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Spatial distribution and floristic composition of trees and lianas in different forest types of an Amazonian rainforest

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Abstract A quantitative inventory of trees and lianas was conducted (1) to compare floristic composition, diversity and stem density variation between three different forest types (tierra firme, floodplain and swamp), and (2) to analyse the relationships between floristic similarity and forest structure in two regions ~60 km apart in Yasuní National Park, Amazonian Ecuador. A total of 1,087 species with a diameter at breast height ≥ 2.5 cm were recorded in 25 0.1-ha plots. Tierra firme was the habitat with the highest number of species and stem density for trees and lianas, followed by floodplain and swamp in both regions. Two hypotheses that have been independently proposed to describe plant distribution in tropical rain forests, together explain species spatial distribution in this study. The fact that the 30 most important species per forest type (totalling 119 species) accounted for 48.2% of total individuals supports the oligarchy hypothesis. Likewise, 28 out of these 119 species are reported as restricted to a single forest type, which supports the environmental-determinism hypothesis. In general, both canopy and understorey trees and lianas showed rather similar floristic patterns across different forest types and regions.

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Introduction

The flora of Ecuador is among the best-known in the Neotropics. However, in the Amazonian region there still remain important gaps of plant diversity knowledge and comparisons of floristic diversity and species composition between habitats and regions (through quantitative inventories) are very scarce (e.g. Balslev et al. 1987; Burnham 2004). In the lowlands of Amazonian Ecuador (0–500 m elevation), 3,996 plant species have been found (26.1% of all Ecuadorean vascular plants), of which 54.4% are woody plants including trees, treelets, lianas and hemiepiphytes (Jørgensen and León-Yánez 1999). Such a relatively well-known and diverse region offers a good opportunity to understand spatial distribution and similarity of species between different habitats at regional scales.

This is the case of Yasuní National Park and the Huaorani Ethnic Reserve, referred to hereafter as Yasuní, which represent one of the best-known areas in plant diversity in northwestern Amazonia. Several quantitative floristic inventories of woody plants have been carried out in the last 23 years, indicating that the alpha diversity of woody plants in Yasuní is among the highest in the tropics (Romoleroux et al. 1997; Pitman et al. 2002; Bass et al. 2010). For instance, there were 1,104 tree species and morpho-species in 152,353 individuals of free-standing woody stems with a diameter at breast height (dbh) ≥ 1 cm, in a tierra firme 25-ha permanent plot (Valencia et al. 2004). Another study of large trees ≥ 10 cm dbh in 15 tierra firme 1-ha plots found a total of 1,017 species-level taxa in 9,809 individuals (Pitman et al. 2001), while other papers also recorded high species counts for large trees in 1-ha plot inventories (Balslev et al. 1987; Cerón 1997). For lianas, there were 311 species among 4,348 climbing stems ≥ 1 cm dbh in 0.2-ha subsamples from 12 1-ha plots established in both tierra firme and floodplain habitats (Burnham 2002, 2004). In another study, there were 138 species and 606 individuals of lianas ≥ 1 cm dbh in two 0.2-ha tierra firme forest plots (Nabe-Nielsen 2001). Finally, there have also been quantitative inventories of particular families such as Arecaceae (Svenning 1999; Vormisto et al. 2004; Montúfar and Pintaud 2006), pteridophytes and Melastomataceae (Tuomisto et al. 2002, 2003a).

Quantitative floristic inventories including all habits of woody plants are scarce in most tropical vegetation types, although patchily distributed in tropical rain forests (e.g. Gentry and Dodson 1987; Duivenvoorden 1994; Duque et al. 2002; Macía 2008). Most of these studies have focused on a physiographic forest unit, mainly well-drained upland tierra firme forests and to a lesser degree on well-drained floodplain forests, but rarely on poorly drained and permanently flooded forests or swamps. Species counts of vascular plants exhibited lower alpha diversity and density in swamp forests than in well-drained forests (Lieberman et al. 1985; Campbell et al. 1992). Tierra firme forests tend to be more species-rich and with higher stem density than floodplain habitats (Campbell et al. 1986; Balslev et al. 1987; Duivenvoorden 1994; Duque et al. 2002; Burnham 2004), but the extent to which the species composition varies with the geographic distance between different and similar habitats defined by inundation history is poorly known.

This article includes a quantitative inventory of all woody plant habits (particularly trees and lianas) within the same plots. New analyses of Romero-Saltos et al.'s (2001) data are performed to further explain the extent of diversity and density variation in two regions ~60 km apart (Dicaro and Guiyero; Fig. 1) and three different forest types (tierra firme, floodplain and swamp) in Yasuní by six life-form subdivisions. More specifically, I ask (i) whether floristic similarity is higher between different forest types of the same region than between similar forest types of different regions, for different life-forms and

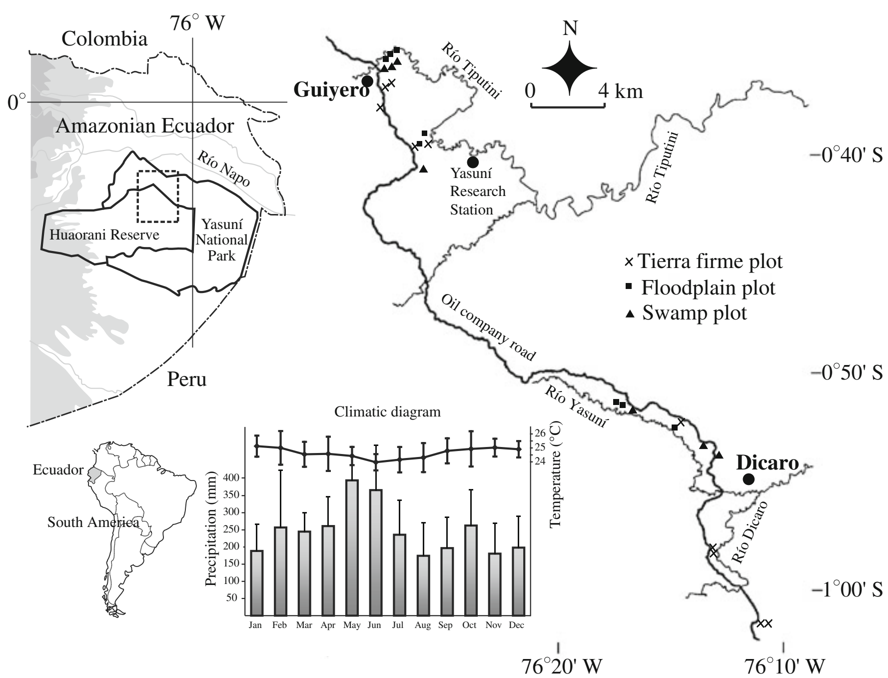

Fig. 1 Location of the study area and 25 0.1-ha plots of tierra firme (*cross*), floodplain (*filled square*) and swamp (*filled triangle*) forest types inventoried around two indigenous communities (Dicaro and Guiyero) in Yasuní National Park and the Huaorani Ethnic Reserve, Amazonian Ecuador. The climatic diagram shows temperature and precipitation average values ± standard deviation from the Yasuní Research Station for the period 1995–2007

size classes, and (ii) if the species diversity, stem density and forest structure, through the relative distribution in diameter classes of trees and lianas, shows significant differences between these two regions.

Methods

Study area

Fieldwork was carried out in Yasuní, the largest protected area in Amazonian Ecuador with ~1.6 million ha. Yasuní is located at the foot of the Andean range on a landscape of rolling piedmont hills, mostly covered by mature tropical rain forest and lacking large deforested areas. Mature forests were studied within the Huaorani indigenous territories around the Dicaro and Guiyero communities, ~60 km apart, at 250–300 m elevation (Fig. 1). Three different broad habitats can be recognised: (i) well-drained upland tierra firme forests, never flooded by rivers, (ii) well-drained floodplain forests, periodically flooded by rivers or streams, and (iii) permanently inundated, poorly drained swamp forests. Probably more than 90% of the Yasuní landscape is covered by tierra firme forests, whereas most floodplain and swamp habitats are confined to narrow bands close to streams and rivers (Macía personal observations). According to climatic data obtained from Yasuní Research Station for the period 1995–2007, mean annual precipitation is ~2800 mm with a peak of rainfall during the months of May and June, and mean annual temperature is ~25°C (see also Romero-Saltos et al. 2001; Valencia et al. 2004; Bass et al. 2010). Soils of the Yasuní region are poorly studied. According to Malo and Arguello (1984), most are composed of alluvial sediments which came from the Andean range. Vegetation types, climatic conditions and elevation were very similar in the two regions studied.

