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Alpha and beta diversity of Lianas in Yasuní, Ecuador

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Abstract

Stems of 4348 lianas from 12 subsampled 1 ha plots in Yasuní, Ecuador represented more than 311 species of climbing woody plants. The plots (each 0.2 ha in area), which individually included up to 106 species among 314 stems, were established in the Huaorani Ethnic Reserve and Yasuní National Park and represent terra firme and floodplain habitats. Yasuní is one of the richest areas sampled for liana diversity in the neotropics. A relatively small group of species (~38) comprise the dominants in this forest, as defined by species contributing consistently to 50% of all stems to samples from either habitat. Distance-related diversity (i.e., beta) is low across both spatially adjacent and distant plots. Floodplain habitats show a slightly higher decay of similarity with distance than either terra firme habitats or cross-habitat comparisons. Cross-habitat comparisons are significantly less similar than same-habitat comparisons at all distances. Habitat-related beta diversity probably contributes to total richness in Yasuní although abundant liana species in Yasuní rarely show absolute restriction to one habitat or the other. A comparison of these data to other sampled sites in the neotropics highlights the problems inherent in comparisons among areas sampled by different methods.

Keywords: Climbers; Liana sampling; Species richness; Amazon; Dominance; Endemism; Plant communities

1. Introduction

The number of species coexisting in a single habitat or in one biogeographic region has been a source of fascination for naturalists for over 125 years (Wallace, 1878; Wright, 2002). This interest continues today with a theoretical focus on how species are packed into habitats and regions (Harte et al., 1999a,b; Plotkin et al., 2000; Hubbell, 2001) and how biodiversity can be maintained in the face of continuing anthropogenic disturbance (Phillips, 1997; Bawa and Dayanandan, 1998; Levitus et al., 2001; Laurance et al., 2002; Phillips et al., 2002).

The maximum number of tree species that can coexist in a $100\,\mathrm{m} \times 100\,\mathrm{m}$ area (1 ha) has been a holy grail of plant systematists and ecologists working in the neotropics. A newly surveyed and collected hectare inevitably raises the question of just how many tree species were encountered ≥ 10 cm diameter at 1.3 m above the ground (dbh) (e.g., Valencia et al., 1994; De Oliveira and Mori, 1999; Duque et al., 2002). Within the neotropics, compilation of many surveyed hectares suggests that the equatorial lowlands, in areas of high rainfall and moderate soil fertility (usually within 100–200 km of the base of the Andes Mountains) harbor more tree species than any other area (Gentry, 1988; Valencia et al., 1994; Clinebell et al., 1995; De Oliveira and Mori, 1999). Comparisons are made to other hectares elsewhere and tentative proposals are tendered to explain the differences among regions (Gentry, 1988; Phillips et al., 1994; Ter Steege et al., 2000; Condit et al., 2002). Yet we still have no firm idea of exactly where the highest diversity in tree

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species is, or why that place holds the record. The importance of characterizing continental-scale patterns in plant richness derives from long open questions regarding Pleistocene refugia (Colinvaux et al., 2002; Bush et al., 2002), centers of endemism (Young et al., 2002; Valencia et al., 2000), and recently designated ''hotspot conservation areas'' (Myers, 1990; Myers et al., 2000). Pinpointing such high diversity areas should invoke scientific and conservation interest and contribute to the demarcation of large tracts of land for special protection.

Although reporting the number of species in a given area is the quickest and most common means to compare diversity among areas, it is not a universally accepted approach. There are strong arguments for the protection of areas that include the maximum amount of morphological or genetic diversity, rather than species diversity (Humphries et al., 1995; Faith, 1996; Sechrest et al., 2002). Morphological or nucleotide diversity can be inferred from phylogenetic trees, with the degree of difference observed between any two taxa serving as a measure of phylogenetic diversity. For example, geographic regions that include 25 species of *Paullinia* (family Sapindaceae) would not represent as much phylogenetic diversity as regions that include 15 species of *Paullinia* in addition to a single species of each of 10 other genera within Sapindaceae, even though species richness counts would declare these regions equivalent. Measures of phylogenetic diversity have been proposed (Linder, 1995; Faith, 1992, 2002) but details of how values should be calculated and applied are far from standardized. The obvious and immediate drawback to these reasonable measures is that without well supported and widely accepted phylogenies, conservation priorities are difficult to establish.

In tropical forests, lianas (woody climbers) add both physical structure and resources to the forest. Their flowers and fruits provide nutrients to a wide variety of invertebrates and vertebrates and their leaves are used as oviposit hosts for lepidopterans and resources for other forest insects (DeVries, 1987; Ødegaard, 2000). Their tangled stems accumulate leaf litter that provides habitat for invertebrates as well as the birds that feed on those invertebrates (Greenberg, 1987). Even the physical structure created by lianas via their stems crossing from tree to tree is used as perches and walkways for vertebrates whose lives may be spent almost entirely in the canopy. The importance of lianas to forest structure and dynamics cannot be overstated, yet we have only a vague idea of the liana composition of any large area of forest in the neotropics, nor the role that any one species of liana plays in those forests.

