

Woody plants diversity, floristic composition and land use history in the Amazonian rain forests of Madidi National Park, Bolivia

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Abstract A floristic inventory of woody plants was carried out to analyse the relationships between floristic similarity and geographical distance, and to compare the effect of land use history on the floristic composition between sites. Three lowland and two submontane sites were studied in Madidi, Bolivia. In one site, there is evidence of an Inca ruin. A total of 877 species and 12,822 individuals of woody plants with a diameter at breast height ≥ 2.5 cm were recorded in 44 0.1-ha plots. Fisher's Alpha index values were slightly higher for the lowlands than for the submontane. Floristic similarity was higher within sites than between sites as measured by both Sørensen and Steinhaus indexes. The fact that the 30 most important species per site (totalling 94 species) accounted for 61.7% of total individuals, support the hypothesis that Amazonian plant communities are dominated by a limited set of species, genera and families. On the other hand, 18 out of the 94 species were reported in a single site, suggesting that some species are patchy in distribution and may be environmentally determined. Both the oligarchy and environmental-determinism hypotheses can be complementary in order to understand floristic patterns of this region. The Ruins submontane site is floristically the most distinct, and past human disturbance is likely to be the main reason. Since species diversity (ranging from 53 to 122 species per plot) and density (ranging from 157 to 503 per plot) are highly variable in Madidi, to characterize the diversity of a site, it is necessary to quantify an average of 10 0.1-ha plots in a relatively small geographical area.

Keywords Beta diversity · Floristic patterns · Lianas · Past human disturbance · Plant communities · Sampling protocols · Southwest Amazonia · Tropical rain forest · Tropical trees

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Introduction

Floristic inventories in tropical rain forests practically never include all vascular plant habits, because a complete inventory would be excessively time consuming. This is mainly due to the high alpha diversity, the taxonomically poorly known flora and the presence of some life-forms, such as climbers and epiphytes, that are more difficult to sample and quantify. Most inventories have focused on trees, which traditionally have been considered as woody self-supporting stems with a diameter at breast height (dbh) greater than or equal to 10 cm, though other dbh cut-off limits, mainly 2.5 cm, have been used as well (e.g. Gentry 1988; Smith and Killeen 1998; Pitman et al. 2001; Romero-Saltos et al. 2001; Phillips et al. 2003a; ter Steege et al. 2003). Focusing on trees is logical, because they define the overall physical forest structure, contribute the main part of forest biomass and represent a substantial part of plant species diversity. However, other woody plants life-forms such as lianas, contribute notably to species richness of a given region but only a minority of woody plants studies include the inventory of trees and lianas within the same localities (Gentry and Dodson 1987; Clinebell et al. 1995; Pérez-Salicrup et al. 2001; Duque et al. 2002).

Recent assessments of the two most widely used plot or transect based protocols of floristic sampling (multiple 0.1-ha plots/transects including all woody plants ≥ 2.5 cm dbh, vs. a 1-ha plot just for trees ≥ 10 cm dbh) conclude that the 0.1-ha method is the more efficient approach for studying floristic diversity and composition (Phillips and Miller 2002; Phillips et al. 2003b).

The first vascular plants checklist of the larger Madidi region, defined as the area which includes three protected areas (the Madidi National Park, Apolobamba Biosphere Reserve, and Área Natural de Manejo Integrado Pilón-Lajas) plus a region surrounding these areas, contains 3,981 species from 23,515 collections (2,741 species for the Madidi National Park) which characterize the region as the most plant-species rich of any forest in Bolivia (Parker and Bailey 1991; Jørgensen et al. 2005a). The region includes 35 vegetation types in an elevational gradient from Amazonian forests and savanna vegetation at ca 150 m, through broad montane forests to subnival vegetation patches higher than 5,500 m (Navarro et al. 2004; Fuentes 2005). The focus of this study is the Amazonian rain forests (<1,100 m), which contain the highest vascular plant alpha diversity (Jørgensen et al. 2005a).

The Madidi region has been reported as nearly without long-term human perturbation (Parker and Bailey 1991), but there is evidence of Inca ruins dated to be more than 300-years old, in the northern part of the National Park (Armentia 1897; Renard-Casevitz et al. 1988; Macía and Svenning 2005). To what extent such long-term human disturbances have affected current composition and structure of plant community of tropical rain forest, is an unstudied issue in this region. Nevertheless, it has been reported that past anthropogenic disturbance may have long-lasting effects on the patterns of woody plant species composition (Balée and Campbell 1990; Thompson et al. 2002; Chazdon 2003; Heckenberger et al. 2003; cf. White and Hood 2004).

This study performs a comparative analysis of the woody plant diversity in the Amazonian region of the Madidi National Park, Bolivia within the framework of a joint research effort by the Herbario Nacional de Bolivia, Missouri Botanical Garden and Real Jardín Botánico de Madrid, established to inventory the poorly known vascular plant flora and vegetation of the Madidi region (Jørgensen et al. 2005b and papers cited therein). The objectives of the present paper were: (i) to determine species richness, floristic composition and structure of different life-forms in five study sites in the lowlands and submontane regions of the Madidi National Park; (ii) to analyse the relationships between floristic similarity and geographical distance, as measured within sites and between sites; and

(iii) to compare the effect of land use history on the floristic composition and forest structure of the Ruins site with respect to the other study sites.

Methods

Study area

Fieldwork was carried out in Madidi National Park, Amazonian Bolivia. The park protects a total of 18,854 km², ranging from 150 m to ca 6,000 m elevation, but we focused on the lowland and submontane regions in the east-southeastern part of the Park, at elevations between 260 and 1,070 m (Fig. 1). The study area contains the last foothills of the eastern Andes and often has a sharply dissected and steep topography which makes the area difficult to access. Rainfall varies considerably with elevation and topography. Mean annual precipitation is 2,335 mm and mean annual temperature 26.1°C (Navarro et al. 2004). The area experiences a dry period of between 3 and 4 months (from May to August) a year, during which periodic Patagonian winds (locally named *sur* or *surazo*) may occasionally drop the temperature to as low as 4.5°C (Macía and Svenning 2005). The inventoried plots were located in valleys and foothills landscapes where soil texture measured as the percentage of sand (>57% in all sites), clay and silt was rather homogeneous between sites (Macía et al. 2007).

The vegetation in the study area is old-growth mature tropical rain forest, with more than 90% of the landscape being non-inundated tierra firme forest and less than 10% being sporadically flooded forest by streams and rivers (Macía, personal observation). Permanently-flooded swamp forests were not found in the study area. Some high prized timber tree species (e.g. *Swietenia macrophylla*, *Cedrela odorata*, *Amburana cearensis*) had been logged in several areas with easy access near larger rivers before the area was declared a National Park in 1995. A preliminary classification of different vegetation types for the Madidi region is given in Fuentes (2005) and the first annotated checklist of the vascular plants for the region can be found in Jørgensen et al. (2005a).