Data collection and plant identification

A total of 25 non-permanent plots of 0.1-ha (50 × 20 m) were established in three different broad forest types: 10 plots in tierra firme (5 Dicaro, 5 Guiyero), 8 plots in floodplains (3 Dicaro, 5 Guiyero), and 7 plots in swamps (3 Dicaro, 4 Guiyero). The selection of sites was based on Landsat TM satellite imagery and according to accessibility. Each plot was placed in well-developed forest with no signs of recent anthropogenic disturbance, excluding big canopy gaps and avoiding heterogeneity in forest physiognomy or soils, and therefore installed in a single broad forest type (tierra firme, floodplain or swamp). Plots within the same region were at least 500 m apart.

Trees and lianas with stems rooted within a plot and with a dbh (diameter measured at 1.3 m above ground) equal to or greater than 2.5 cm were measured, inventoried and identified to species or to a field-temporary name allocated to a morphological species concept (morphospecies). Hemiepiphytes rooted within a plot were also inventoried using this method, measuring the diameters of their descending roots and analysed separately from lianas, as recommended by Gerwing et al. (2006). Multiple stems were measured separately, but all stems rooting in the same place were counted as one individual. Specimens were collected to voucher each name and in doubtful cases to identify a stem. All specimens were first sorted to species or morphospecies level. Then, the sterile vouchers were identified by matching them with vouchers identified by specialists or professional botanists which are deposited at AAU, MO, NY, QCA and QCNE herbaria (acronyms according to Holmgren et al. 1990). Classical taxonomy have been used to facilitate floristic comparisons with past papers, although there are recent changes (e.g. Bombacaceae, Sterculiaceae and Tiliaceae rather than Malvaceae).

Duplicates of the specimens were distributed to taxonomic specialists worldwide who agreed to identify them. A full set of duplicates is deposited at QCA and a nearly complete set at AAU, MA, MO and QCNE. Unicates were kept at QCA. All voucher specimens can be accessed at the TROPICOS website maintained by the Missouri Botanical Garden (http://www.tropicos.org).

Data analyses

Species diversity, floristic composition and similarity were measured with quantitative indexes. For each of these analyses, woody plants were divided into six life-forms: (i) all woody plants: trees, lianas and hemiepiphytes with dbh ≥ 2.5 cm, (ii) all trees with dbh $\geq$ 2.5 cm, (iii) large trees with dbh $\geq$ 10 cm, (iv) small trees with 2.5 $\geq$ dbh < 10 cm, (v) all lianas with dbh $\geq$ 2.5 cm, and (vi) hemiepiphytes with dbh $\geq$ 2.5 cm. The hemiepiphytes were too rare for meaningful analyses and were therefore excluded (see Table 1). Palms and tree ferns were included in the tree categories to facilitate analyses interpretation, although they are not properly trees. In the following analyses, specimens identified to subspecific taxa were lumped under their species. Morphospecies were included in all analyses.

Species diversity values were broken down into different life-forms, and expressed in terms of species richness for each plot and averaged per habitat and region. The Fisher's Alpha diversity index was calculated to relate the total number of woody plants species and the total number of individuals for each plot and then averaged per habitat and region (Fisher et al. 1943). This index is relatively insensitive to sample size and provides good estimates of the overall diversity of tropical forests, even in the case of small samples (Condit et al. 1998).

To quantify and compare floristic composition between habitats and regions, the species importance value index (IVI) was calculated as the sum of its relative density, its relative dominance and its relative frequency (Curtis and McIntosh 1951). The frequency of a species for each habitat and region was defined as the number of 0.1-ha plots in which it occurred, and thus the sum of all frequencies gives the total number of plots per habitat and region. Family importance value index (FIVI) was calculated as the sum of relative density, relative diversity and relative dominance for a family (Mori et al. 1983). To calculate IVIs and FIVIs, data from plots in the same forest type and region were pooled together.

To analyse the degree of floristic similarity within and between inventoried habitats and regions, very rare species represented by five or less individuals in the entire sample area were removed. Two similarity indexes were calculated: the Sørensen index and the Steinhaus index. These two indexes are mathematically identical, but the Sørensen index uses only presence-absence species data whereas the Steinhaus index also includes species abundance, measured as the number of individuals per species (Legendre and Legendre 1998). Both indexes were used because it is recommendable to compare differences in results between presence–absence and abundance data. Similarity matrices were calculated separately for different life-forms: (i) all woody plants, (ii) all trees, (iii) large trees, (iv) small trees, and (v) all lianas.

In order to visualise the floristic patterns among the plots, principal coordinates analysis (PCoA) were run using floristic distance matrices based on the Steinhaus index. The resemblance matrices (S) first needed to be transformed to distance matrices (D) using the formula $D = \sqrt{1 - S}$, following Legendre and Legendre (1998, p. 266). In the obtained PCoA ordination diagrams, plots that displayed close to each other are floristically more similar than plots that displayed far apart, which are floristically more different.

Structural composition for each habitat and region was analysed by comparing the distribution of all trees and lianas according to dbh classes.

Multiple comparisons analysis between habitats and regions were performed with a Tukey 'honest significant difference' (HSD) test, where variables showed normal distribution or were transformed following a Box–Cox transformation to make the data more normal distribution-like. Coefficients with positive values indicate pairs of means that were significantly different from each other and from all other means at the $\alpha = 0.05$ error rate. To analyse forest structure, mean of stems in the smallest diameter class for both trees and lianas were used to run the analysis. All these tests were computed in JMP 3.2.1. Sørensen and Steinhaus similarity indexes, resemblance matrices and principal coordinates analyses were computed in the program Le Progiciel R (available online at http://www.bio.umontreal.ca/legendre/indexEn.html).

Results

Diversity and density of woody plant species

A total of 6,953 individuals belonging to 1,087 species (368 genera and 85 families) of trees, lianas and hemiepiphytes $\geq$ 2.5 cm dbh were recorded in 25 0.1-ha plots. In the Dicaro region, 750 species (302 genera and 78 families in 3,214 stems) were found in 11 plots, whereas in the Guiyero region 782 species (318 genera and 82 families in 3,739 stems) were found in 14 plots. Well-drained forests (tierra firme and floodplain) were much more diverse and

Table 1 Total number of species (Spp.) and individuals (Ind.) in different woody plant life-forms in three different forest types in two study regions, as recorded in 25 0.1-ha plots inventoried in Yasuní National Park and the Huaorani Ethnic Reserve, Ecuadorean Amazon

Attributes	Dicaro ($n = 11$)			Guiyero ($n = 14$)		
	Tierra firme ($n = 5$)	Floodplain ($n = 3$)	Swamp ($n = 3$)	Tierra firme ($n = 5$)	Floodplain ($n = 5$)	Swamp ($n = 4$)
Woody plants (dbh ≥ 2.5 cm)						
Spp.	568 (166–212)	354 (158–169)	109 (41–45)	524 (154–187)	346 (63–153)	190 (25–103)
Ind.	1750 (328–393)	1071 (345–371)	393 (113–165)	1858 (289–437)	1301 (220–301)	580 (82–197)
All trees (dbh ≥ 2.5 cm)						
Spp.	488 (139–184)	319 (145–157)	91 (35–39)	464 (137–165)	293 (48–144)	155 (23–89)
Ind.	1554 (285–339)	955 (297–340)	351 (105–136)	1643 (243–386)	1152 (193–288)	504 (79–165)
Large trees (dbh ≥ 10 cm)						
Spp.	205 (46–60)	122 (44–53)	27 (11–14)	219 (45–70)	128 (25–46)	44 (6–21)
Ind.	327 (51–78)	215 (60–81)	159 (44–62)	402 (68–108)	262 (41–71)	203 (43–59)
Small trees (dbh < 10 cm)						
Spp.	408 (113–146)	274 (115–135)	83 (30–33)	382 (107–143)	243 (38–117)	129 (19–76)
Ind.	1227 (234–261)	740 (216–280)	192 (48–83)	1241 (174–313)	890 (144–217)	301 (36–119)
Lianas (dbh ≥ 2.5 cm)						
Spp.	80 (16–29)	35 (12–17)	18 (2–11)	68 (14–26)	50 (9–21)	23 (1–11)
Ind.	191 (23–59)	112 (31–47)	40 (2–29)	209 (22–55)	139 (10–55)	59 (2–26)
Hemiepiphytes (dbh ≥ 2.5 cm)						
Spp.	5 (1–2)	4 (1–3)	2 (1–1)	5 (1–3)	9 (1–3)	13 (1–8)
Ind.	5 (1–2)	4 (1–3)	2 (1–1)	6 (1–3)	10 (1–3)	17 (1–9)
Mean Fisher's Alpha diversity index	155.9 (131.6–187.7)	119.7 (112.8–126.3)	22.8 (20.4–24.9)	131.1 (105.0–178.9)	67.4 (28.0–124.5)	41.1 (12.2–87.1)