Lianas contribute roughly 20% of the woody plant species in surveys of lowland, neotropical forests (Bullock, 1985; Gentry, 1991; Schnitzer and Bongers, 2002; Burnham, 1997, 2002). With such high relative species importance, increasing interest has been focused on the role of lianas in tropical forest dynamics (Putz and Chai, 1987; Laurance et al., 2001; Perez-Salicrup et al., 2001a; Phillips et al., 2002). Still, lianas contribute relatively little biomass to the majority of forests outside of patches of ''liana forest'', which are both relatively small in area and exceedingly difficult to study (Balee and Campbell, 1990; Perez-Salicrup et al., 2001b). In the few areas where total contribution of lianas to biomass has been estimated, their contribution in primary forest is on the order of 3–8% of total biomass, whereas in disturbed or low-stature forests the contribution is variable, and generally lianas contribute twice the biomass proportion as in undisturbed forest (Putz, 1983; Gerwing and Farias, 2000; Restom and Nepstad, 2001).

Species turnover across large geographic areas or between habitats represents ''beta diversity''. Beta diversity has been the focus of theories relating species-area and richness to habitat and distance (Tuomisto et al., 1995, 2003; Harte et al., 1999a,b; Hubbell, 2001; Arita and Rodríguez, 2002; Balvanera et al., 2002; Condit et al., 2002). It is a central theme of theoretical ideas on the origin and maintenance of species diversity in tropical areas as well as on the application of those theories to conservation biology, where preserved area size and habitat heterogeneity are, in part, the basis for decision making (Freemark and Merriam, 1986). Studies addressing data from wet and dry tropical forests have reported estimates of beta diversity with virtually no consensus on the importance of habitat heterogeneity or distance on the maximum species richness of an area. In dry forests of Mexico, where insolation is clearly an important ecological factor, as much as 42% of the beta diversity of trees was attributed to insolation (Balvanera et al., 2002). However, in comparisons over thousands of kilometers in South America, distance appears to have little effect on beta diversity (Condit et al., 2002; but see Tuomisto et al., 2003). Clearly, the geographic distribution of a species may interact with habitat distribution to create a mosaic that places similar communities in similar habitats, separated by very wide geographic distances (Arita and Rodríguez, 2002). How lianas fit into this puzzle of tropical beta diversity is not clear, but because of the high propensity for lianas to vegetatively regenerate, it stands to reason that lianas might show a distance effect in patterns of beta diversity.

In managed or damaged ecosystems, lianas can overtop trees, causing ''arrested'' succession and promoting fast-growing weedy tree species over slow-growing tree species more typical of undisturbed forests (Schnitzer and Carson, 2001). In areas where timber extraction dictates some liana management, liana cutting decreases biodiversity (Gerwing and Vidal, 2002), but the species of lianas that remain or regenerate after cutting have not yet been classified as either invaders or primary forest species. Because liana cutting does result in abundant resprouting (Gerwing and Vidal, 2002), it is important not only to monitor changes in stem density, but also in species composition. Liana cutting is a labor-intensive management practice (Vidal et al., 1997; Perez-Salicrup et al., 2001a), thus the silvicultural benefits of liana cutting must be weighed against the biodiversity loss and other deleterious effects on forests. Because lianas are not phylogenetically unified (derived in the neotropics from >80 angiosperm families as well as one gymnosperm: data from the Field Museum of Natural History Rapid Reference Collection), it is logical to propose that certain species will cause agricultural and silvicultural problems, while others will be less successful in the high light and high disturbance regime of human-managed areas.

Recent investigations indicate that some liana species respond strongly to elevated CO_2 (Sasek and Strain, 1988; Condon et al., 1992; Granados and Körner, 2002). Liana response appears to level off at very high CO_2 levels, but the unique combination of increased growth rates of lianas under elevated CO_2 and increasingly disturbed forests due to human intervention is a situation requiring attention. The assumption that disturbed forests ultimately can recover and regain biodiversity and ecosystem function, given sufficient time, may not be warranted if arrested succession takes over under CO_2 conditions not experienced previously. As with any biological process, the differences among species responses must be evaluated because management practices that treat all species of lianas as equivalent are unlikely to be successful.

In spite of the pressure to make management and conservation decisions based on limited data, the species composition of liana communities remains the key element to understanding the implications of climate change and human disturbance on lianas in modern tropical forests. Liana surveys pioneered by Alwyn Gentry provide species composition in small undisturbed plots (0.1 ha) scattered throughout the neotropics and worldwide (Gentry, 1991; Phillips and Miller, 2002). The Gentry data set, although limited in scope and taxonomic resolution for lianas, is our current best estimate for phytogeographic patterns of lianas in the neotropics. While the density of lianas alone helps us describe the physical structure of forests, without species identifications we cannot approach the role of any one species, its potential for being invasive, and the implications of its loss or spread.

This paper reports the results of a study of liana species composition, distribution and diversity in 12 spatially distinct ha of intact primary forest in western Amazonia (Yasuní, Ecuador). It represents one of the first reports of liana beta diversity in the western Amazon basin. The questions addressed here are: How species rich are lianas in 1 ha plots in Yasuní? Given limited sampling, is there consistency in the estimates of species richness? Are habitats similar in their species composition, particularly of the dominant species? Do liana species show restriction to specific habitats? Does habitat or distance influence the similarity between any two sampled hectares? Is Yasuní more diverse than other sampled areas in Amazonia?