Data collection

A total of 44 0.1-ha (50 × 20 m) plots were inventoried at five different sites along a north-south geographical gradient (Fig. 1). The selection of the sites was based on satellite imagery, available maps and accessibility. Three of them were located in the lowlands at 260–610 m elevation in the vicinity of the Aguapolo, Tequeje and Yariapo rivers with 6–11 plots per site, totalling 24 plots. The other two sites were in submontane forests at 735–1,070 m, in the surroundings of Inca ruins (Fig. 2) and in the Serranía de Tumupasa, with 8 and 12 plots per site respectively. All plots were placed in closed-canopy mature forests with no sign of any recent disturbance, with the exception of the Ruins site albeit human disturbance was more than 300 years ago (Armentia 1897; Renard-Casevitz et al. 1988). The forest structure at the Ruins site was indistinguishable from any other mature forest in the region. Plots were located to span the available habitat heterogeneity at each site, but each plot was placed to avoid heterogeneity in forest physiognomy or soils and therefore installed in a single broad forest type (tierra firme or floodplain) and excluding big canopy gaps. Plots within the same site were at least 500 m apart. Further information on plot location, geographical coordinates and elevations can be found appended to Macía and Svenning (2005).

All woody plants (trees, lianas and hemiepiphytes) with stems rooted independently within a plot and with a dbh (measured at 1.3 m above ground for all life-forms) equal to or

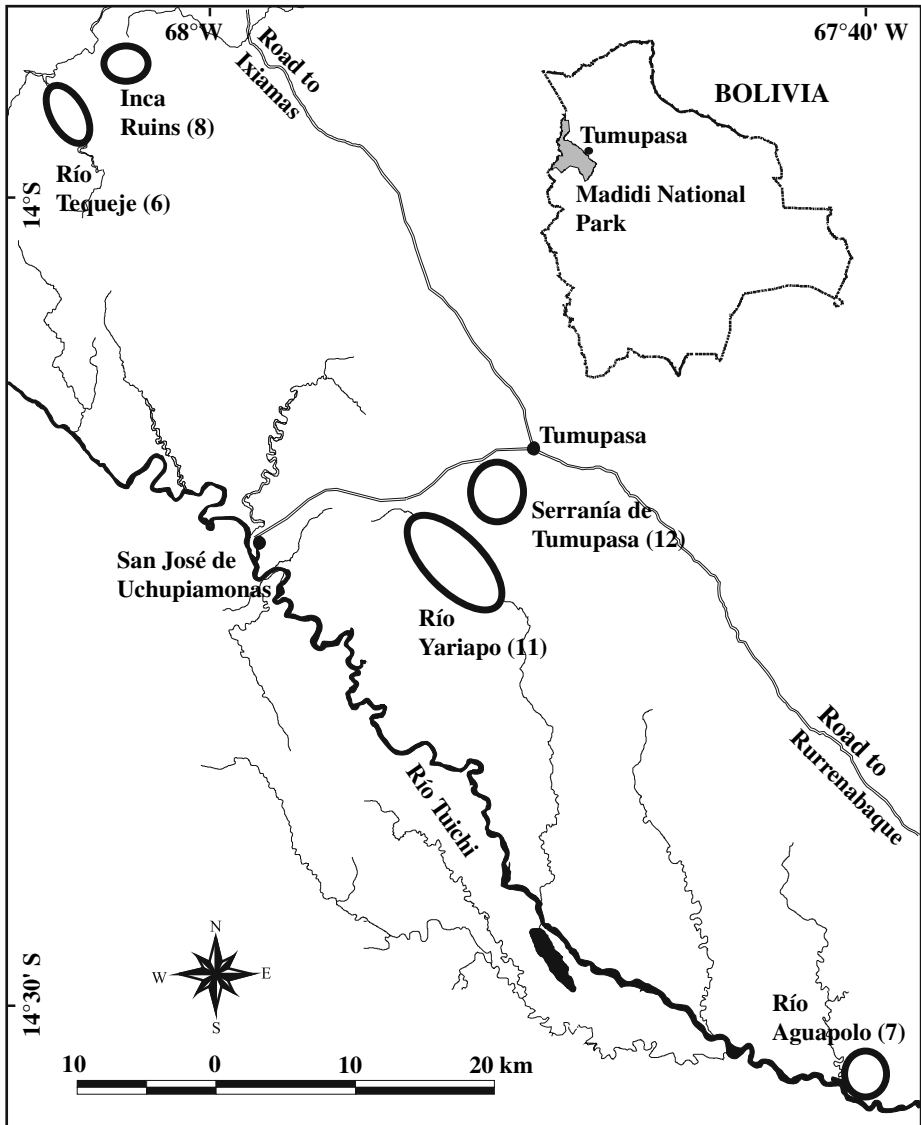


Fig. 1 Location of study area and the five study sites in Madidi National Park, Bolivian Amazonia. The number of plots in each site is given in parentheses

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). Multiple stems were measured separately, but all stems rooting in the same place were counted as one individual. Specimens (Macía et al. 3,876–7,051) were collected in 2001 and 2002 to voucher each name (per site) and in all doubtful cases to identify a stem. All voucher specimens can be found in the TROPICOS web page (<http://www.mobot.mobot.org/W3T/Search/vast.html>). 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



Fig. 2 Inca fort ruins at 950 m elevation in Madidi National Park, Amazonian Bolivia. In the surroundings of the ruins, eight 0.1-ha plots were inventoried

professional botanists which are deposited at LPB, MA, MO, NY and USZ herbaria (acronyms according to Holmgren et al. 1990). Duplicates of the specimens were distributed to taxonomic specialists worldwide who agreed to identify them (see Acknowledgements). A full set of duplicates is deposited at LPB and MA, and a nearly complete set at MO. Unicates are kept at LPB. In the following analyses, specimens identified to subspecific taxa were lumped under their species. All morphospecies were treated in the same way as identified species.

Data analyses

For the inventoried sites, species diversity, floristic composition and similarity were measured with quantitative and qualitative indices. For each of these analyses, woody plants were divided into six life-forms: (a) all woody plants (trees, lianas and hemiepiphytes ≥ 2.5 cm dbh); (b) all trees (≥ 2.5 cm dbh); (c) large trees (≥ 10 cm dbh); (d) small trees ($2.5 \geq \text{dbh} < 10$ cm); (e) all lianas (≥ 2.5 cm dbh); and (f) hemiepiphytes (≥ 2.5 cm dbh). The hemiepiphytes were too rare for meaningful analyses and were therefore excluded (see Table 1). Palms were included in the tree categories to facilitate analyses interpretation, although they are not properly trees.

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

To quantify and compare floristic composition between sites, the species Important 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 site is defined as the number of 0.1-ha plots in which it is present, and the sum of all frequencies as the total number of plots per site. 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).

Table 1 Total number of woody plant species and individuals per life-form at five study sites, totalling 44 0.1-ha plots inventoried in Madidi National Park, Bolivia