Mean plot Fisher's Alpha diversity index is also given per habitat and region, respectively. Range values between plots are given in parentheses; n = number of plots

Table 2 Tukey HSD test coefficients comparing mean species diversity and mean species density between three different habitats and two studied regions, as recorded in 25 plots of 0.1-ha in Yasuní National Park and the Huaorani Ethnic Reserve, Ecuadorean Amazon

Attribute	Habitats	Dicaro	Guiyero	All plots
Diversity	Tierra firme vs. floodplain	−8.78	22.28	17.84
	Tierra firme vs. swamp	113.22	59.15	88.08
	Floodplain vs. swamp	92.43	−13.85	32.75
Density	Tierra firme vs. floodplain	−48.68	27.41	8.05
	Tierra firme vs. swamp	162.79	136.31	160.78
	Floodplain vs. swamp	161.40	26.51	93.67

Positive values indicate a statistically significant difference at $P < 0.05$

with higher stem density than poorly drained forests (swamp) in both regions for trees and lianas (Table 1). According to mean plot Fisher's Alpha diversity index, tierra firme had the highest diversity while swamp the lowest (Table 1). In the whole region, significant differences were found between the three habitats for both mean diversity and density (Table 2), as recorded in Romero-Saltos et al. (2001). However, when analyses were performed within each region, only the comparison between tierra firme and swamp resulted consistently a significant difference in both diversity and density. In the case of density, floodplain, and swamp also differed from each other in both regions, but all other comparisons gave equivocal results between the two regions.

All trees represented 83.4% of total species and 88.6% of total individuals, whereas values for lianas were 16.6 and 10.8% and for hemiepiphytes 2.5 and 0.6%, respectively (Table 1). The total species percentages sum to more than 100 because some liana species in their juvenile stages were found growing as free-standing treelets. The highest liana diversity and density values were reported in tierra firme and the lowest in swamp forests at the two study regions. Hemiepiphytes were poorly represented in this inventory, although density and diversity values were higher in Guiyero than in Dicaro in all habitats.

In the whole region, statistically significant differences between the three habitats were found in all life-forms for diversity (as recorded in Romero-Saltos et al. (2001), but not for density, where significant differences between forest types were only found in all trees category (Table 3). However, when Tukey HSD test coefficients were compared between regions for diversity taking into account all life-forms, significant differences were only found between tierra firme and swamp. In the case of comparison for density, just the categories, all trees and small trees showed significant differences between swamp and the two other habitats, but not between tierra firme and floodplain.

The five most common tree species per habitat showed important differences in their relative densities between regions, especially in floodplain and to a lesser degree in swamp (Table 4). It is outstanding that three species in the genus *Matisia* were among the most important in tierra firme and three palms in swamp. However, the five most common liana species per forest type showed more similar relative densities values between regions (Table 4). The species *Machaerium cuspidatum* was among the most important in all habitats and *Combretum laxum* and *Uncaria guianensis* in two of them.

Family and species composition

According to the FIVI, Leguminosae (comprising 127 species), Moraceae (45) and Arecaceae (24) were among the most important families in all habitats of both regions (Table 5). Two other families, Lauraceae (75) and Rubiaceae (64), were also among the most important, except in floodplain and tierra firme of Guiyero, where Lauraceae and Rubiaceae were not among the top ten most important families, respectively. Overall, Leguminosae, Lauraceae and Rubiaceae were the most species-rich tree families whereas the richest for lianas were Leguminosae (28), Bignoniaceae (19) and Malpighiaceae (17). The ten most important families per region and habitat (totalling 18 families; Table 5) accounted for 56.1% of the species and 70.7% of the individuals. In swamp forest, the highest values were recorded for Arecaceae followed by Leguminosae, which was also the dominant family in both tierra firme and floodplain. Five families were among the most important in only one habitat: Cecropiaceae and Polygonaceae in Dicaro swamp plots, Cyatheaceae and Ochnaceae in Guiyero swamp and Violaceae in Dicaro floodplain. The families Euphorbiaceae and Sapotaceae ranked among the most important only in well-drained

Table 3 Tukey HSD test coefficients comparing mean species diversity and mean species density for different life-forms between three different habitats and two studied regions, as recorded in 25 plots of 0.1-ha in Yasuní National Park and the Huaorani Ethnic Reserve, Ecuadorean Amazon

Attribute	Life forms	Habitats	Dicaro	Guiyero	All plots
Diversity	All trees ≥ 2.5 cm dbh	Tierra firme vs. floodplain	−19.19	17.06	12.02
		Tierra firme vs. swamp	83.19	49.98	76.45
		Floodplain vs. swamp	63.99	−17.02	27.73
	Large trees ≥ 10 cm dbh	Tierra firme vs. floodplain	−10.24	10.47	5.50
		Tierra firme vs. swamp	23.19	26.47	29.52
		Floodplain vs. swamp	18.50	2.07	13.52
	Small trees < 10 cm dbh	Tierra firme vs. floodplain	−20.07	8.13	6.01
		Tierra firme vs. swamp	63.37	35.15	58.32
		Floodplain vs. swamp	51.15	−17.05	20.67
	Lianas ≥ 2.5 cm dbh	Tierra firme vs. floodplain	−3.03	−0.06	2.36
		Tierra firme vs. swamp	4.97	5.78	9.14
		Floodplain vs. swamp	−3.59	−1.82	1.29
Density	All trees ≥ 2.5 cm dbh	Tierra firme vs. floodplain	−47.74	21.66	5.01
		Tierra firme vs. swamp	116.69	120.97	143.31
		Floodplain vs. swamp	118.84	22.77	84.01
	Large trees ≥ 10 cm dbh	Tierra firme vs. floodplain	−15.20	6.28	−2.82
		Tierra firme vs. swamp	−9.60	6.47	4.38
		Floodplain vs. swamp	−5.64	−20.53	−9.05
	Small trees < 10 cm dbh	Tierra firme vs. floodplain	−52.92	−0.61	−1.44
		Tierra firme vs. swamp	107.28	97.53	129.29
		Floodplain vs. swamp	111.97	26.32	83.03
	Lianas ≥ 2.5 cm dbh	Tierra firme vs. floodplain	−27.32	−11.05	−7.39
		Tierra firme vs. swamp	−6.32	−0.28	7.57
		Floodplain vs. swamp	−12.15	−12.68	−1.55

Positive values indicate a statistically significant difference at $P < 0.05$

forests, and Melastomataceae only in poorly drained swamp forests at both regions.

Based on IVI, the 30 most important species per forest type at each of the two regions (totalling 119 species) accounted for 48.2% of all individuals (Table 6). The liana *Machaerium cuspidatum* was among the most important species, reaching high values in almost all sites. The large trees (≥10 cm dbh) *Eschweilera coriacea*, *Guarea macrophylla*, *Iriartea deltoidea* and *Iryanthera hostmannii* were present in the majority of sites. All these most important species reached 10 cm dbh, except 14 which were understorey species and nine which were lianas (Table 6).

Some species showed distributions clearly associated with a particular habitat. In swamp forests, *Cespedesia spathulata*, *Cyathea pungens*, and *Mauritia flexuosa* were only found in this habitat, and *Euterpe precatoria*, *Licaria triandra* and *Macrolobium angustifolium* were very common in this forest type (Table 6). In tierra firme forests, *Zygia heteroneura* and *Z. lathetica* were exclusively reported for this habitat and *Guarea kunthiana*, *Matisia longiflora*, *Memora cladotricha*, *Protium sagotianum* and *Siparuna decipiens* were common species in this habitat. All these seven species from tierra firme never occurred in swamp forests. In floodplain forests, the species *Gustavia longifolia*, *Perebea xanthochyma* and *Phytelephas tenuicaulis* were commonly although not exclusively found in this habitat.