2. Materials and methods

2.1. Site description and sampling methodology

Yasuní National Park and the Huaorani Ethnic Reserve in eastern Ecuador comprise a combined area of about 1.6 million ha (Pitman, 2000), referred to

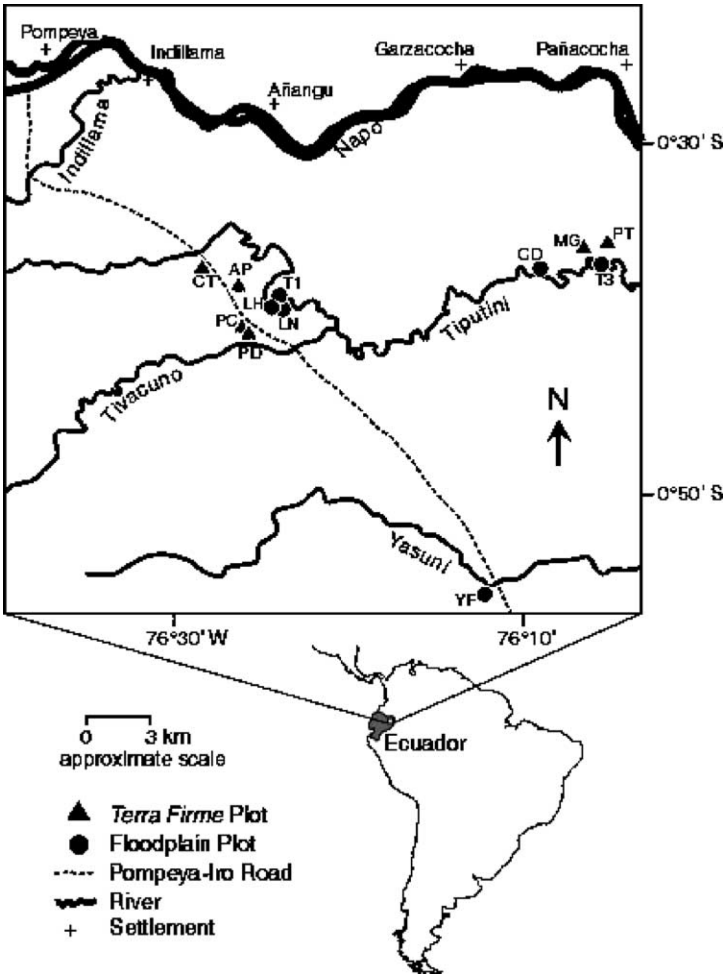

Fig. 1. Location of study area and 12 liana plots in two different habitats in Yasuní, Ecuador.

here as 'Yasuní'. Twelve one hectare (1 ha) plots were established in Yasuní: six in terra firme habitat and six in floodplain habitat. Plots are located in three regions within the park as indicated in Fig. 1. In each plot five parallel 4 m × 100 m transects (with 16 m between transects) were sampled, in which all lianas $\geq$1 cm diameter were located, measured for diameter, identified, and vouchers collected if field identification was not possible. Stems were included in the census if they were rooted in or crossed the sampled area $\leq$2 m from the ground. Care was taken to follow stems to their root to avoid counting any individual more than once. Diameter measurements were made close to ground level, above any basal swelling or nodal enlargements of the stems. Vouchers are deposited at the National Herbarium of Ecuador (QCNE), the University of Michigan (MICH), and The Field Museum of Natural History (F). Specimens have been sorted and identified to species-level categories for 93% of all stems counted, with the remaining 7% unidentified.

An analysis of completely sampled hectare plots (unpublished data) indicates that the total species richness of a hectare sampled by the method I used misses less than 20% additional species. Therefore, the species richness numbers are absolute minimum numbers of species/ha^{-1}, but are deemed comparable to other surveys using the same diameter limits. Density of stems/ha^{-1} is overestimated by this sampling method if density is simply multiplied by five. Density measures reported here should only be compared with 1 ha plots in which each stem has been followed to its rooting position, even if outside the sampled area.

Floodplain hectares are generally within about 100 m of the river floodplain of the Tiputini or Yasuní Rivers (Fig. 1). These habitats are flooded 2–3 times per year, often to a depth of 2 m. Floodwaters can remain in the floodplain for up to 2 weeks (pers. obs.), but for the majority of the year, these areas do not contain standing water. Terra firme habitats are areas that are never inundated by high river levels, and may include hills and flat areas, further from the river floodplains. Comparative soil analyses have been carried out in the context of large-scale surveys of biodiversity of the western Amazon Basin (Tuomisto et al., 2003; supplementary data), but Ecuadorian sites tend to cluster closely, relative to the scale of differences seen over the whole basin. Within Yasuní, the available data from Pitman (2000) classified terra firme habitat soils as Inceptisols. More detailed analysis of the physical attributes of each habitat in Yasuní is needed.