Attributes	Lowlands			Submontane		
	Aguapolo	Tequeje	Yariapo	Ruins	Tumupasa	
Total woody plant species	285 (70–101)	312 (80–137)	335 (53–103)	313 (61–97)	416 (58–122)	
Total woody plant families	62 (38–44)	72 (42–52)	66 (26–46)	66 (33–46)	77 (36–46)	
Total woody plant individuals	1936 (228–349)	2075 (277–416)	2626 (157–295)	2811 (209–503)	3374 (208–471)	
Trees \geq 2.5 cm dbh species	220 (63–83)	249 (64–111)	258 (48–91)	256 (51–87)	337 (54–103)	
Trees \geq 2.5 cm dbh individuals	1715 (203–297)	1866 (246–363)	2343 (129–275)	2576 (191–475)	3125 (202–431)	
Trees \geq 10 cm dbh species	120 (26–38)	126 (27–46)	140 (18–41)	147 (28–43)	206 (26–56)	
Trees \geq 10 cm dbh individuals	423 (47–72)	485 (71–95)	749 (47–91)	743 (69–119)	852 (49–105)	
Trees $<$ 10 cm dbh species	174 (49–63)	212 (51–89)	219 (39–67)	218 (33–69)	280 (40–89)	
Trees $<$ 10 cm dbh individuals	1292 (142–229)	1381 (151–277)	1594 (78–195)	1833 (116–364)	2273 (135–337)	
Lianas \geq 2.5 cm dbh species	65 (8–19)	67 (7–25)	75 (2–16)	59 (4–21)	79 (4–19)	
Lianas \geq 2.5 cm dbh individuals	214 (12–52)	199 (8–61)	278 (2–62)	231 (16–93)	242 (4–39)	
Hemiphytes \geq 2.5 cm dbh species	5 (0–4)	5 (0–2)	5 (0–1)	4 (0–3)	5 (0–3)	
Hemiphytes \geq 2.5 cm dbh individuals	7 (0–4)	10 (0–5)	5 (0–1)	4 (0–3)	7 (0–3)	
Mean Fisher's Alpha index	43.7 (33.0–51.0)	51.1 (37.7–71.3)	41.7 (21.7–62.1)	35.1 (19.7–51.1)	42.1 (26.7–63.0)	
Number of plots	7	6	11	8	12	
Mean elevation (m a.s.l.)	330 (260–420)	480 (425–550)	530 (460–610)	915 (735–1045)	880 (800–1,070)	

Mean plot Fisher's Alpha index and elevation are also given per site. Range values between plots are shown in brackets

To analyse the degree of floristic similarity within and between inventoried sites, two similarity indices were calculated: the Sørensen index and the Steinhaus index. These two indices 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). It is convenient to compare whether the results obtained with abundance data are different from the results obtained with presence-absence data. Similarity matrices were calculated separately for different life-forms: (a) all woody plants; (b) all trees; (c) large trees; (d) small trees; and (e) all lianas.

Cluster analyses were computed to classify the five inventoried sites on the basis of their floristic similarity, according to both the Sørensen and Steinhaus indices. An agglomerative cluster which uses a proportional-link linkage algorithm was applied; the connectedness level was set to 0.5 (i.e. midway between single and complete linkage). Clusters were performed separately for the five life forms, but because clusters obtained for all trees and small trees were very similar to the total woody plants cluster, they are not included here.

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

Sørensen and Steinhaus similarities and cluster analyses were computed in the program Le Proiciel R (available online at <http://www.bio.umontreal.ca/legendre/index-English.html>).

Owing to the sharply dissected topography in the study area, floods are sporadic and of short duration compared to those further downriver in rolling landscapes, where forests may be inundated for several weeks or months at a time. Therefore, the dichotomy of flood-plain and tierra firme forests is not important for defining floristic patterns in the Madidi region (see Macía and Svenning 2005; Macía et al. 2007 for details).

Results

Species diversity and density

A total of 12,822 individuals representing 877 species (359 genera and 94 families) of woody plants ≥ 2.5 cm dbh were found in 44 inventoried 0.1-ha plots. Mean total numbers of woody plant species and individuals were slightly smaller in the lowland sites than in the submontane sites (Table 1). The lowland Yariapo and the submontane Tumupasa sites had both the highest species richness and density for all studied life-forms and size classes.

Free-standing trees represented 90.7% of the total individuals and 78.3% of the total species, whereas values for lianas were 9.1% and 24.6% and hemiepiphytes 0.2% and 1.9%, 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 trees or rarely vice versa. In the lowland Aguapolo site, the lowest tree species richness was reported and in the submontane Ruins site the lowest liana species richness was reported. Hemiepiphytes were poorly represented in all sites, with similar number of species and individuals.

The five most common tree species in terms of number of individuals were *Rinorea viridifolia* (770), *Iriartea deltoidea* (720), *Rinorea guianensis* (274), *Styloceras brokawii* (267) and *Pseudolmedia laevis* (224); they accounted for 19.4% of tree individuals. The five most common liana species, *Roentgenia bracteomana* (69), *Byttneria pescapriifolia* (44), *Petrea maynensis* (35), *Combretum laxum* (29) and *Dalbergia frutescens* (26), accounted for 17.4% of liana individuals.

Table 2 Comparison of the 10 most important families (in bold) at five study sites, totalling 44 0.1-ha plots in Madidi National Park, Bolivia

Family	Lowlands			Submontane	
	Aguapolo	Tequeje	Yariapo	Ruins	Tumupasa
Annonaceae	9.79	13.63	5.27	7.25	6.60
Arecaceae	21.93	29.80	31.81	11.15	19.43
Bignoniaceae*	11.84	7.23	9.61	9.15	8.50
Buxaceae	–	1.98	11.52	1.45	3.71
Cecropiaceae	1.50	2.42	4.92	8.16	1.99
Chrysobalanaceae	14.60	4.84	3.32	6.87	5.92
Euphorbiaceae*	2.88	12.87	18.13	10.08	8.62
Flacourtiaceae	6.05	11.37	7.99	4.86	9.18
Lauraceae	9.59	7.59	13.22	9.42	9.27
Leguminosae*	21.28	17.95	22.27	18.56	18.60
Melastomataceae	2.48	4.17	2.90	18.36	3.65
Meliaceae	11.73	20.79	14.32	5.43	19.37
Moraceae	17.83	20.34	19.13	20.94	18.67
Myrtaceae	11.12	4.84	3.24	7.54	7.08
Piperaceae	2.87	1.23	9.93	4.53	7.41
Rubiaceae*	8.90	10.93	9.75	32.19	16.96
Violaceae	25.36	13.17	6.94	10.60	25.69

Numbers indicate the Family Importance Value Index (FIVI), which was obtained as the sum of their relative density, relative dominance and relative diversity. Families with the symbol * include liana species

Mean plot Fisher's Alpha index values were slightly higher for the lowlands than for the submontane region (Table 1). The highest diversity value was recorded in the lowland Tequeje site, whereas the lowest value was recorded in the submontane Ruins site.

Family and species composition

According to the FIVI, the most important families were Arecaceae (comprising 11 species), Lauraceae (47), Leguminosae (100) and Moraceae (31) (Table 2). The families Bignoniaceae (43 species, mainly lianas), Euphorbiaceae (24), Meliaceae (20), Rubiaceae (55) and Violaceae (5) also had high FIVI values in four study sites. Overall, Leguminosae, Rubiaceae and Lauraceae were the most species rich tree families whereas the richest for lianas were Bignoniaceae (40 species), Leguminosae (31) and Malpighiaceae (30). The ten most important families per site (totalling 17 families; Table 2) accounted for 66.4% of the individuals and 56.2% of the species. In the lowland Yariapo site, Buxaceae (only represented by the small tree *Styloceras brokawii*) was among the most important families, but in Aguapolo not a single stem of this species was found. The families Chrysobalanaceae and Myrtaceae were among the most important only in Aguapolo, and Piperaceae only in Yariapo. Cecropiaceae and Melastomataceae only ranked among the most important families at the submontane Ruins site.

According to the IVI, the 30 most important species per site (totalling 94 species) accounted for 61.7% of the total individuals, and both *Iriartea deltoidea* and *Rinorea viridifolia* were the sole species that reached high values in all five sites (Table 3). In the lowlands, nine species (*Celtis schippii*, *Leonia crassa*, *Lunania parviflora*, *Meliosma herbertii*, *Otoba parvifolia*, *Pseudolmedia laevis*, *Socratea exorrhiza*, *Sorocea briquetii* and *Tetragastris altissima*) were recorded as the most important on all three inventoried sites, and all of them

reached ≥ 10 cm dbh (Table 3). However, in the submontane forests only *Piper obliquum*, *Pseudolmedia laevigata* and *Quararibea wittii* were important species shared in both sites.