Floristic resemblance between forest types

Overall, floristic similarity was higher among plots from the same broad forest type and region than

Table 4 The five most common tree and liana species and their relative densities broken down by habitats and regions as recorded in 25 0.1-ha plots inventoried in Yasuní National Park and the Huaorani Ethnic Reserve, Amazonian Ecuador

Habitat	Trees				Lianas			
	Species	Total number of individuals	Relative density Dicaro	Relative density Guiyero	Species	Total number of individuals	Relative density Dicaro	Relative density Guiyero
Tierra firme	*Matisia oblongifolia*	66	–	3.55	*Machaerium cuspidatum*	37	1.03	1.08
	Zygia lathetica	64	1.71	1.83	*Callichlamys latifolia*	25	0.23	1.13
	Matisia longiflora	48	1.71	0.97	*Combretum laxum*	18	0.57	0.43
	Rinorea lindeniana	47	1.71	0.91	*Adenocalymna impressum*	16	0.69	0.21
	Matisia malacocalyx	42	1.14	1.18	*Arrabidaea florida*	15	0.11	0.70
	Memora cladotricha	42	0.86	1.45				
Floodplain	*Phytelephas tenuicaulis*	73	1.40	4.46	*Machaerium cuspidatum*	49	2.70	1.61
	Coussarea macrophylla	72	–	5.53	*Bauhinia rutilans*	22	0.37	1.61
	Quararibea wittii	64	0.19	4.76	*Cuervea kappleriana*	9	0.84	–
	Rinorea lindeniana	61	4.20	1.23	*Byttneria asterotricha*	9	0.75	0.08
	Sorocea steinbachii	59	0.19	4.38	*Uncaria guianensis*	9	–	0.69
Swamp	*Mauritia flexuosa*	138	18.32	11.38	*Machaerium cuspidatum*	15	0.76	2.07
	Euterpe precatoria	64	7.38	6.03	*Bauhinia tarapotensis*	12	0.76	1.55
	Attalea butyracea	44	–	7.59	*Combretum laxum*	9	2.03	0.17
	Macrolobium angustifolium	34	5.09	2.41	*Uncaria guianensis*	7	0.25	1.03
	Cyathea pungens	30	1.02	4.48	*Clitoria javitensis*	6	1.02	0.34

between habitats and regions, as measured with both Sørensen and Steinhaus indexes, although there are some exceptions for large trees in all habitats and lianas in well-drained forest types just for abundance data (Tables 7, 8, respectively).

When floristic resemblance mean values for presence/absence data were compared within each of the regions, different patterns were found: average similarity values for the Dicaro floodplains were higher than those for tierra firme, but in the case of Guiyero the opposite was found (Table 7). Swamp forests had the lowest values in both regions. This was true for all life forms with the exception of large trees, which reached the highest values in swamp forests in both Dicaro and Guiyero. When abundance data were considered, the same pattern was found for Dicaro with the exception of large trees which reached the highest values in swamp forests (Table 8). But in the case of Guiyero, mean resemblance values were higher for swamps in all the cases with the exception of small trees and lianas where tierra firme forests reached higher values.

However, when floristic similarity average values were compared between Dicaro and Guiyero for both presence/absence data and abundance data, the values obtained followed in general terms the pattern above described for Guiyero. For presence/absence data, tierra firme forests reached the highest values with the exception of large trees in swamps (Table 7). For abundance data, swamp forests reached the highest values (together with tierra firme for both all woody plants and all trees), with the only exception of lianas which reached the highest values for floodplain forests (Table 8).

The PCoA ordinations in all tree size-classes showed clear differences in floristic patterns between tierra firme and swamp plots, with floodplain plots scattered between these two extremes but closely related to tierra firme forests (Fig. 2a, b, c), as recorded in Romero-Saltos et al. (2001) using DCA ordinations. There is also a good separation of the floodplain forests from the other habitats when using all trees and small trees, except for a few outliers. For

Table 5 Comparison of the 10 most important families (in bold) between three different forest types and two study regions, totalling 25 0.1-ha plots inventoried in Yasuní National Park and the Huaorani Ethnic Reserve, Ecuadorean Amazon

Family	Dicaro			Guiyero		
	Tierra firme	Floodplain	Swamp	Tierra firme	Floodplain	Swamp
Annonaceae	8.44	**15.97**	2.49	**10.57**	**13.78**	5.50
Arecaceae*	**10.47**	**11.92**	**93.38**	**12.21**	**20.23**	**91.20**
Bombacaceae	**9.49**	8.55	5.41	**18.25**	**15.74**	**9.20**
Cecropiaceae	4.09	2.71	**10.17**	5.12	4.04	1.98
Cyatheaceae	0.95	–	2.33	0.88	–	**7.66**
Euphorbiaceae*	**15.69**	**20.55**	5.51	**9.82**	**11.16**	3.52
Lauraceae	**19.59**	**9.69**	**13.09**	**13.55**	7.69	**8.16**
Lecythidaceae	7.87	**13.74**	1.57	**9.90**	**9.26**	3.95
Leguminosae*	**39.25**	**43.86**	**45.49**	**38.70**	**34.35**	**40.95**
Melastomataceae*	5.45	3.44	**18.29**	7.55	3.95	**8.07**
Meliaceae	**18.97**	8.73	**10.77**	**13.47**	6.28	2.09
Moraceae	**14.58**	**11.38**	**6.93**	**16.87**	**20.15**	**10.03**
Myristicaceae	**14.89**	7.36	**8.58**	7.79	**9.04**	**8.81**
Ochnaceae	–	0.41	1.54	0.28	–	**8.32**
Polygonaceae	1.57	1.29	**7.49**	1.76	2.91	2.64
Rubiaceae*	**12.79**	**12.06**	**10.49**	9.05	**30.73**	**10.37**
Sapotaceae	**10.79**	**13.11**	–	**10.23**	**10.13**	7.02
Violaceae	5.86	**12.25**	2.85	6.27	8.05	1.84

Numbers indicate the family importance value index (FIVI), which were obtained as the sum of their relative density, relative dominance and relative diversity, respectively. Families with the symbol * include species of lianas

large trees, well-drained forests were not so clearly discriminated. The ordination based on lianas showed the same general pattern although less clear differences in species composition between forest types, since some plots in all habitats displayed at intermediate positions (Fig. 2d).

Community structure between habitats

The distribution of tree individuals in different dbh classes showed an inverse J-shaped curve with higher similarity between well-drained habitats than swamp forests (Fig. 3). Compared to tierra firme and floodplain habitats, swamp forests had a lower percentage of small trees (<10 cm dbh) and a higher percentage of canopy trees (≥20 cm dbh) at both regions. Trees showed significance differences in class diameter between swamp and the two other habitats for all regions, but not between tierra firme and floodplain (Table 9). In tierra firme were recorded a higher number of liana stems than in floodplain forests, whereas in swamp forest were found the lowest number of individuals. Structurally, lianas showed more variability in the number of individuals than trees in all habitats and regions (Fig. 3) and furthermore, no statistical differences were found between them (Table 9).

Discussion

Differences in broad forest types

Well-drained tierra firme forest is the most species-rich habitat and has the highest stem density in Yasuní for both trees and lianas, whereas the least diverse and dense stand is the poorly drained waterlogged swamp forest, as recorded in Romero-Saltos et al. (2001). Well-drained floodplain habitats showed intermediate diversity and density values, although both floristic similarity coefficients and PCoA ordinations showed values on plot positions closer to tierra firme than to

Table 6 Comparison of the 30 most important species (in bold) between three different forest types and two study regions, totalling 25 0.1-ha plots inventoried in Yasuní National Park and the Huaorani Ethnic Reserve, Amazonian Ecuador