2.2. Data analysis

Average species richness (alpha diversity) and average density of lianas on 1 ha plots in Yasuní were calculated (Burnham, 2002). Average proportional abundance per plot of the 10 most common species of lianas in Yasuní is summarized in Table 1, which also shows average density per habitat type, and the significance of any differences between habitats. Comparisons among all 66 pairwise combinations of plots sampled in Yasuní were made using Sorenson's index of diversity, which measures the proportion of species shared between any two plots. The index weights species equally, rather than being influenced by frequency measures. The decay of the index over distance and between habitats was used as a preliminary measure of beta diversity. No correction was made for comparisons between hectares with different species richness. Jaccard similarity indices also were calculated for all comparisons, but because the results were always parallel to the Sorenson's index and their interpretation is slightly less straightforward (Vellend, 2001), they are not reported here. Similarity indices were calculated for both the full data set of 311 species and for a subset of the data, which included only species that comprise the dominants in Yasuní.

Literature was compiled on surveys of lianas in the neotropics in which stem density and species richness are reported for the majority of stems. The available liana compositional data were compared to data from Yasuní for the dual purposes of: (1) evaluating Yasuní as a site of high liana species richness and (2) illustrating the variety of methods and approaches that have been taken in sampling and reporting of liana density and diversity. Some studies were excluded from comparison because methodologies or data reported could not be compared with the data gathered in Yasuní.

Table 1
Ten most abundant lianas ($\geq$1 cm diameter) on twelve 1 ha plots, Yasuní, Ecuador

Species (family)	Average percentage abundance			Habitat differences, *P*-value
	All plots	Terra firme	Floodplain	
Machaerium cuspidatum (Fabaceae)	10.9	8.23	13.29	0.076
Paragonia pyramidata (Bignoniaceae)[a]	3.22	1.17	5.05	0.031[b]
Tetracera volubilis (Dilleniaceae)[a]	2.65	0.39	4.66	0.052
Celtis iguanea (Ulmaceae)[a]	2.53	0.63	4.23	0.007[b]
Clitoria pozuzoensis (Fabaceae)	2.09	2.34	1.87	0.565
Sciadotenia toxifera (Menispermaceae)	2.05	1.02	2.96	0.02[b]
Petrea maynensis (Verbenaceae)	2.02	4.04	0.22	0.053
Combretum laxum (Combretaceae)[a]	1.96	1.46	2.40	0.252
Clitoria javitensis (Fabaceae)	1.63	1.51	1.74	0.953
Doliocarpus major (Dilleniaceae)[a]	1.59	0	3.01	0.143

[a] These species are distributed at least as far north as Panama.

[b] Significant differences are found between proportional abundances for different hectares.

3. Results

3.1. Yasuní alpha diversity and dominance

Species richness of lianas in 1 ha plots (based on subsamples) ranged from 62 to 109 species (mean = 88 spp.). Species richness values exclude all stems whose identities have not yet been determined to a species-level category, and represent an estimated decrease of about 2.5% of the species richness per plot, if all censused specimens had been identified. Species richness on terra firme plots was significantly higher than on floodplain plots with average richness of 98 and 77 species, respectively (t-test, $P < 0.002$). Liana species richness for the twelve plots combined was 311.

Collections of lianas made by the author and other botanists throughout Yasuní indicate a total richness for the Yasuní area of >450 liana species (Burnham, 2002). This Yasuní liana catalog includes only climbers originally rooted as seedlings in the ground that maintain a connection to the ground throughout their life. Both woody and herbaceous species are included, but members of the Araceae, Marcgraviaceae, and Clusiaceae are excluded because of the mix of habits (hemi-epiphytes, epiphytes, lianas) within these families and the difficulty in measuring stem diameters in some individuals. Assuming that liana collections represent an equivalent level of sampling effort as that for trees, lianas total roughly 20% of the known woody flora $\geq$1 cm dbh from Yasuní, which has been estimated to include ca. 2000 species of trees (G. Villa, N. Pitman, pers. comm., November 2002). In Ecuador, 11% (1686 spp.) of the catalogued flora is classified as ‘lianas and vines’ by Jørgensen and León-Yánez (1999). Excluding all species listed as occurring only in the highlands trims the list to 545 species, which may include some species that occur only west of Yasuní, as covered here (species lists available from the author).

A total of 38 species of lianas are dominant across Yasuní, as measured by a contribution to the top 50% of all stems counted in either habitat (details of criteria used for defining the dominants are given in Burnham, 2002). These 38 species represent the Yasuní oligarchy among lianas (oligarchy as used by Pitman et al., 2001). Ten species are present as dominants in both habitat types (*Machaerium cuspidatum*, *Paragonia pyramidata*, *Sciadotenia toxifera*, *Combretum laxum*, *Paullinia bracteosa*, *Clitoria pozuzoensis*, *Clitoria javitensis*, *Maripa* aff. *peruviana*, *Curarea toxicofera*, and *Piptadenia anolidurus*). Habitat preference by some members of the oligarchy is evident, with six species found only in one of the two habitats (floodplain only: *Doliocarpus major*, *Uncaria guianensis*, *Byttneria ancistrodonta*, *Byttneria catalpifolia*; terra firme only: *Stizophyllum inaequilaterum*, *Stizophyllum riparium*), while the remaining species are found in both habitats, even when not abundant in one habitat. These results suggest a moderate level of habitat preference (although little habitat specificity) among oligarchic liana species in Yasuní.