Based on IVI, a total of 18 species were very important at a single site, especially in the submontane Ruins which was characterized by its specific suite of 9 species (*Amaioua guianensis*, *Aspidosperma marcgravianum*, *Connarus perrottetii*, *Helicostylis tomentosa*, *Hippotis* sp., *Miconia pyrifolia*, *M. splendens*, *Pourouma guianensis*, and *Sacoglottis mattogrossensis*; Table 3). Of the other nine species, five of them were found only at Aguapolo (*Brosimum alicastrum*, *Cheilochlinium cognatum*, *Hirtella racemosa*, *Pachira* sp., and *Trichilia* aff. *pleeana*), two in Tumupasa (*Condaminea elegans* and *Rinorea guianensis*) and one each in Tequeje (*Oxandra* aff. *acuminata*) and Yariapo (*Mollinedia ovata*). Ten out of the 94 species were small trees that never reached 10 cm dbh, and three other species were lianas (*Byttneria pescapriifolia*, *Petrea maynensis* and *Roentgenia bracteomana*), which were reported only in the lowlands.

Floristic similarity between sites

Floristic similarity was clearly higher within sites than between sites for all life-forms and size classes as measured with both Sørensen and Steinhaus indexes (Tables 4 and 5, respectively). The coefficients obtained with the Sørensen index were generally higher than the coefficients obtained with the Steinhaus index, but overall patterns were similar.

The submontane Ruins site showed the lowest floristic similarity values in comparison with the other four sites for all life-forms and using both indexes (Tables 4 and 5). In general terms, the resemblance coefficients were similar between the lowland and submontane Tumupasa sites for all life-forms with the exception of lianas, which were slightly higher among the lowlands with both indexes. The lowland Yariapo and Tequeje sites had the highest coefficients between sites albeit in the case of lianas, values were much more similar.

The floristic similarity clusters based on the Sørensen and Steinhaus indexes were similar for all the life-forms (Fig. 3). The Ruins site was separated from the other sites in all the plant group dendrograms. The Yariapo, Tequeje and Tumupasa sites were closer together whereas Aguapolo site was slightly more different than the other lowland sites.

Community structure

The distribution of tree diameter classes showed an inverse J-shape curve with high similarity among all the study sites (Fig. 4). Within the tree category, small trees (< 10 cm dbh) represented 72% of the individuals whereas large trees (≥ 10 cm dbh) comprised 28% of the individuals. Structurally, lianas showed more variability in the mean number of individuals per site than trees. The lowlands region had higher number of liana stems than the submontane region, and Aguapolo was the most abundant liana site. The community structure of the Ruins site was very similar to the other inventoried sites (Fig. 4).

Discussion

Diversity and floristic composition of Madidi lowlands and submontane forests

Species diversity and density are highly variable in the Madidi Amazonian rain forests, with total woody plant species ranging from 53 to 122 and the total number of individuals

Table 3 Comparison of the 30 most important species (in bold) at five study sites, totalling 44 0.1-ha plots in Madidi National Park, Bolivia

Family	Scientific name	Lowlands			Submontane	
		Aguapolo	Tequeje	Yariapo	Ruins	Tumupasa
Anac.	<i>Tapirira guianensis</i> Aubl.	1.08	1.54	1.48	1.61	2.01
Anno.	<i>Oxandra</i> aff. <i>acuminata</i> Diels		7.34			
	<i>Unonopsis floribunda</i> Diels	5.75	3.31	1.77	0.81	0.76
Apoc.	<i>Aspidosperma marcgravianum</i> Woodson					5.18
Aral.	<i>Dendropanax arboreus</i> (L.) Decne. & Planch.	0.92	2.35	1.95	0.20	0.86
Arec.	<i>Astrocaryum murumuru</i> Mart.	5.29	0.31	2.66		1.28
	<i>Euterpe precatorea</i> Mart.	6.39	3.31	2.13	1.51	
	<i>Iriartea deltoidea</i> Ruiz & Pav.	6.22	21.16	20.82	8.53	18.07
	<i>Socratea exorrhiza</i> (Mart.) H. Wendl.	2.40	5.01	4.01	1.87	0.49
Bign.	**Roentgenia bracteomana (K. Schum. ex Sprague) Urb.	2.95	1.76	2.00		
Bomb.	<i>Pachira</i> (MJM 6897)	2.68				
	<i>Quararibea wittii</i> K. Schum. & Ulbr.		1.59	4.80	2.39	5.73
Burs.	<i>Protium rhynchophyllum</i> (Rusby) D.C. Daly	3.90	2.85	1.78		0.60
	<i>Protium spruceanum</i> (Benth.) Engl.				6.25	0.29
	<i>Tetragastris altissima</i> (Aubl.) Swart	3.06	2.73	2.85	1.81	4.56
Buxa.	<i>*Styloceras brokawii</i> A.H. Gentry & R.B. Foster		2.14	12.28	1.29	4.45
Capp.	<i>Capparis prisca</i> J.F. Macbr.				0.38	1.84
Cecr.	<i>Pourouma guianensis</i> Aubl.				7.51	
Cela.	<i>Gymnosporia urbaniana</i> (Loes.) Liesner		1.95	0.63		1.86
Chry.	<i>*Hirtella racemosa</i> Lam.	12.18				
	<i>Licania kunthiana</i> Hook. f.	1.96			3.72	0.68
Comb.	<i>Terminalia oblonga</i> (Ruiz & Pav.) <i>Steud.</i> Cambess.	0.43	2.05	2.29		0.69
Conn.	<i>Connarus perrottetii</i> (DC.) Planch.				3.82	
Cyat.	<i>Cyathia delgadii</i> Sternb.				2.74	0.49
Dich.	<i>Tapura juruana</i> (Ule) Rizzini	2.75	0.98	0.54	0.65	3.21
Elae.	<i>Sloanea eichleri</i> K. Schum				2.34	1.10
	<i>Sloanea fragrans</i> Rusby	0.25	0.31	2.35		
Euph.	<i>Alchornea glandulosa</i> Poepp. <i>*Aparisthium cordatum</i> (Juss.) Baill.			1.50	2.45	0.29
	<i>Drypetes</i> (MJM 4967)		6.73	0.29	4.26	0.28
	<i>Hieronyma alchorneoides</i> Allemão	0.27	2.23	2.76		0.14
	<i>Mabea anadena</i> Pax & K. Hoffm.		0.75	3.29		
Flac.	<i>Hasseltia floribunda</i> Kunth	1.54	4.36	2.46	1.36	4.82
	<i>Lunania parviflora</i> Spruce ex Benth.	2.68	4.88	4.65		2.94
Hipp.	<i>*Cheiloclinium cognatum</i> (Miers) A.C. Sm.	4.22				
Humi.	<i>Sacoglottis mattogrossensis</i> Malme				2.64	
Laci.	<i>Lacistema aggregatum</i> (P.J. Bergius) Rusby	1.66	0.23	0.17	2.32	0.16
Laur.	<i>Ocotea obovata</i> (Ruiz & Pav.) Mez	0.58	0.47	2.62		0.99
Lecy.	<i>Eschweilera</i> (MJM 7018)				4.04	0.29
Legu.	<i>Inga thibaudiana</i> DC. <i>Swartzia myrtifolia</i> Sm.	0.25			2.56	0.14
		2.11		0.21		
Mela.	<i>Miconia pyriformis</i> Naudin				4.17	
	<i>Miconia splendens</i> (Sw.) Griseb.				2.55	
Meli.	<i>Guarea guidonia</i> (L.) Sleumer	3.68	1.03	0.36	0.27	2.36
	<i>Guarea kunthiana</i> A. Juss.	0.73	0.22	1.80	0.41	3.28
	<i>Guarea macrophylla</i> Vahl		5.70	2.75		0.86
	<i>Guarea pterorhachis</i> Harms		4.68	3.71	0.58	4.11
	<i>Guarea purusana</i> C. DC.		2.19	0.71		