Family	Scientific name	Dicaro			Guiyero		
		Tierra firme	Floodplain	Swamp	Tierra firme	Floodplain	Swamp
Anno.	*Anaxagorea brevipes* Benth.				**2.53**	0.85	
	Anaxagorea (MJM 1914)				0.20	1.62	**3.32**
	Annonaceae (MJM 1422)		**3.78**				
Apoc.	*Aspidosperma darienense* Woodson ex Dwyer		**2.06**			1.36	1.18
Arec.	*Astrocaryum urostachys* Burret					**2.02**	0.77
	Attalea butyracea (Mutis ex L. f.) Wess. Boer					**2.49**	**27.31**
	Euterpe precatoria Mart.		0.75	**17.71**	0.48	1.93	**14.16**
	Iriartea deltoidea Ruiz & Pav.	**3.92**	**5.30**	1.14	**5.02**	**3.78**	0.84
	Mauritia flexuosa L. f.			**67.83**			**44.47**
	Oenocarpus bataua Mart.	**2.06**		1.49	**1.71**		**1.71**
	Phytelephas tenuicaulis (Barfod) A.J. Hend.	0.37	**3.47**		0.30	**9.29**	1.70
	Socratea exorrhiza (Mart.) H. Wendl.	0.43	0.84	**3.86**	0.53	1.77	0.73
Bign.	***Callichlamys latifolia* (Rich.) K. Schum.	0.53			**2.19**		
	***Clytostoma binatum* (Thunb.) Sandwith			1.09			**1.72**
	Memora cladotricha Sandwith	**1.80**	1.25		**2.68**	0.30	
Bomb.	*Ceiba samauma* (Mart.) K. Schum.			**3.19**			1.42
	Matisia bracteolosa Ducke	**1.64**	0.78	**1.93**	**2.37**	0.80	1.32
	Matisia longiflora Gleason	**3.14**	0.33		**1.94**	0.31	
	Matisia malacocalyx (A. Robyns & S. Nilsson) W.S. Alverson	**2.46**	**2.63**		**2.97**	0.51	
	Matisia oblongifolia Poepp. & Endl.		0.57		**7.66**	0.62	0.76
	Quararibea wittii K. Schum. & Ulbr.	0.22	0.46			**9.58**	**3.03**
Bora.	**Cordia nodosa* Lam.	0.31	0.34		0.37	1.21	**1.78**
Burs.	*Protium aracouchini* (Aubl.) Marchand	0.48			**1.72**	0.36	
	Protium nodulosum Swart	1.07	**2.20**		0.58	1.32	
	Protium sagotianum Marchand	**1.76**	0.33		**1.66**	0.31	
Cecr.	*Cecropia ficifolia* Warb. ex Snethl.	0.20		**6.74**	0.32	0.60	
Comb.	***Combretum laxum* Jacq.	1.39	0.93	**3.34**	1.37		0.63
Cyat.	**Cyathea pungens* (Willd.) Domin			**2.96**			**6.78**
Euph.	**Acalypha cuneata* Poepp.	**2.86**	1.20		0.45		
	Alchornea triplinervia (Spreng.) Müll. Arg.				**1.64**		
	Aparisthmium cordatum (Juss.) Baill.	**1.52**					
	Hieronyma alchorneoides Allemão		**2.41**	**3.70**		0.73	0.66
	Mabea klugii Steyerm.			1.09		**2.60**	
	Mabea piriri Aubl.	1.15			**2.99**	0.30	
	Pausandra trianae (Müll. Arg.) Baill.	**2.27**	**3.46**		0.19	0.93	
	Sagotia racemosa Baill.	0.94	**2.21**			1.05	
Hipp.	***Cuervea kappleriana* (Miq.) A.C. Sm.		**1.74**				
Laur.	*Aniba guianensis* Aubl.	**1.55**			0.20	0.30	
	Licaria triandra (Sw.) Kosterm.		0.66	**6.97**			**1.81**
	Pleurothyrium (MJM 2348)	0.44		**2.23**			
	Rhodostemonodaphne crenaticupula Madriñán	0.24		**1.96**	0.19	0.30	
	Lauraceae (MJM 3614)	1.16				1.26	**2.65**

Table 6 continued

Family	Scientific name	Dicaro			Guiyero		
		Tierra firme	Floodplain	Swamp	Tierra firme	Floodplain	Swamp
Lecy.	*Eschweilera coriacea* (DC.) S.A. Mori	**2.10**	**4.62**	1.42	**5.10**	1.39	**1.77**
	Eschweilera (MJM 2933)	0.49			0.94	**2.89**	
	Grias neuberthii J.F. Macbr.	**1.55**	1.53		1.43	**2.63**	
	Gustavia longifolia Poepp. ex O. Berg	1.30	**5.59**		0.47	**1.99**	0.65
Legu.	*Bauhinia arborea* Wunderlin	0.24	**1.72**		0.27	0.52	
	Bauhinia brachycalyx Ducke	0.66	**3.44**		0.79	1.55	1.43
	***Bauhinia rutilans Spruce ex Benth.	**1.48**	0.75			**3.49**	
	**Bauhinia tarapotensis Benth.	0.19		1.82			**3.43**
	Brownea grandiceps Jacq.	**2.26**	**4.25**		**3.29**	0.91	1.34
	Browneopsis ucayalina Huber				0.47	**2.85**	
	**Clitoria javitensis (Kunth) Benth.			**2.14**	0.44		0.91
	Crudia glaberrima (Steud.) J.F. Macbr.					0.84	**2.71**
	Inga auristellae Harms	**2.63**			0.98		
	*Inga bourgoni (Aubl.) DC.	0.39	**2.38**		0.28	0.61	0.89
	*Inga cayennensis Sagot ex Benth.	0.20		**1.97**			0.87
	Inga cordatoalata Ducke	1.25			**1.74**		
	Inga nobilis Willd.	0.70	0.70	**2.05**	0.42	**2.31**	**3.45**
	Inga spectabilis (Vahl) Willd.	0.76	0.37			**4.73**	1.31
	**Machaerium cuspidatum Kuhlm. & Hoehne	**2.05**	**4.79**	1.69	**2.08**	**3.23**	**3.68**
	***Machaerium floribundum Benth.			**8.08**	0.19		
	Macrolobium acaciifolium (Benth.) Benth.						**2.66**
	Macrolobium angustifolium (Benth.) R.S. Cowan		0.71	**13.36**		0.66	**7.30**
	Macrolobium stenocladum Harms	0.19	**1.82**		**2.08**		
	Pterocarpus rohrii Vahl		**1.96**				1.24
	Zygia cataractae (Kunth) L. Rico	0.38	**6.10**	1.40			
	Zygia heteroneura Barneby & J.W. Grimes	**2.00**			**2.20**		
	*Zygia inaequalis (Humb. & Bonpl. ex Willd.) Pittier		0.49	**3.32**			0.63
	*Zygia lathetica Barneby & J.W. Grimes	**3.20**			**3.19**		
Malp.	**Malpighiaceae (MJM 2475)			**2.02**			
Mela.	*Miconia grandifolia* Ule	0.19		**2.37**	0.86	0.32	0.62
	*Miconia spennerostachya Naudin			1.09			**1.70**
	Miconia splendens (Sw.) Griseb.				0.23	**2.57**	**2.56**
	Miconia (MJM 2582)		0.37	**5.84**			
Meli.	*Guarea kunthiana* A. Juss.	**2.34**	0.89		**2.19**		
	Guarea macrophylla Vahl	**1.91**	**3.06**	**7.84**	0.63	**2.80**	
	Guarea pubescens (Rich.) A. Juss.	**1.53**		1.08			
	Trichilia elsae Harms	**2.35**	0.44		0.69		
Mora.	*Ficus piresiana* Vázq. Avila & C.C. Berg			1.59			**1.97**
	Ficus schultesii Dugand	0.21				**2.27**	
	Ficus (MJM 2448)			**4.03**	0.52		0.65
	Maquira calophylla (Poepp. & Endl.) C.C. Berg				**1.70**		
	Naucleopsis krukovii (Standl.) C.C. Berg	1.07	0.32		**1.68**		
	Perebea xanthochyma H. Karst.	0.90	**1.74**		0.88	**2.97**	1.63

Table 6 continued

Family	Scientific name	Dicaro			Guiyero		
		Tierra firme	Floodplain	Swamp	Tierra firme	Floodplain	Swamp
	Pseudolmedia laevis (Ruiz & Pav.) J.F. Macbr.	**1.88**	0.88		**2.19**	0.60	0.67
	Pseudolmedia rigida (Klotzsch & H. Karst.) Cuatrec.	0.21	0.68			**2.28**	
	Sorocea steinbachii C.C. Berg	1.11	0.61		1.57	**8.91**	0.66
Myri.	*Iryanthera hostmannii* (Benth.) Warb.	**2.87**	**1.75**		**2.10**	0.43	**2.23**
	Otoba parvifolia (Markgr.) A.H. Gentry	1.08			0.82	**2.62**	
	Virola duckei A.C. Sm.	**2.00**			0.53		
	Virola pavonis (A. DC.) A.C. Sm.	**1.85**	1.35	**4.66**	0.38	1.59	**3.17**
	Virola surinamensis (Rol. ex Rottb.) Warb.			**4.41**			
Myrt.	*Calyptranthes simulata* McVaugh						**3.89**
	Eugenia florida DC.	1.21	**1.76**		0.40	0.45	1.39
Nyct.	*Neea* (MJM 2909)	0.44	**2.18**		0.19	**6.23**	0.64
	Neea (MJM 1498)	**1.62**	0.37		**1.91**	0.31	
	**Neea* (MJM 2451)	0.20	0.33	**2.20**			
Ochn.	*Cespedesia spathulata* (Ruiz & Pav.) Planch.			**2.18**			**7.79**
Olac.	*Heisteria acuminata* (Humb. & Bonpl.) Engl.	0.27	1.28		0.29	**2.27**	0.70
Poly.	*Coccoloba densifrons* C. Mart. ex Meisn.	1.17	1.61		0.64	**2.63**	
	Triplaris americana L.	0.19		**6.01**		0.50	0.94
Rham.	*Colubrina spinosa* Donn. Sm.	0.89	**3.94**			1.01	
Rubi.	**Coussarea longiflora* (Mart.) Müll. Arg.					**3.27**	
	**Coussarea macrophylla* Müll. Arg.					**9.37**	
	**Coussarea revoluta* Steyerm.					**2.45**	
	**Pentagonia williamsii* Standl.		0.98	1.38	0.26	0.45	**1.73**
	***Uncaria guianensis* (Aubl.) J.F. Gmel.			1.10		1.23	**1.94**
Sapo.	*Pouteria torta* (Mart.) Radlk.	0.19	1.08		0.66	1.14	**2.35**
Sipa.	*Siparuna decipiens* (Tul.) A. DC.	**1.49**	0.35		**2.17**		
Ster.	*Sterculia apeibophylla* Ducke				**1.64**	0.33	**3.47**
	Sterculia colombiana Sprague	1.09	0.33	**3.83**	1.20		
Tili.	*Apeiba aspera* Aubl.	1.31	**2.35**		**1.90**	0.74	0.73
	Pentaplaris huaoranica Dorr & C. Bayer		**5.08**			1.96	
Viol.	*Leonia crassa* L.B. Sm. & A. Fernández	0.93	0.32	**2.71**	0.77	**3.29**	**2.14**
	Leonia glycycarpa Ruiz & Pav.	1.06	0.96		**3.32**	0.30	
	Rinorea apiculata Hekking		**1.78**				
	**Rinorea lindeniana* (Tul.) Kuntze	**2.91**	**7.27**		1.63	**2.04**	
	Rinorea viridifolia Rusby	0.48	1.67			**2.38**	

