

Oligarchic dominance in western Amazonian plant communities

Manuel J. Macía*¹ and Jens-Christian Svenning†

* Real Jardín Botánico de Madrid (CSIC), Plaza de Murillo 2, E-28014 Madrid, Spain

† Department of Biological Sciences, Section for Systematic Botany, University of Aarhus, Herbarium, Build. 137, Universitetsparken, DK-8000 Aarhus C, Denmark
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Abstract: The oligarchy hypothesis proposes that large areas of Amazonian plant communities are dominated by limited sets of species. We tested this hypothesis by (1) quantifying dominance of the 10 most common species, genera and families in each region; and (2) assessing the consistency of relative abundance ranks between areas and across scales in dominance patterns for trees and lianas in two distant Amazonian regions (~1900 km), the Yasuní and Madidi National Parks in Ecuador and Bolivia, respectively. The analyses were based on sixty-nine 0.1-ha plots in which all woody plants with a diameter at breast height (dbh) ≥ 2.5 cm were inventoried (19 775 individuals and 1729 species in total). The plots were located at two Yasuní and five Madidi sites, with an average of 10 plots per site. Overall, oligarchic dominance was pronounced at all the spatial scales investigated, although decreasing with increasing scale. Cross-scale relative abundance ranks were more consistent in Yasuní than in Madidi, while no such difference was apparent within single sites. Quantitative dominance and consistency of relative abundance ranks increased with taxonomic rank, being stronger at the family level than at genus and species levels. Species-level dominance was somewhat stronger within the 10 most common families in either region, than in other families. Dominance was similarly strong for canopy (dbh ≥ 10 cm) and understorey trees (dbh < 10 cm), and less pronounced among lianas. In conclusion, our results provide strong evidence that western Amazonian forests can be dominated by limited oligarchies of species, genera and families over large expanses.

Key Words: Bolivia, Ecuador, environmental heterogeneity, life forms, neutral theory, oligarchy hypothesis, relative abundance, species dominance, taxonomic levels, tropical rain forests

INTRODUCTION

Amazonia is a global hotspot for plant diversity, with extraordinarily high plant species richness not only at the regional scale, but also within single small localities (Balslev *et al.* 1998, De Oliveira & Mori 1999, Gentry 1988a, ter Steege *et al.* 2000). However, the spatial patterning of plant species richness and composition in Amazonia remains much less known and is currently subject to strong debate (Condit *et al.* 2002, Terborgh & Andresen 1998, Tuomisto *et al.* 2003). An important focal point is currently the degree and spatial scale of species dominance (Campbell 1994, Pitman *et al.* 2001, Terborgh *et al.* 1996, Tuomisto *et al.* 2003, Vormisto *et al.* 2004a). While monodominant stands (Connell & Lowman 1989, Hart *et al.* 1989) seem to be rare in Amazonia under non-extreme environmental conditions (but cf. Nascimento *et al.* 1997), any given small forested

area (1–50 ha) within Amazonia generally seems to be composed of a limited set of relatively common species and large number of sparse species (Campbell 1994, Gentry 1988b, Pitman *et al.* 2001, Valencia *et al.* 2004). While Gentry (1988b) emphasized that relative abundances of species were highly variable among localities, recent studies have found Amazonian lowland forests to be dominated by limited sets of species that combine high landscape-scale frequency with high local abundance and at least sometimes form predictable oligarchies over wide landscapes (Burnham 2002, 2004; Pitman *et al.* 2001, Terborgh *et al.* 1996, Vormisto *et al.* 2004a). Pitman *et al.* (2001) predicted this to be a general phenomenon across Amazonia (the so-called oligarchy hypothesis). However, the degree of oligarchic dominance has been found to vary between regions (Vormisto *et al.* 2004a), and some still challenge the notion of oligarchic dominance altogether (Tuomisto *et al.* 2003). In contrast, it is well accepted that floristic composition at the family-level is highly consistent among lowland tropical moist and wet forest sites not only within the Neotropics, but also globally (Gentry 1988b, Richards 1996).