Table 3 continued

Family	Scientific name	Lowlands			Submontane	
		Aguapolo	Tequeje	Yariapo	Ruins	Tumupasa
	<i>Guarea</i> (MJM 6832)	0.50		2.41		0.90
	<i>Trichilia inaequilatera</i> T.D. Penn.	1.24	0.78	0.64	0.20	1.83
	<i>Trichilia pallida</i> Sw.	1.15	2.09		0.51	0.83
	<i>Trichilia pleeana</i> (A. Juss.) C. DC.	0.76	3.69	1.76	0.52	3.13
	<i>Trichilia</i> (MJM 4662)		0.79	0.77	0.46	2.68
	<i>Trichilia</i> aff. <i>pleeana</i> (A. Juss) C. DC.	2.50				
Moni.	* <i>Mollinedia ovata</i> Ruiz & Pav.			4.87		
Mora.	<i>Brosimum alicastrum</i> Sw.	4.03				
	<i>Clarisia biflora</i> Ruiz & Pav.	0.51	1.44	2.85		0.46
	<i>Clarisia racemosa</i> Ruiz & Pav.	1.17	0.24	1.03	0.40	1.96
	<i>Helicostylis tomentosa</i> (Poepp. & Endl.) Rusby				5.67	
	<i>Poulsenia armata</i> (Miq.) Standl.	0.38	1.02	2.86		1.80
	<i>Pseudolmedia laevigata</i> Trécul		1.22		10.86	3.31
	<i>Pseudolmedia laevis</i> (Ruiz & Pav.) J.F. Macbr.	6.51	6.83	6.91	0.21	4.77
	<i>Sorocea briquetii</i> J.F. Macbr.	4.05	2.97	2.64	0.20	0.32
	<i>Trophis caucana</i> (Pittier) C.C. Berg			0.49		2.08
Myri.	<i>Otoba parvifolia</i> (Markgr.) A.H. Gentry	4.17	2.65	5.34	0.21	3.83
	<i>Virola calophylla</i> (Spruce) Warb.		2.45		0.76	
	<i>Virola sebifera</i> Aubl.	0.82	2.94	1.33	0.49	0.22
Myrs.	<i>Stylogyne cauliflora</i> (Mart. & Miq.) Mez		3.34	3.16		0.51
Myrt.	<i>Myrcia paivae</i> O. Berg	0.24			2.80	
	<i>Myrciaria floribunda</i> (H. West ex Willd.) O. Berg	3.14		0.34	2.49	0.19
Nyct.	<i>Neea</i> (MJM 5577)		2.16		2.23	0.90
Pipe.	* <i>Piper heterophyllum</i>			1.82		3.39
	* <i>Piper obliquum</i> Ruiz & Pav.	0.41	1.01	2.42	2.58	2.01
	* <i>Piper pseudo-arboreum</i> Yunck.			0.17	3.15	
Poly.	<i>Triplaris setosa</i> Rusby	3.58	0.56	1.61	0.95	1.05
Rubi.	<i>Amaioua guianensis</i> Aubl.				13.77	
	<i>Bathysa peruviana</i> K. Krause				8.30	0.48
	<i>Condaminea elegans</i> Delprete					1.85
	<i>Hippotis</i> (MJM 6235)				4.65	
	<i>Macrocneum roseum</i> (Ruiz & Pav.) Wedd.		1.00	1.87		2.33
Sabi.	<i>Meliosma herbertii</i> Rolfe	2.69	3.46	2.33	0.21	1.66
Sapi.	<i>Allophylus petiolulatus</i> Radlk.	0.23	0.91		0.22	3.30
Sipa.	* <i>Siparuna bifida</i> (Poepp. & Endl.) A. DC.	0.25	6.51	3.31	0.48	0.28
	* <i>Siparuna guianensis</i> Aubl.	6.22			0.20	0.73
Sola.	<i>Solanum</i> (MJM 6036)		0.23	0.17		2.73
Ster.	** <i>Bytneria pescarpiifolia</i> Britton		0.23	2.52		
	<i>Theobroma cacao</i> L.	1.54	1.07	1.82	0.43	2.60
Tili.	<i>Pentaplaris davidsmithii</i> Dorr & C. Bayer	8.11	0.83	2.26		1.63
Ulma.	<i>Celtis schippii</i> Standl.	3.98	2.16	4.36	0.20	1.45
Verb.	** <i>Petrea maynensis</i> Huber	3.27	0.59	0.34		
Viol.	<i>Leonia crassa</i> L.B. Sm. & A. Fernández	3.15	2.44	3.71		0.72
	<i>Leonia glycyarpa</i> Ruiz & Pav.			0.20	5.02	
	<i>Rinorea guianensis</i> Aubl.					15.85
	<i>Rinorea viridifolia</i> Rusby	23.65	11.37	3.42	6.02	10.76

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

Table 4 Pair-wise comparison of floristic similarity as measured by the Sørensen index (for presence/absence data) between three lowland and two submontane study sites as recorded at 44 0.1-ha plots in Madidi National Park, Bolivia

Life-form	Sites	Lowlands			Submontane	
		Aguapolo	Tequeje	Yariapo	Ruins	Tumupasa
Total woody plants	Aguapolo	0.38 ± 0.12				
	Tequeje	0.23 ± 0.06	0.39 ± 0.06			
	Yariapo	0.23 ± 0.10	0.28 ± 0.10	0.32 ± 0.12		
	Ruins	0.11 ± 0.05	0.11 ± 0.05	0.09 ± 0.06	0.31 ± 0.14	
	Tumupasa	0.20 ± 0.06	0.23 ± 0.05	0.23 ± 0.08	0.12 ± 0.09	0.32 ± 0.09
Trees ≥ 2.5 cm dbh	Aguapolo	0.41 ± 0.14				
	Tequeje	0.25 ± 0.07	0.42 ± 0.06			
	Yariapo	0.26 ± 0.12	0.30 ± 0.11	0.36 ± 0.13		
	Ruins	0.13 ± 0.06	0.12 ± 0.06	0.10 ± 0.07	0.33 ± 0.15	
	Tumupasa	0.21 ± 0.07	0.25 ± 0.05	0.25 ± 0.09	0.13 ± 0.10	0.35 ± 0.10
Trees ≥ 10 cm dbh	Aguapolo	0.35 ± 0.16				
	Tequeje	0.21 ± 0.10	0.27 ± 0.11			
	Yariapo	0.22 ± 0.13	0.23 ± 0.10	0.28 ± 0.12		
	Ruins	0.07 ± 0.04	0.07 ± 0.05	0.07 ± 0.05	0.26 ± 0.14	
	Tumupasa	0.17 ± 0.08	0.19 ± 0.07	0.18 ± 0.10	0.08 ± 0.07	0.24 ± 0.09
Trees <10 cm dbh	Aguapolo	0.38 ± 0.14				
	Tequeje	0.24 ± 0.06	0.39 ± 0.06			
	Yariapo	0.23 ± 0.11	0.28 ± 0.11	0.32 ± 0.13		
	Ruins	0.12 ± 0.06	0.12 ± 0.06	0.09 ± 0.08	0.30 ± 0.14	
	Tumupasa	0.19 ± 0.07	0.23 ± 0.05	0.23 ± 0.09	0.12 ± 0.09	0.33 ± 0.11
Lianas ≥ 2.5 cm dbh	Aguapolo	0.20 ± 0.11				
	Tequeje	0.10 ± 0.07	0.19 ± 0.11			
	Yariapo	0.10 ± 0.08	0.11 ± 0.11	0.13 ± 0.12		
	Ruins	0.04 ± 0.06	0.03 ± 0.04	0.02 ± 0.04	0.11 ± 0.12	
	Tumupasa	0.08 ± 0.07	0.08 ± 0.07	0.09 ± 0.08	0.04 ± 0.06	0.10 ± 0.09