M. cuspidatum Kuhlm. and Hoehne (Fabaceae) represents the most abundant liana species based on numbers of stems averaged over all sampled plots in Yasuní. *M. cuspidatum* represents 10.9% of all stems sampled but is slightly less abundant on terra firme plots (mean = 8.2% of stems ha^{-1}), when compared to floodplain plots (mean = 13.3% of stems ha^{-1}). These differences are not statistically significant (arcsine square root transformations applied, t-test, $P = 0.08$). *M. cuspidatum* is the most abundant species on eight of the 12 sampled plots, while *Petraea maynensis* is most abundant on two plots. The top 10 liana species in stem abundance on all plots are listed in Table 1. Three species within the top 10 most common lianas show significant difference in their average abundances between habitats. *P. pyramidata* (Bignoniaceae), *Celtis iguanea* (Ulmaceae) and *S. toxifera* (Menispermaceae) are all significantly more common in floodplain than in terra firme habitats. The 10 most abundant lianas in Yasuní (Table 1) are distributed with varying degrees of breadth across the neotropics. All are found in Peru (Brako and Zarucchi, 1993) and half are also found as far north as Panama (distribution from TROPICOS data base, Missouri Botanical Garden).

M. cuspidatum is represented by many small stems across all plots (Fig. 2). This distribution appears to reflect the abundant regeneration from latent axillary buds (pers. obs.) present in severed or fallen stems. Small stems may be derived from seedlings, but there have been few collections or observations of fallen fruits or germinating seeds and very few vouchered fertile specimens have been collected throughout Yasuní, given the abundance of the species (Burnham,

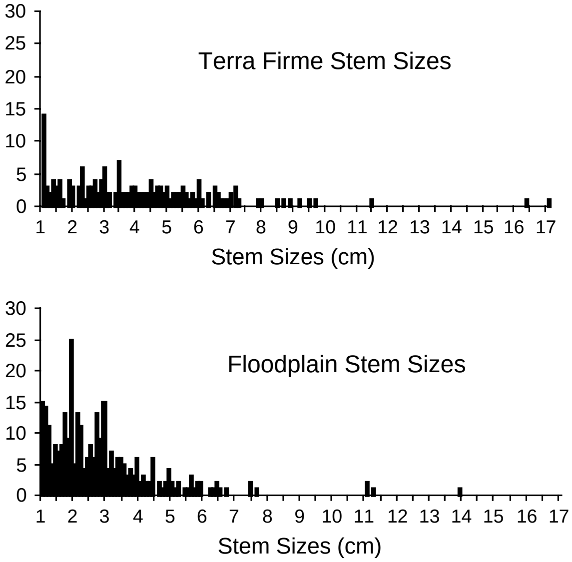

Fig. 2. Stem size distribution of all stems of *M. cuspidatum* in 12 plots in Yasuní, Ecuador. Top panel shows only terra firme stems from six plots while lower panel shows only floodplain stems from six plots.

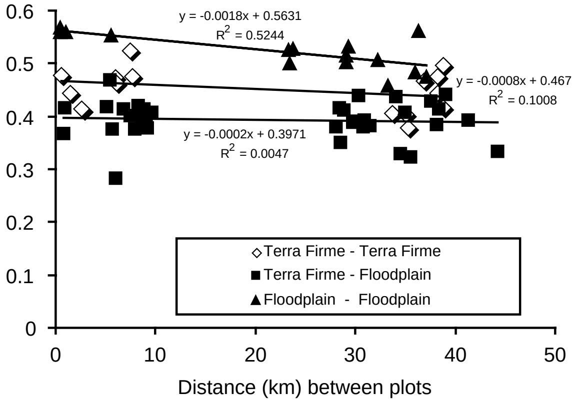

Fig. 3. Effect of distance and habitat on liana composition in comparisons between plots in Yasuní National Park, Ecuador. Sorenson's similarity index based on presence or absence of species on plots.

unpublished data; V. Persson, pers. comm., September 2002). Stems as large as 17 cm diameter were encountered during plot censuses, and stems 7–8 cm diameter are regularly encountered in the forest during random surveys of areas beyond the sampled hectares. For this species, the pattern of size distribution relative to habitat shows that of the 50 largest stems (each $\geq$6 cm), 35 are from terra firme habitats. In addition, a significantly larger proportion of small stems ($\leq$2.5 cm diameter) are found in floodplain habitats than in terra firme habitats (arcsine square root transformations applied, *t*-test, $P \ll 0.01$, Fig. 2).