Numbers indicate species importance value index (IVI), which were obtained as the sum of their relative density, relative dominance and relative frequency, respectively. The species with * symbol are understorey trees (species whose stems did not reach 10 cm dbh in the inventory), those with ** symbol are lianas, and those with *** symbol are both trees and lianas

swamp forests. This is in agreement with earlier quantitative floristic studies for both trees and lianas in Amazonian forests, which also found floristic differences between well-drained tierra firme and floodplain forests (Lieberman et al. 1985; Campbell et al. 1986; Balslev et al. 1987; Duivenvoorden 1994; Romero-Saltos et al. 2001; Duque et al. 2002; Burnham 2004). The fact that floodplain habitats conform a large gradient from high to low diversity, density and drainage between tierra firme and swamp stands can be explained by the particular flooding history in each of the sites, i.e., depending on

Table 7 Pair-wise comparison of floristic similarity as measured by Sørensen index (for presence/absence data) between three broad forest types (Tierra firme [TF], Floodplain [FP] and Swamp [SW]) in two different study regions as recorded at 25 0.1-ha plots in Yasuní National Park and the Huaorani Ethnic Reserve, Amazonian Ecuador

Life-form	Sites	Dicaro			Guiyero		
		Tierra firme	Floodplain	Swamp	Tierra firme	Floodplain	Swamp
All woody plants	Dicaro-TF	0.44 ± 0.07					
	Dicaro-FP	0.38 ± 0.04	0.53 ± 0.03				
	Dicaro-SW	0.09 ± 0.04	0.12 ± 0.05	0.33 ± 0.07			
	Guiyero-TF	0.42 ± 0.07	0.33 ± 0.06	0.09 ± 0.03	0.46 ± 0.10		
	Guiyero-FP	0.24 ± 0.07	0.30 ± 0.10	0.12 ± 0.04	0.22 ± 0.10	0.33 ± 0.11	
	Guiyero-SW	0.15 ± 0.06	0.20 ± 0.12	0.25 ± 0.08	0.15 ± 0.07	0.23 ± 0.10	0.28 ± 0.07
All trees (dbh ≥ 2.5 cm)	Dicaro-TF	0.44 ± 0.07					
	Dicaro-FP	0.38 ± 0.04	0.53 ± 0.02				
	Dicaro-SW	0.09 ± 0.05	0.12 ± 0.05	0.37 ± 0.08			
	Guiyero-TF	0.43 ± 0.07	0.34 ± 0.06	0.07 ± 0.04	0.46 ± 0.10		
	Guiyero-FP	0.24 ± 0.08	0.30 ± 0.11	0.12 ± 0.04	0.23 ± 0.10	0.32 ± 0.11	
	Guiyero-SW	0.15 ± 0.06	0.20 ± 0.11	0.25 ± 0.09	0.15 ± 0.07	0.23 ± 0.10	0.29 ± 0.05
Large trees (dbh ≥ 10 cm)	Dicaro-TF	0.27 ± 0.14					
	Dicaro-FP	0.34 ± 0.10	0.44 ± 0.10				
	Dicaro-SW	0.05 ± 0.07	0.11 ± 0.11	0.66 ± 0.08			
	Guiyero-TF	0.36 ± 0.11	0.33 ± 0.10	0.09 ± 0.07	0.36 ± 0.15		
	Guiyero-FP	0.23 ± 0.15	0.30 ± 0.14	0.19 ± 0.12	0.20 ± 0.11	0.26 ± 0.16	
	Guiyero-SW	0.08 ± 0.08	0.14 ± 0.10	0.44 ± 0.10	0.14 ± 0.10	0.16 ± 0.12	0.41 ± 0.07
Small trees (dbh < 10 cm)	Dicaro-TF	0.44 ± 0.08					
	Dicaro-FP	0.35 ± 0.04	0.48 ± 0.01				
	Dicaro-SW	0.07 ± 0.04	0.11 ± 0.05	0.26 ± 0.11			
	Guiyero-TF	0.41 ± 0.08	0.30 ± 0.05	0.05 ± 0.03	0.44 ± 0.12		
	Guiyero-FP	0.20 ± 0.08	0.27 ± 0.13	0.09 ± 0.05	0.20 ± 0.11	0.31 ± 0.15	
	Guiyero-SW	0.15 ± 0.07	0.20 ± 0.12	0.22 ± 0.11	0.14 ± 0.07	0.22 ± 0.12	0.26 ± 0.05
All lianas (dbh ≥ 2.5 cm)	Dicaro-TF	0.36 ± 0.15					
	Dicaro-FP	0.36 ± 0.15	0.38 ± 0.17				
	Dicaro-SW	0.15 ± 0.16	0.18 ± 0.13	0			
	Guiyero-TF	0.34 ± 0.16	0.25 ± 0.16	0.15 ± 0.11	0.46 ± 0.13		
	Guiyero-FP	0.23 ± 0.15	0.31 ± 0.14	0.16 ± 0.22	0.16 ± 0.17	0.39 ± 0.22	
	Guiyero-SW	0.16 ± 0.15	0.17 ± 0.19	0.20 ± 0.24	0.15 ± 0.15	0.16 ± 0.21	0.25 ± 0.25

Species represented by five or less individuals in the entire sample area were removed. Mean ± standard deviation Sørensen coefficients are presented for different life-forms and size classes

Table 8 Pair-wise comparison of floristic similarity as measured by Steinhaus index (for abundance data) between three broad forest types (Tierra firme [TF], Floodplain [FP] and Swamp [SW]) in two different study regions as recorded at 25 0.1-ha plots in Yasuní National Park and the Huaorani Ethnic Reserve, Amazonian Ecuador