Mean ± standard deviation Sørensen coefficients are presented for different life-forms and size classes

ranging from 157 to 503 among the 0.1-ha plots. This clearly indicates that maximizing understanding of the diversity of a site requires inventory of several 0.1-ha plots to be installed in different sites with evidence of variation in environmental variables (soil, flooding and topography) and historical features, both of which strongly influence alpha diversity (Gentry 1988; Duivenvoorden 1995; Svenning 1999; Tuomisto et al. 2003; Vormisto et al. 2004b; Fine et al. 2005).

The most species-diverse 0.1-ha plots were also the plots with the highest density. For trees, this is a common pattern also shown in many other past studies (Romero-Saltos et al. 2001; Duque et al. 2002; Phillips and Miller 2002) but in the case of lianas it is unclear. This could be due to sampling error caused by the smaller number of liana individuals inventoried per plot. In any case, liana density and diversity were relatively high (9.1% of total individuals, representing 24.6% of total species); this confirms earlier observations that Madidi region has high concentration of lianas compared to other Neotropical sites (Foster 1991; Foster and Gentry 1991; Burnham 2004). This could be due to the high density of large trees that seem to be greater than normal in Amazonia (Macía and Svenning 2005).

The coefficients obtained in the Fisher's Alpha diversity index indicate that there is no clear differences in species richness between the lowland and submontane sites, although there is high variability in plot-diversity coefficients, which in some cases is greater than

Table 5 Pair-wise comparison of floristic similarity as measured by the Steinhaus index (for abundance data) between three lowland and two submontane study sites as recorded in 44 0.1-ha plots in the Madidi National Park, Bolivia

Life-form	Sites	Lowlands			Submontane	
		Aguapolo	Tequeje	Yariapo	Ruins	Tumupasa
Total woody plants	Aguapolo	0.38 ± 0.16				
	Tequeje	0.20 ± 0.08	0.33 ± 0.10			
	Yariapo	0.16 ± 0.09	0.23 ± 0.11	0.24 ± 0.12		
	Ruins	0.09 ± 0.08	0.09 ± 0.08	0.07 ± 0.07	0.23 ± 0.13	
	Tumupasa	0.16 ± 0.07	0.21 ± 0.06	0.19 ± 0.09	0.10 ± 0.09	0.28 ± 0.11
Trees ≥ 2.5 cm dbh	Aguapolo	0.41 ± 0.17				
	Tequeje	0.22 ± 0.09	0.35 ± 0.11			
	Yariapo	0.17 ± 0.10	0.24 ± 0.11	0.26 ± 0.13		
	Ruins	0.10 ± 0.09	0.10 ± 0.08	0.07 ± 0.08	0.24 ± 0.13	
	Tumupasa	0.17 ± 0.08	0.22 ± 0.07	0.20 ± 0.09	0.10 ± 0.10	0.29 ± 0.12
Trees ≥ 10 cm dbh	Aguapolo	0.30 ± 0.15				
	Tequeje	0.18 ± 0.09	0.27 ± 0.13			
	Yariapo	0.18 ± 0.12	0.23 ± 0.13	0.25 ± 0.15		
	Ruins	0.06 ± 0.05	0.09 ± 0.08	0.09 ± 0.09	0.24 ± 0.13	
	Tumupasa	0.15 ± 0.08	0.19 ± 0.08	0.19 ± 0.11	0.10 ± 0.09	0.25 ± 0.11
Trees <10 cm dbh	Aguapolo	0.33 ± 0.15				
	Tequeje	0.18 ± 0.09	0.31 ± 0.09			
	Yariapo	0.13 ± 0.07	0.20 ± 0.09	0.22 ± 0.12		
	Ruins	0.08 ± 0.10	0.08 ± 0.09	0.05 ± 0.06	0.20 ± 0.13	
	Tumupasa	0.14 ± 0.07	0.18 ± 0.07	0.16 ± 0.08	0.09 ± 0.10	0.27 ± 0.12
Lianas ≥ 2.5 cm dbh	Aguapolo	0.19 ± 0.11				
	Tequeje	0.08 ± 0.07	0.13 ± 0.08			
	Yariapo	0.08 ± 0.06	0.08 ± 0.09	0.09 ± 0.10		
	Ruins	0.02 ± 0.04	0.01 ± 0.02	0.02 ± 0.04	0.06 ± 0.07	
	Tumupasa	0.05 ± 0.05	0.06 ± 0.06	0.06 ± 0.06	0.03 ± 0.05	0.07 ± 0.07

Mean ± standard deviation Steinhaus coefficients are presented for different life-forms and size classes

100% within sites. The average diversity value for the Tumupasa submontane site was similar to the average values for the lowland sites, although the Tequeje lowland site clearly showed the highest value and the submontane Ruins site showed the lowest.

The results obtained here confirm past observations that dominant families represented in tropical forests are highly predictable (e.g. Gentry 1988; Richards 1996; Terborgh and Andresen 1998; ter Steege et al. 2000). Families found with the highest FIVI are basically among the same most important families reported in many other Amazonian floristic studies and particularly in Bolivia, when using the same sampling protocol (Foster and Gentry 1991; Kessler and Helme 1999; Phillips and Miller 2002; Araujo-Murakami 2005a, b, c). In some families, the FIVI was high because they were among the most species-rich (e.g. Leguminosae, Rubiaceae and Lauraceae), while other families scored high because they include extremely abundant species (e.g. *Iriarteia deltoidea* in the Arecaceae, *Styloceras brokawii* in the Buxaceae or *Rinorea viridifolia* and *R. guianensis* in the Violaceae). For the lianas, the most important families were the most species-rich (Bignoniaceae, Leguminosae and Malpighiaceae).

