), although it was not the dominant liana in biomass. Pérez-Salicrup *et al.* (2001) reported *Tynanthus schumannianus* (Kuntze) A. H. Gentry as the most abundant liana (8.5%) in a 25-ha area in eastern Bolivia where over 2200 liana stems were censused.

Habitat specialization

The majority of liana species in Yasuní can be categorized as habitat generalists (63%), geographically widespread (100%), and present at moderate population sizes (88.5%). Even so, a large number of species (~25% of those analysed here) were habitat-restricted with moderate to large population sizes. These species may be habitat specialists. Additional sampling can reject this hypothesis simply by documenting their presence in habitats distinct from those found here. The rarity values for lianas in Yasuní are remarkably similar to values reported for trees in Amazonian Peru (Pitman *et al.* 1999, Table 5) where 68% of tree species were widespread and present at moderate population sizes, while 19% of tree species were habitat restricted but with moderate population sizes. Rarity analysis of lianas ≥ 2.5 cm by Romero-S. *et al.* (2001) indicated greater habitat specialization, which can be attributed to a smaller sample size and larger diameter limit than used here.

Relatively large population sizes and wide geographic distributions in liana and tree species may appear surprising in light of popular focus on tropical species and endemism (Myers *et al.* 2000). The results are concordant with those of Valencia *et al.* (2000) on Ecuadorian lianas, who indicated that only 1% of all endemic Ecuadorian vascular plant species were lianas and that only three endemic lianas were known from Yasuní National Park (not one of which was encountered during this study).

Species dominance

The small size of the liana oligarchy (38 species) in this diverse flora (∼500 species of lianas) indicates that some consistency in dominance throughout Yasuní does exist. DeWalt *et al.* (2000) found even fewer dominant species in central Panama: only five species contribute 50% of all liana stems. Based on the range of values encountered during this census of Yasuní lianas, if a new liana plot were to be established in Yasuní, it is predicted that stems of the most abundant species would contribute < 14% to all *terra firme* stems or < 19% to all floodplain stems. The 20 most abundant lianas are predicted to contribute > 35% of all stems on *terra firme* plots while they would contribute > 50% on floodplain plots. At least the 10 most important species should be found in the oligarchy list in Table 3. The dominant species are very likely to be among the species represented at high abundance in each habitat, however neither absolute abundance nor the exact rank order of these species on specific 1-ha plots is predictable. Lianas may be more subject to spatially variable population sizes than tree species because of the capacity of lianas to regenerate vegetatively from fallen branches or ground-touching stems (Gentry 1991*b*). Vegetative reproduction in a favourable environment would produce a relatively dense local population of a species that is sparsely distributed elsewhere.

Gentry (1991*b*) proposed that individual lianas (ramets) may be able to persist over many hundreds of years and only infrequently reproduce sexually, indicating that we should expect broad spatial fluctuations in population densities, even among the dominants. *Machaerium cuspidatum* vigorously spreads vegetatively (*pers. obs.*), thus even a large population may include little genetic variability. Pathogens and disease can exterminate such a population and may be the cause for the more restricted geographic dominance than seen in the dominant palm species of western Amazonia. Very little is known about the population genetic structure of liana species that resprout (Caballé 1977, 1994; Peñalosa 1984) versus those that do not (Foster & Sork 1997).

This study represents one of the largest censuses of exclusively neotropical lianas (DeWalt *et al.* 2000, Laurance *et al.* 2001, Paz y Miño 1990, Putz 1984, Schnitzer 2001), yet the area over which the plots were sampled is still small. This study included five times more liana stems than the 25 0.1-ha plot study of Yasuní trees and lianas by Romero-S. *et al.* (2001) and seven times more liana stems than the two 0.2-ha Yasuní study by Nabe-Nielsen (2001). Their results on rarity and habitat differentiation in liana communities are broadly congruent with those presented here and an outline of the liana community of Yasuní is emerging. The population structure and basic reproductive biology of the dominants, as well as the complete geographic range of liana species in Yasuní, remain to be clarified.

CONCLUSIONS

The liana community of Yasuní is species-rich, with marked heterogeneity in species composition, even within a single habitat type. While the majority of species are not habitat-restricted, some species do indicate habitat preference. *Machaerium cuspidatum* is the most common liana in Yasuní with > 10% of all stems accounted for by this species, and it is the most uniformly distributed of all species encountered. Using CV and dominance rank to identify a liana oligarchy in the broad landscape of Yasuní provided a means for comparison with areas in which time-limited surveys have been made (Alverson *et al.* 2000, Gentry 1991*a*). Research focused on individual species of the oligarchy will improve our knowledge of the role of vegetative reproduction, sexual reproduction and dispersal biology in the population structure of high-diversity forests. Additional sampling of lianas should be focused on more restricted habitats in Yasuní, such as permanently inundated swamp habitats, margins of floodplain channels, and habitats disturbed by a variety of human activities (road building, oil extraction, cultivation). Learning to recognize the 38 liana species included in the oligarchy for both habitats is a simple task compared with learning the ~500 species likely to be encountered within Yasuní. This census indicates that ~50% of all stems encountered would be represented by these 38 species.

The results presented here, in the form of a list of the dominant liana species over a large area, are recommended as a starting point in evaluation of adjacent areas that have been subject to human disturbance. Significant deviation from the listed oligarchy found at a newly sampled *terra firme* or floodplain plot may indicate substantial human or natural disturbance. However, comparison with adjacent intact forests is important, because the dominant lianas in the study by Romero-S. *et al.* (2001) included only 50% overlap with the oligarchy species identified here. This difference is due partly to differences in methodology and taxonomy, but also demonstrates the high degree of variability to be expected in each lowland tropical plot investigated.

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