3.2. Beta diversity of lianas in Yasuní

The Sorenson's index (Fig. 3) indicates only a slight negative correlation between distance and compositional similarity between plots. First, among all plots, very little difference in species composition is evident across 50 km (slope $= -0.0005$, $r^2 = 0.02$, $P = 0.30$). Second, when habitats are analyzed separately, little difference is detected in closely-spaced versus widely-spaced plot comparisons. In terra firme-to-terra firme plots comparisons, similarity is not significantly higher when the plots are closely spaced than when plots are up to 50 km apart (slope $= -0.0008$, $r^2 = 0.10$, $P = 0.25$). In cross-habitat comparisons, there is also no higher similarity between plots located close to one another than those at large distances (terra firme-to-floodplain comparisons, slope $= -0.0002$, $r^2 = 0.005$, $P = 0.69$). Floodplain-to-floodplain comparisons do indicate a decay in similarity over distance does occur (slope $= -0.0018$, $r^2 = 0.52$, $P = 0.002$), even though that decay is fairly small. Jaccard's index of similarity, which has been used in some other analyses of tropical diversity (Balvanera et al., 2002; Tuomisto et al., 2003), shows parallel results and is not reported here.

A comparison of cross-habitat similarities with within-habitat similarities is used here to evaluate habitat-related beta diversity. When cross-habitat comparisons are made for both complete species lists and oligarchy-only species lists, mean similarities are lower than for within-habitat comparisons (Table 2 and Fig. 3). Floodplain species composition shows a higher degree of similarity from plot to plot than terra firme species compositions show to one another. Significant differences are found among all mean similarity values for these comparisons when all species are included. When only dominants are included in the comparisons, terra firme and floodplains are comparable in plot similatity but cross-habitat comparisons are significantly lower than either terra firme or floodplain comparisons (Table 2). The difference between dominant and full species list comparisons reflects the

Table 2
Mean similarities of habitat comparisons using Sorenson's coefficient of similarity[a]

Comparison between plots from habitats:	All taxa mean Sorenson's similarity and range	Oligarchy-only mean Sorenson's similarity and range
Floodplain × floodplain	0.52 (0.46–0.57)	0.79 (0.71–0.88)
Terra firme × terra firme	0.45 (0.40–0.52)	0.78 (0.67–0.86)
Terra firm × floodplain	0.39 (0.28–0.44)	0.67 (0.50–0.79)

[a] Mean similarities are shown for: (1) all species comparisons and (2) only dominant species comparisons. Means are compared using t-tests and all comparisons show significantly different mean values ($P > 0.01$), except oligarchy-only floodplain × floodplain means compared to terra firme × terra firme means.

far higher species richness of terra firme habitats as a group. Values obtained using the Jaccard index are parallel to those shown and are not presented here.

4. Discussion

Species richness of lianas in lowland forests of eastern Ecuador surpasses or rivals the richness in any other neotropical area sampled. Liana species richness across Yasuní is variable, with single plots including from 62 to 109 species each. Liana species richness is higher in terra firme habitats than floodplains, although stem density is not different. Only 10 liana species are dominant on both floodplain and terra firme hectare plots, among the 38 oligarchy species, indicating that liana species do demonstrate some habitat preference in Yasuní. Strict liana restriction to habitat is suggested, thus far, in only six species among the oligarchy lianas.

Beta diversity of lianas in Yasuní is similar over short and long distances, with the exception of the floodplain habitats. Floodplains show slight, but significantly greater similarity to one another at short distances than over long distances. These data suggest that the influence of beta diversity over distances up to 50 km does not contribute strongly to the high diversity of lianas in Yasuní. However, floodplain plots are more similar, as a group, than are terra firme plots, a result that indicates that at least some of the diversity in Yasuní can be attributed to habitat differences (beta diversity). This result pertains only to the full data set of 311 species, not to the species that comprise the oligarchy in Yasuní (Table 2). The difference between the pattern of similarity among the dominants and that among the full species list reflects the high diversity of terra firme habitats in Yasuní. When the long tail of diversity is removed (by evaluating only oligarchy) this difference between levels of similarity within-habitats disappears. These results also may indicate that beta diversity patterns can be informed only generally by using common species, although these results should be verified with additional data sets.

A much larger number of liana species contribute to the terra firme flora than to the floodplain flora (254 versus 179, respectively), and terra firme habitat represents an estimated 80% of all land area in the 1.6 million ha of Yasuní (Pitman, 2000), so the effect of total area and total species pool on these statistics must be taken into consideration. Ecuadorian tree communities of Yasuní, compared over similar distances, show similar levels of beta diversity (as measured by Sorenson's index) to those shown here (Condit et al., 2002; Fig. 3). However, the comparisons of Condit and colleagues were made among samples from a single habitat: terra firme. The results shown here indicate that habitat differences do contribute to liana species richness in Yasuní, by preferential representation of some relatively common species largely to floodplain habitats (e.g., *D. major*, *B. catalpifolia*, *U. guianensis*).