The fact that the 30 most important species per site (totalling 94 species) accounted for 61.7% of total individuals and more specifically, the five most abundant tree and liana species accounted for 19.4% and 17.4% of all individuals respectively, support the hypothesis that Amazonian plant communities are dominated by a limited set of species, genera and families (Pitman et al. 2001; Burnham 2004; Vormisto et al. 2004a; Macía and Svenning

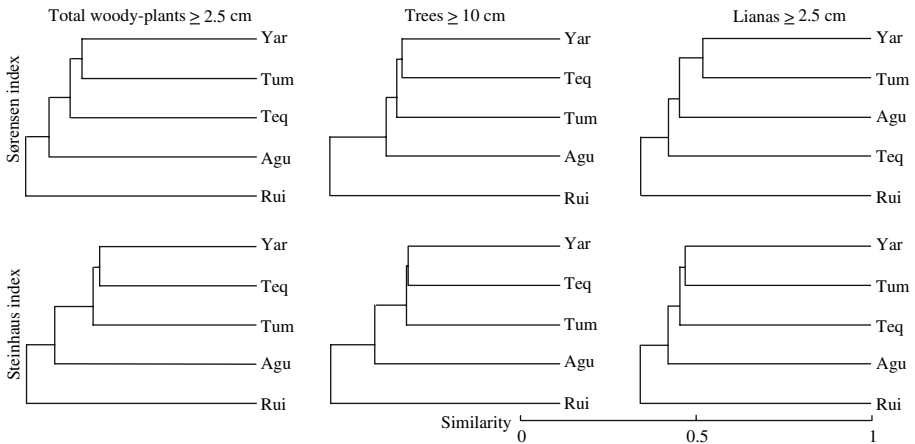


Fig. 3 Floristic similarity clusters for different life-forms at five inventoried sites, totalling 44 0.1-ha plots in the lowlands and submontane areas of the Madidi National Park, according to both Sørensen index (species presence-absence data) and Steinhaus index (species abundance data). The clusters for all trees (dbh ≥ 2.5 cm) and small trees ($2.5 \geq$ dbh < 10 cm) are not included in this figure because they were very similar to the total woody plant cluster. The site abbreviations are as follows: Agu. for Aguapolo; Rui. for Ruins; Teq. for Tequeje; Tum. for Tumupasa; and Yar. for Yariapo

2005; cf. Tuomisto et al. 2003). These observations also add support to several studies that report the canopy palm *Iriartea deltoidea* is frequently one of the most abundant species in both 0.1-ha and 1-ha plot inventories in Western Amazonia (Clark et al. 1999; Pitman et al. 2001; Vormisto et al. 2004a). Similarly, *Rinorea* species (here *R. viridifolia* and *R. guianensis*) are remarkably dominant in Bolivian lowland forests (Foster and Gentry 1991; Flores et al. 2002; Araujo-Murakami et al. 2005a, b) as well as in other Western Amazonia rain forests (Romoleroux et al. 1997; Romero-Saltos et al. 2001; Phillips and Miller 2002). Future studies are needed to clarify the ecological mechanisms creating such large-scale community structure, and particularly for *Rinorea* species.

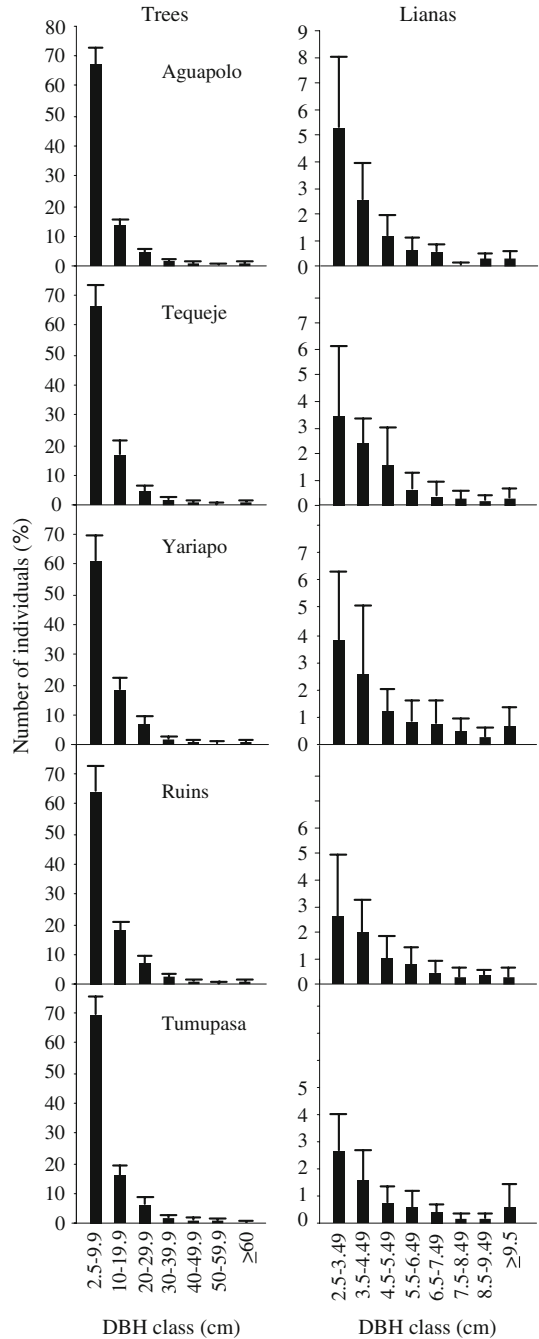
A total of 18 dominant species were reported in a single site in this study (Table 3) which could be explained by several factors including deterministic characteristics, such as soil or other environmental site variables that create defined forest mosaics (Gentry 1988; Tuomisto et al. 1995, 2003) and to a lesser degree by random effects (Hubbell 2001). Both hypotheses have been reported as important in explaining differences in species composition among sites (Duque et al. 2002; Phillips et al. 2003; Tuomisto et al. 2003; Vormisto et al. 2004a; Macía et al. 2007). Further studies which quantitatively measure the environmental heterogeneity for the dominant species would be of great interest to understand patterns of patchy distribution of Amazonian plants.

Two of these points of view (oligarchic dominance and environmental-determinism hypotheses) have usually been considered as opposite lines of thinking to explain plant distribution in Western Amazonia (Tuomisto et al. 2003). However, both views are not mutually exclusive and may in fact be complementary and necessary in order to understand floristic patterns in the Amazonian rain forests of the Madidi region.

Long-term effects of human disturbance

The Ruins submontane site is notably different floristically from all inventoried sites for the following evidences. First, mean plot Fisher's Alpha index was the lowest in the study area,

Fig. 4 Relative distribution of diameter classes between trees and lianas ≥ 2.5 cm dbh respectively, for the five inventoried sites in the lowlands and submontane areas of Madidi National Park, Bolivia. Bars indicate standard deviation



and also the minimum value for all plots was recorded here. Second, the families Cecropiaceae and Melastomataceae showed very high FIVI values compared with other sites. These two families are characteristic of gaps in rain forests and are predominant in second growth (Gentry 1993). Third, according to the IVI values it contains the highest number of

exclusive dominant species (9) which were found only at this site. Fourth, the highest dissimilarity, i.e. lowest similarity values between sites as measured with both species presence/absence data (Sørensen index) and species abundance data (Steinhaus index), was found in the pair-wise comparison involving the Ruins site for all life-forms. Fifth, floristic similarity clusters computed with both Sørensen and Steinhaus indexes showed the Ruins site as the most dissimilar for all plant groups. However, its forest structure was similar to the other studied sites and indistinguishable from other mature forests, although lianas showed more structural variability than trees.

Some studies have reported that past human disturbance may have long-lasting effects on plant community (Balée and Campbell 1990; Thompson et al. 2002; Chazdon 2003; van Gernerden et al. 2003) although others did not find any current anthropogenic effect (White and Hood 2004). The present study adds to the first series of observations and infer past human disturbance is likely to be the main reason of floristic differences in the Ruins site.