Life-form	Sites	Dicaro			Guiyero		
		Tierra firme	Floodplain	Swamp	Tierra firme	Floodplain	Swamp
All woody plants	Dicaro-TF	0.29 ± 0.07					
	Dicaro-FP	0.25 ± 0.04	0.42 ± 0.02				
	Dicaro-SW	0.05 ± 0.02	0.07 ± 0.02	0.33 ± 0.12			
	Guiyero-TF	0.28 ± 0.07	0.21 ± 0.04	0.04 ± 0.02	0.31 ± 0.10		
	Guiyero-FP	0.13 ± 0.06	0.20 ± 0.10	0.06 ± 0.02	0.12 ± 0.07	0.20 ± 0.14	
	Guiyero-SW	0.07 ± 0.04	0.10 ± 0.08	0.28 ± 0.13	0.07 ± 0.05	0.11 ± 0.08	0.32 ± 0.13
All trees (dbh ≥ 2.5 cm)	Dicaro-TF	0.30 ± 0.08					
	Dicaro-FP	0.25 ± 0.04	0.42 ± 0.01				
	Dicaro-SW	0.04 ± 0.02	0.06 ± 0.02	0.36 ± 0.12			
	Guiyero-TF	0.28 ± 0.07	0.21 ± 0.04	0.03 ± 0.02	0.30 ± 0.10		
	Guiyero-FP	0.13 ± 0.07	0.19 ± 0.12	0.05 ± 0.02	0.11 ± 0.07	0.19 ± 0.16	
	Guiyero-SW	0.07 ± 0.04	0.10 ± 0.07	0.28 ± 0.14	0.06 ± 0.05	0.11 ± 0.07	0.33 ± 0.14
Large trees (dbh ≥ 10 cm)	Dicaro-TF	0.22 ± 0.12					
	Dicaro-FP	0.26 ± 0.09	0.34 ± 0.04				
	Dicaro-SW	0.02 ± 0.03	0.05 ± 0.05	0.54 ± 0.16			
	Guiyero-TF	0.25 ± 0.10	0.25 ± 0.08	0.03 ± 0.02	0.29 ± 0.13		
	Guiyero-FP	0.15 ± 0.12	0.20 ± 0.13	0.06 ± 0.04	0.13 ± 0.09	0.18 ± 0.18	
	Guiyero-SW	0.03 ± 0.03	0.05 ± 0.05	0.44 ± 0.23	0.05 ± 0.04	0.08 ± 0.09	0.48 ± 0.23
Small trees (dbh < 10 cm)	Dicaro-TF	0.29 ± 0.08					
	Dicaro-FP	0.23 ± 0.05	0.42 ± 0.01				
	Dicaro-SW	0.04 ± 0.02	0.06 ± 0.02	0.16 ± 0.08			
	Guiyero-TF	0.26 ± 0.08	0.18 ± 0.03	0.03 ± 0.02	0.28 ± 0.10		
	Guiyero-FP	0.11 ± 0.07	0.17 ± 0.13	0.04 ± 0.03	0.10 ± 0.07	0.18 ± 0.16	
	Guiyero-SW	0.07 ± 0.04	0.10 ± 0.08	0.15 ± 0.08	0.06 ± 0.05	0.10 ± 0.08	0.17 ± 0.06
All lianas (dbh ≥ 2.5 cm)	Dicaro-TF	0.19 ± 0.13					
	Dicaro-FP	0.26 ± 0.13	0.37 ± 0.10				
	Dicaro-SW	0.11 ± 0.13	0.13 ± 0.13	0			
	Guiyero-TF	0.23 ± 0.14	0.20 ± 0.13	0.10 ± 0.10	0.33 ± 0.12		
	Guiyero-FP	0.17 ± 0.15	0.27 ± 0.16	0.12 ± 0.18	0.15 ± 0.14	0.26 ± 0.17	
	Guiyero-SW	0.12 ± 0.13	0.17 ± 0.19	0.14 ± 0.17	0.12 ± 0.13	0.16 ± 0.21	0.26 ± 0.25

Species represented by five or less individuals in the entire sample area were removed. Mean ± standard deviation Steinhaus coefficients are presented for different life-forms and size classes

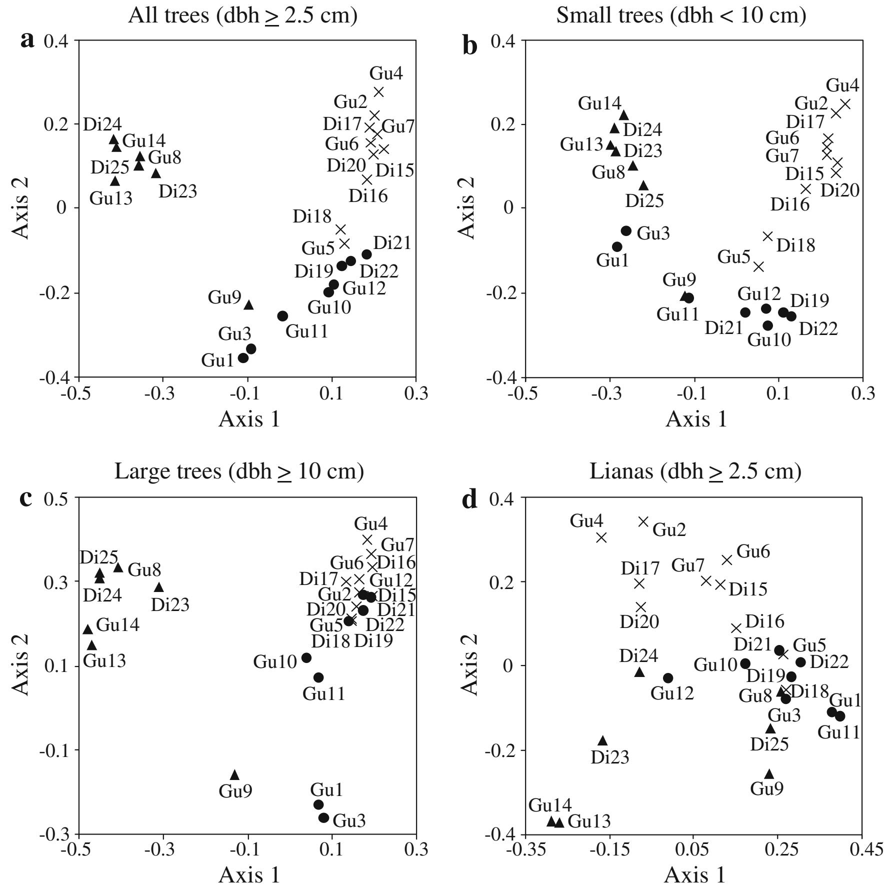

Fig. 2 Floristic ordination diagrams (PCoA) obtained for each of the four life-forms separately (**a** all trees ≥ 2.5 cm dbh, **b** small trees ≥ 2.5 cm dbh, **c** large trees ≥ 10 cm dbh, **d** all lianas ≥ 2.5 cm dbh) for the 25 inventoried 0.1-ha plots in Yasuní National Park and the Huaorani Ethnic Reserve, Ecuadorean Amazon. For both regions, Dicaro (Di) and Guiyero (Gu), plot habitats are represented as follows: tierra firme (*cross*), floodplains (*filled circle*) and swamps (*filled triangle*). Similarity matrices for floristic composition were based on Steinhaus index (for abundance data)

frequency (seasonal or sporadically) and duration of flooding (Campbell et al. 1992; Ferreira 1997).

According to the quantitative indexes used, the swamp is the most distinct habitat in terms of both floristic composition and similarity for the following reasons. First, average plot Fisher's Alpha diversity index was the lowest among the forest types. Second, the families Cecropiaceae, Cyatheaceae, Melastomataceae, Ochnaceae and Polygonaceae showed very high FIVI values compared with other forest types. Some of these families (Cecropiaceae, Melastomataceae) or genera (*Cespedesia* in Ochnaceae and *Triplaris* in Polygonaceae) are prevalent in gaps in rain forests and predominant in second growth forests (Gentry 1993). Because stem abundance in swamps is lower than in the other studied habitats, these forests are more open stands and, therefore, light penetrates more easily to the lower strata and is more favourable to these heliophyte species. Third, the lowest floristic similarity values between habitats were found in the pair-wise comparison involving swamp forests, as measured with the Sørensen index with the exception of large trees which were mainly represented by the palm *Mauritia flexuosa*. Fourth, PCoA ordinations showed that swamp and tierra firme forests are floristically the most different habitats since they displayed far apart. Fifth, tree forest structure exhibited a lower number of understorey trees (<10 cm dbh) compared to well-drained habitats that showed very similar values and a higher number of large trees (≥20 cm dbh), represented mostly by *Mauritia flexuosa*.