Species richness of lianas in Yasuní appears to be at least as high as in other comparably sampled areas in Amazonia, if not higher. Recent studies summarized in Table 3 suggest that both Yasuní and Cuyabeno, Ecuador, are richer than other areas sampled, although analysis is hampered by the difference in sampling and reporting methodology among studies. This conclusion is in accord with data derived from very small samples made by Gentry (Gentry, 1991; Phillips and Miller, 2002). However, species richness of lianas in forests of Para, Brazil (Gerwing and Vidal, 2002) is impressive. Both liana density and liana richness are

Table 3
Neotropical lowland liana censuses: although some plots were established for both tree and liana censuses, only liana statistics are reported here

Reference	Geographic region	Plot dimensions (total area sampled)	Diameter limit and stem density	Number of spp. lianas
Balee and Campbell (1990)	Xingu river, Brazil	Two 1 ha plots (20,000 m^2)	≥10 cm dbh, 9 liana stems >10 cm dbh	3 spp. ≥ 10 cm dbh; non-quantitative survey of lianas includes 59 spp. (with 7 Araceae); 30 spp. (with 2 Araceae)
Burnham (this study)	Yasuní, Ecuador	Twelve 1 ha plots sampled in five 4 m × 100 m transects (24,000 m^2)	≥1 cm: 362 stems/0.2 ha; ≥2 cm: 250 stems/0.2 ha	88 spp. (≥1 cm)/ha (0.2 ha sampled); 69 spp. (≥2 cm)/ha (0.2 ha sampled)
Gentry (1991) and Missouri Botanical Garden	Jatun Sacha, Ecuador	2 m × 500 m transects (1000 m^2)	≥2.5 cm dbh; 83 stems/1000 m^2	50 spp./0.1 ha
Gerwing and Farias (2000)	Paragominas, Para, Brazil	Thirty 0.01 ha plots (3000 m^2)	>2 m tall; 40 stems/0.01 ha	78 spp. = all plots; 9.4–21.7 spp./plot; 31–66 spp. in 0.1 ha
Gerwing and Vidal (2002)	Paragominas, Para, Brazil	2 m × 1000 m plot (2000 m^2)	≥1 cm dbh; 2495 stems/ha	80 spp./0.2 ha
Laurance et al. (2001)	Manaus, Brazil	Three 10 ha fragments: 24 plots each (12 edge and 12 interior); plots 400 m^2 (28,800 m^2)	≥2 cm dbh; 1023 individuals, 24 plots, all fragments	83 spp. in 2.88 ha of sampled area (2 habitat types)
Lott et al. (1987)	Jalisco, Mexico	Thirty 2 m × 50 m transects: two habitats (3000 m^2)	≥2.5 cm dbh; 4–14 stems/100 m^2	8–22 spp./1000 m^2; 2–5 spp./100 m^2
Nabe-Nielsen (2001)	Yasuní, Ecuador	Two 20 × 100 plots (4000 m^2)	No dbh limit: 606 stems/0.4 ha; 151.5 stems/0.1 ha; ≥1 cm dbh limit: 94.5 stems/0.1 ha	138 spp. in 0.4 ha; 61.8 spp. in 0.1 ha; 44.3 spp. >1 cm in 0.1 ha
Paz y Miño (1990)	Cuyabeno, Ecuador	100 m × 100 m (10,000 m^2)	≥0.5 cm dbh; 2119 stems	90 spp./ha (after Romero-S., 1999)
Perez-Salicrup et al. (2001b)	Oquiriquia, Bolivia	Twenty-four 900 m^2 plots, (21,600 m^2)	≥2 cm dbh; subsampled in 12 of the 24 plots; 2471 stems/ha	51 spp./ha
Putz (1983)	Rio Negro, Brazil	Twenty 100 m^2 circular plots (2000 m^2)	≥2 m tall; 34.5 = mean stem number/plot	45 spp.: all 20 plots; 11.4 spp./plot
Putz (1984)	Barro Colorado Island, Panama	Ten 40 m × 25 m plots and ninety 100 m^2 circular plots (10,000 + 9000 m^2)	≥1 cm dbh; 773 stems/ha	65 spp.: all plots (1 ha)
Romero-S. (1999)	Chuwitayo, Ecuador	50 m × 100 m (5000 m^2)	≥0.5 cm dbh; 1085 stems/0.5 ha; ≥1 cm dbh: 192 stems/0.2 ha	137 spp./0.5 ha with ≥0.5 cm dbh limit; 65 spp./0.2 ha with ≥1 cm dbh limit
Schnitzer and Bongers (2002)	South American Tropics, review	0.1 ha plots (1000 m^2)	≥2.5 cm dbh; 61.6 (±22.2 stems/0.1 ha)	33.7 (±10.9) spp./0.1 ha
Solórzano et al. (2002)	Chamela, Jalisco, Mexico	35,000 ha	n/a	71 spp.
Solórzano et al. (2002)	Chajul, Chiapas, Mexico	100,000 ha	n/a	128 spp.
Van Andel (2001)	Northwest, Guyana. Barama (B): white water floodplain and Moruco (M): black water floodplain	Two sites, each with two 10 ha × 1000 ha plots. 10 × 10 plots every 100 m (4000 m^2)	≤10 cm dbh; ≥1.5 m tall (no stems >10 cm dbh)	Lianas spp. ≥10 and ≤10 added together (B1 = 41, B2 = 43, M1 = 36, M2 = 48)
Vidal et al. (1997)	Fazenda Sete, Paragominas, Para, Brazil	Two 2 m × 1400 m transects, 400 m apart (5400 m^2)	≥1 cm dbh; 1872 stems/0.54 ha	63 spp. (43 genera, 24 families)

surprisingly high there, in light of the distance from the site at Paragominas to the rich soils of the Andean flanks. These forests are maintained in a patchwork of human activity, which may stimulate the growth of liana species not encountered frequently in less disturbed forest (Uhl, 1987; Uhl et al., 1997; Gerwing and Vidal, 2002). Until more areas are sampled in comparable ways, it can only be hypothesized that liana species richness/ha^{-1} should diminish from west to east across the Amazon Basin.