It is widely accepted that disturbance promotes liana abundance in secondary and fragmented forests (Putz 1984; Schnitzer and Carson 2000; Schnitzer 2005), but in cases of very old disturbance, liana regeneration is lower (DeWalt et al. 2000). In the case of the Ruins site, where disturbance occurred more than 300 years ago, liana density was similar to other inventoried sites, but its diversity was the lowest.

Comparison of woody plants in 0.1-ha inventories in Bolivia

Using the 0.1-ha plot/transect protocol, the Amazonian rain forests of Bolivia (<1000 m elevation) proved to be its most diverse forests (Table 6; Jørgensen et al. 2005a). However, there are some dry forest plots in the Department of Pando, which challenge these lowland rain forests as having the highest diversity (Phillips and Miller 2002).

The present study supports the observation that liana abundance is higher in seasonal regions (Schnitzer 2005) since Bolivian dry forests overall have a higher number of liana individuals compared to other wet habitats (Table 6).

The Gentry-transect sampling protocol (2 × 500 m) produced higher values of woody plant diversity and density as compared to a single 0.1-ha plot in all habitats (Table 1 vs. Table 6). The plot sampling protocol (20 × 50 m and 10 × 100 m) produced similar diversity and density data. These diversity and density differences between transects and plots may be due to several factors. It is clear that a narrow transect protocol will study a more heterogeneous area than a plot protocol, and therefore the number of species should be higher, but it is unclear why plant density would be higher. Perhaps, the Gentry-transects did not strictly follow a compass-direction line and changed periodically to incorporate some new woody plants to the inventory. In any case, this transect vs. plot comparison indicates that to gain a more comprehensive overall idea of woody plant richness patterns in a given region, it is necessary to inventory several plots/transects at an average of 10 0.1-ha plots (here between 6 and 12 plots) and at least 500 m apart in a relatively small geographical area (here between 20 and 40 km² per site), as plot diversity and density data can vary more than 100% within sites (Tables 1, 6). Since the two most common 0.1-ha plot protocols produced similar data, their application to inventory woody plants make no qualitative difference. However, in the interest of rigor it is recommended to be consistent and use a single sampling method within a site or region.

It has been suggested that for more rigorous comparisons of diversity at different sites, one should include samples with approximately equal numbers of individuals (ignoring the area), using the same sampling protocol and dbh limit, and preferably with 2,000+ individuals inventoried (Condit et al. 1998). In order to make more precise floristic comparisons of

Table 6 Comparison of diversity and density of woody plants (trees and lianas) in 0.1-ha plot/transect inventories (inv.) carried out in Bolivia

Vegetation type	Elevation (m)	Department	Woody plants ≥ 2.5 cm		Trees ≥ 2.5 cm		Lianas ≥ 2.5 cm		Alpha Fisher dimension (m ²)	Plot/Transect dimension (m ²)	No. Inv.	Reference
			Spp.	Indiv.	Spp.	Indiv.	Spp.	Indiv.				
Lowland forest	260–420	La Paz	285	1,936	220	1715	65	214	92.2	1000 (50 × 20 m)	7	This study
Lowland forest	280	La Paz	204	434	151	341	53	93	150.2	1000 (500 × 2 m)	1	Foster and Gentry (1991)
Lowland forest	300–360	La Paz	310	2,680	274	2369	36	311	90.6	1000 (100 × 10 m)	12	Araujo-Murakami et al. (2005a)
Lowland forest	300–600	La Paz	294	2,776	262	2532	32	244	83.1	1000 (100 × 10 m)	13	Araujo-Murakami et al. (2005b)
Ridge top lowland foothills	360–380	La Paz	175	483	131	398	44	85	98.6	1000 (500 × 2 m)	1	Foster and Gentry (1991)
Lowland forest	425–550	La Paz	312	2,075	249	1866	67	199	101.9	1000 (50 × 20 m)	6	This study
Lowland forest	460–610	La Paz	335	2,626	258	2343	75	278	101.9	1000 (50 × 20 m)	11	This study
Submontane forest	735–1045	La Paz	313	2,811	256	2576	59	231	90.2	1000 (50 × 20 m)	8	This study
Submontane forest	800–1070	La Paz	416	3,374	337	3125	79	242	124.8	1000 (50 × 20 m)	12	This study
Montane rain forest	1240–1385	Cochabamba	–	–	83	328	–	–	35.8	1000 (50 × 20 m)	3	Macía and Fuentes (unpubl.)
Lower montane forest	1500–1550	La Paz	115	268	89	229	17	27	76.3	500 (250 × 2 m)	1	Phillips and Miller (2002)
Lower montane forest	1520–1560	La Paz	159	514	141	470	12	28	78.8	1000 (500 × 2 m)	1	Phillips and Miller (2002)
Ridge top montane rain forest	1560	Cochabamba	–	–	44	437	–	–	12.2	1000 (100 × 10 m)	1	Macía and Fuentes (unpubl.)
Montane rain forest	2380–2450	La Paz	98	550	78	418	16	90	34.7	1000 (500 × 2 m)	1	Phillips and Miller (2002)
Montane forest: <i>ceja de monte</i>	3225–3503	La Paz	–	–	66	3360	–	–	11.6	1000 (100 × 10 m)	10	Araujo-Murakami et al. (2005c)
Moist forest	100	Santa Cruz	116	445	70	288	46	157	51.0	1000 (500 × 2 m)	1	Phillips and Miller (2002)
Moist forest	280	Santa Cruz	111	320	74	218	37	102	60.2	1000 (500 × 2 m)	1	Phillips and Miller (2002)
Moist forest	375	Santa Cruz	63	180	37	105	26	75	34.5	1000 (500 × 2 m)	1	Phillips and Miller (2002)
Dry forest	100	Pando	169	331	130	262	36	66	138.3	1000 (500 × 2 m)	1	Phillips and Miller (2002)
Dry forest	160	Pando	149	358	116	295	32	62	95.8	1000 (500 × 2 m)	1	Phillips and Miller (2002)
Dry forest	300	Santa Cruz	83	395	53	275	30	120	32.0	1000 (500 × 2 m)	1	Phillips and Miller (2002)
Dry forest	700–800	Santa Cruz	47	179	45	169	2	10	20.8	600 (300 × 2 m)	1	Phillips and Miller (2002)
Dry forest	818–1015	La Paz	171	4,709	–	4291	–	418	34.8	1000 (100 × 10 m)	13	Fuentes et al. (2004)
Dry forest	1000	La Paz	79	465	50	331	29	134	27.3	1000 (500 × 2 m)	1	Foster and Gentry (1991)
Dry forest	1020–1200	La Paz	80	339	59	278	–	–	33.0	1000 (500 × 2 m)	1	Kessler and Helme (1999)
Chaco upland thorn forest	250	Santa Cruz	32	360	27	351	5	9	8.5	1000 (500 × 2 m)	1	Phillips and Miller (2002)
Chaco upland thorn forest	350	Santa Cruz	41	420	29	348	12	72	11.2	1000 (500 × 2 m)	1	Phillips and Miller (2002)
Chaco upland thorn forest	350	Santa Cruz	51	366	43	249	8	117	16.1	1000 (500 × 2 m)	1	Phillips and Miller (2002)

Fisher's Alpha diversity index was computed on total woody plants when data were available for trees and lianas, otherwise just for trees

different tropical forests sites and assess their diversity in future forest inventories, the results of the present study support using this approach in the 0.1-ha plot protocol (measuring all woody plants ≥ 2.5 cm dbh) as well as considering this minimum number of approximately 2000 individuals per site.

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