This study adds to earlier papers demonstrating that dominant families are predictable in Amazonian forests (e.g. Gentry 1988; Terborgh and Andresen 1998; Punyasena et al. 2008). Most of the families found with the highest FIVI values were also important in those past studies using the same 0.1-ha plot protocol (Gentry 1988; Duivenvoorden 1994; Macía 2008), following these two general patterns: some families scored high because they are the most

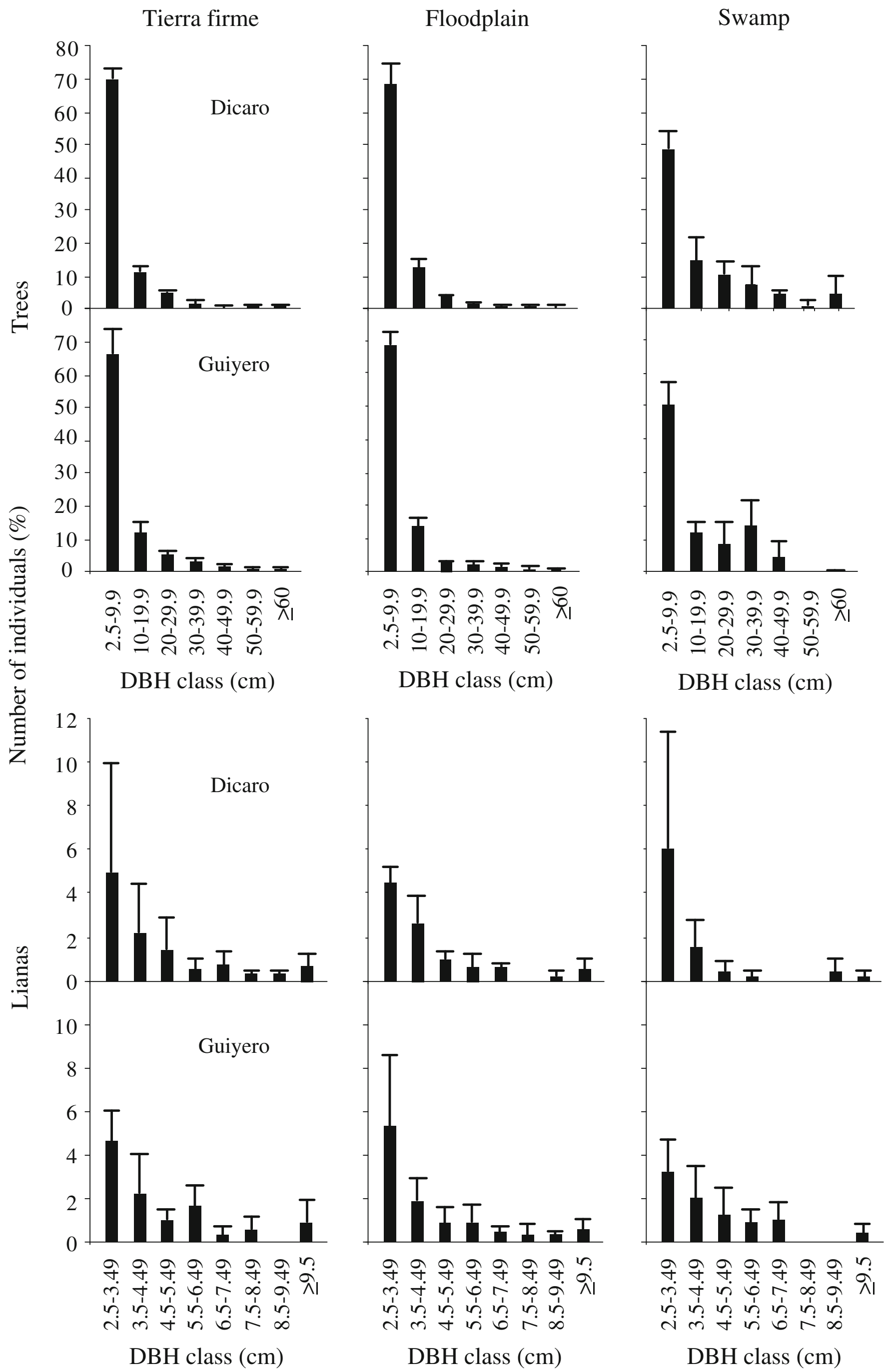

Fig. 3 Diameter class distribution of trees and lianas ≥ 2.5 cm dbh, respectively, for three broad forest types in two regions of the Yasuní National Park and the Huaorani Ethnic Reserve, Amazonian Ecuador. *Bars* indicate standard deviation

species-rich (Leguminosae, Lauraceae, Rubiaceae and Moraceae), while other families with a medium or low number of species, contained species which were greatly abundant in one habitat (e.g. *Mauritia flexuosa* in the Arecaceae, *Cyathea pungens* in the Cyatheaceae and *Cespedesia spathulata* in the Ochnaceae, all in swamp forests) or several broad forest types (e.g. *Rinorea lindeniana* in the Violaceae, *Phytelephas tenuicaulis* and *Euterpe precatoria* in the Arecaceae, *Matisia oblongifolia* and *Quararibea wittii* in the Bombacaceae). These patterns were found for both trees and lianas independently. In the

Table 9 Tukey HSD test coefficients comparing forest structure for both trees and lianas ≥ 2.5 cm dbh between three different habitats and two studied regions, as recorded in 25 plots of 0.1-ha in Yasuní National Park and the Huaorani Ethnic Reserve, Ecuadorean Amazon. Positive values indicate a statistically significant difference at $P < 0.05$

Life-forms	Habitats	Dicaro	Guiyero	All plots
Trees ≥ 2.5 cm dbh	Tierra firme vs. floodplain	−50.87	−1.82	−2.43
	Tierra firme vs. swamp	113.49	96.56	129.12
	Floodplain vs. swamp	110.04	26.36	83.70
Lianas ≥ 2.5 cm dbh	Tierra firme vs. floodplain	−14.45	−7.56	−5.22
	Tierra firme vs. swamp	−7.12	0.11	2.25
	Floodplain vs. swamp	−10.24	−2.89	−0.63

case of lianas, the most species-rich families (Leguminosae, Bignoniaceae and Malpighiaceae) included some of the most abundant species (e.g. *Machaerium cuspidatum*, *Callichlamys latifolia*, *Dicella julianii*) and these three families were also the most important in another Amazonian study which used the same inventory protocol (Macía 2008).

Spatial distribution of woody plants

Two of the most important hypotheses demonstrating plant distribution in tropical rain forests, together explain species spatial distribution in this study. The first one, the oligarchic dominance hypothesis support that western Amazonian upland tree communities tend to be dominated by limited sets of plant species, genera and families (Pitman et al. 2001) and later was also supported to other life-forms and habitats (Burnham 2004; Vormisto et al. 2004; Macía and Svenning 2005). The fact that the 30 most important species per forest types and region (totalling 119 species) accounted for 48.2% of total individuals give support to this hypothesis. At the same time, a total of 28 species with the highest IVI were reported in a single forest type (and in some cases in a single region) which could be explained by the environmental determinism hypothesis, that proposes forests to be a mosaic where plant species composition is determined by edaphic and other environmental site characteristics (Tuomisto et al. 2003b; Fine et al. 2005; John et al. 2007; Queenborough et al. 2007). However, a good demonstration of restriction implies a larger sample size.

Each of the broad forest types exhibited their particular suite of dominant tree species, which combine high landscape scale frequency (percentage of plots occupied) with high local abundance. In tierra firme habitats, three species in the genus *Matisia* and *Rinorea lindeniana*, dominated over large expanses which was also the case of past studies in Yasuní (Romoleroux et al. 1997; Romero-Saltos et al. 2001; Valencia et al. 2004). In floodplains, the five most common species belonged to five different families, including again *Rinorea lindeniana* and the palm *Phytelephas tenuicaulis* as the most abundant. In swamps, the family Arecaceae was the most important numerically with three species (largely *Mauritia flexuosa*, and *Euterpe precatoria* and *Attalea butyracea*) as clearly dominant, which have been reported in past studies in western Amazonia (Kahn 1991).

In general, the two diameter classes of trees showed similar floristic patterns across habitats and regions. Congruence among plant groups suggest that are probably responding to environmental variables and historical factors in the same way (Macía et al. 2007; Ruokolainen et al. 2007; cf. Duque et al. 2002).

In the case of lianas, it is striking the great dominance of the legume *Machaerium cuspidatum* in all broad forest types, which indicates a strong oligarchic dominance in this region (Nabe-Nielsen 2001; Burnham 2004). This could be explained by its high production of independent ramets induced by different environmental conditions (Nabe-Nielsen and Hall 2002). Two other liana species (*Combretum laxum* and *Uncaria guianensis*), were highly abundant in two of the three broad forest types. Past studies concluded that abundant lianas can be considered ecologically more generalist than trees along environmental variables and do not show restriction to one habitat (Burnham 2004; Macía et al. 2007). In any case, the ecological mechanisms creating such a predictable community structure need to be studied further.

As mentioned above, some of the most important species were exclusively distributed in one forest type, but other groups of species are more abundant in one habitat and less common in the other two (Table 6). This can be explained by the dispersal ability and ecological adaptation to environmental conditions of different species by the so-called mass effect hypothesis, which maintains that trees or lianas disperse their seeds over long distances and, therefore, there could be more woody plants growing in habitats where they cannot maintain viable populations in the long term (Shmida and Wilson 1985).

Finally, swamps and lianas were items with smaller sample size than tierra firme or trees and often, noted as differing from other forest types or life-forms. Therefore, conclusions obtained here need to be confirmed in further studies which carry out larger sample size.

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