No endemics to Ecuador were encountered in the survey of lianas in Yasuní. However, almost one third (88 of 311) of the identified taxa from the plots are known from only one specimen among all plots. This indicates that Yasuní harbors many rare species, even though they are not endemics to Ecuador. The protection of an area like Yasuní will conserve not only these rare species (distributed among 28 different plant families), but will also maintain the dominance hierarchy of lianas in a forest in which human disturbance is still relatively minor. The relative stability of species composition among dominants across the plots sampled in Yasuní may indicate the ecological balance that might be expected in well-protected areas of Amazonian Ecuador, even though the flora is one of the richest known.

Few other surveys of lianas have been made in eastern Ecuador on this scale. Four studies from Ecuador (Romero-S., 1999; Nabe-Nielsen, 2001; Gentry, 1991, detailed in Phillips and Miller, 2002; Paz y Miño, 1990) can be compared to this survey of Ecuadorian lianas to explore patterns of distribution and the dominance hierarchy (Table 3). In a survey of 606 stems in Yasuní from two 0.2 ha plots (sites close to those surveyed here), Nabe-Nielsen (2001) encountered 132 species or morphospecies of lianas (in all size classes) and found that *M. cuspidatum* was the most abundant liana. Romero-S. (1999) surveyed lianas of Chuwitayo, Ecuador at 850 m elevation, some 200 km from Yasuní's western border. He found that *Adelobotrys adscendens* (Melastomataceae) was the most abundant of 137 species among 1085 climber stems in 0.5 ha (contiguous samples, ≥0.5 diameter limit). In Cuyabeno, Ecuador (250 m elevation), north of the Napo River from Yasuní, the most abundant liana was *Cydista aequinoctialis* (Bignoniaceae: Paz y Miño, 1990 in Romero-S., 1999), where 2119 liana stems of 90 species were encountered in 1 ha using a 0.5 cm diameter limit. Data from Gentry's unpublished survey of lianas from Jatun Sacha, Ecuador (available from Missouri Botanical Garden) were reanalyzed with updated determinations by the author. These revised data reveal 83 liana stems ≥2.5 cm diameter representing 50 species in a 0.1 ha area, with *C. iguanea* (Ulmaceae) and *Mikania leiostachya* (Asteraceae) as co-dominants (six individuals each).

Equally interesting as the comparison of species richness across the large area of the neotropics reported in Table 3 is the lack of standardized methods for both surveying and reporting liana density and richness. Depending on the diameter limit used and the size of the area sampled, the values of species richness vary enormously. Almost no study reports the number of specimens that were unassignable to species or morphospecies. The compilation of data on large-diameter liana densities across Amazonia recently published by Phillips et al. (2002) was as notable in the lack of species-level identifications as it was in the indication that large-diameter lianas may be increasing in density over time in neotropical forests. Certainly our ability to make large-scale comparisons among liana communities and to interpret the role that lianas play in tropical forests will depend critically on well-documented taxonomic identifications and a standard sampling methodology. Unified sampling methodologies have been proposed by Foster (1998), but no plan has been agreed upon by researchers studying lianas in tropical areas. Standardization is critical for adequate comparison of biodiversity among areas.

Currently there is very little information available on the actual distribution of almost any tropical plant species, including trees. Even the distribution of economically valuable species of *Hevea* and *Sweitenia* (rubber and mahogany) is relatively poorly known in remote areas of Amazonia. This situation is particularly acute for lianas, which can be more difficult to collect in flower or fruit, are known vegetatively to fewer specialists, and have been the focus of less-sustained collecting and monitoring activity over the past 25 years. Complete reporting of species identities, facilitated by exchange of specimens and photographs among experts will vastly improve this situation. Guides, catalogues and web-based inventories to various areas of the neotropics (Brako and Zarucchi, 1993; INBio, 1998; Jørgensen and León-Yánez, 1999; Ribeiro et al., 1999) are our starting points for this venture, with each inventoried liana plot adding information to a rich tapestry of liana biodiversity across the neotropics.

Liana biology has advanced tremendously in recent decades, with substantial interest in a wide range of species, community composition, physiological processes, phylogenetic relationships, morphological adaptations, and ethnobotanical information (see Putz and Mooney, 1991). Still, the most basic of information: 'which species are where' is hard to compile because vouchering, reporting and sampling has been less standardized than for comparable tree communities. Tree censuses generally have followed standard methods, which were pioneered by foresters with specific economic goals in mind. As the importance of tropical forests to global carbon cycling, water resources, and biodiversity maintenance increase, the economic imperative shifts to all species in tropical forests. Therefore, the time is now ripe for liana biologists to agree on a standardized methodology and to provide these data on the structural threads in tropical forest to a global audience.

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