¹ Corresponding author. Email: mmacia@ma-rjb.csic.es

Given that dominance patterns in Amazonia are still controversial, it is hardly surprising that the same applies to the underlying causal processes. One line of thinking proposes that relative abundances are the non-equilibrium outcome of stochastic neutral processes (Gentry 1988b, Hubbell 2001). In contrast, Pitman *et al.* (2001) suggested that oligarchic dominance resulted from the ecological superiority of the dominant species. Notably, at a Peruvian site it has been shown that the same few species dominate scattered tree communities with similar environmental conditions to a degree that cannot be accounted for by neutral processes (Hubbell 2001, Terborgh *et al.* 1996). Hart (1990) suggested that, in the absence of disturbance, tropical forests will become dominated by shade-tolerant species just like extratropical forests (Koike 2001, Pacala *et al.* 1996). Indeed, a recent study from a Panamanian tropical moist forest found that landscape-scale frequency and local abundance of individual tree species both increased with sapling survivorship in shade (Svenning *et al.* 2004).

Here, our aim is to investigate the generality of the oligarchy patterns reported by previous studies from western Amazonia by comparing dominance patterns in two distant regions of divergent macrotopography and climate, namely the Yasuní and Madidi National Parks in Ecuador and Bolivia, respectively. Dominance patterns were described by (1) the quantitative dominance of the 10 most common species, genera and families in each region, and (2) the consistency of relative abundance ranks between areas and across scales (cf. Pitman *et al.* 2001, Vormisto *et al.* 2004b). Additionally, we assess the extent to which dominance patterns vary between areas, taxonomic levels (species, genus, family), families (including common and rare families grouped), life forms and plant size. With exception of family-level dominance, these issues remain largely unexplored.

STUDY SITES

Fieldwork was carried out in two western Amazonian regions, namely the Yasuní National Park in Ecuador and the Madidi National Park in Bolivia (Figure 1). The Yasuní region is located at the base of the Andes at < 500 m elevation and has a rather gently rolling landscape mostly covered by mature tropical forest. More than 80% of the landscape is terra firme, but there are also rather extensive floodplain and swamp areas. Mean annual rainfall is around 2800 mm, and mean annual temperature is 28 °C (see Romero-Saltos *et al.* 2001, Valencia *et al.* 2004 for detailed descriptions). Within Yasuní we selected two study sites with similar topographic characteristics, namely the vicinities of the Huaorani indigenous communities of Guiyero (~ 0°36'S, 76°27'W), and Dicaro (~ 0°56'S, 76°12'W).

The Madidi region is also largely covered with mature tropical forest, but contains the last foothills of the eastern Andes, spanning 260–1070 m in elevation, and has a heterogeneous, often sharply dissected and steep topography. More than 90% of the landscape is *terra firme*, although small periodically flooded areas also occur. Permanent swamps are absent. At Rurrenabaque (14°26'S, 67°28'W; 200 m elevation), records mean annual precipitation is 2550 mm and mean annual temperature 25.9 °C (DeWalt *et al.* 1999). In the 3–4-mo dry period, between May and August, periodic cold winds from the south may cause the temperature to drop as low as 4.5 °C (see Pitman *et al.* 2001 for southern Peru). We selected five study sites within Madidi. Three of the sites were in lowland forest at 260–610 m elevation: near the Aguapolo stream in the Tuichi river basin (~ 14°33'S, 67°40'W); in the vicinity of Yariapo river (~ 14°12'S, 67°56'W); and nearby the Tequeje river (~ 13°55'S, 68°12'W). The two other sites were in submontane forest at 780–1070 m elevation: Serranía de Tumupasa (~ 14°10'S, 67°55'W) and ~ 15 km south of Ixiamas village in the proximity of some Inca ruins (~ 13°53'S, 68°09'W).

In the following the usage of 'region' is restricted to meaning Yasuní or Madidi as a whole, 'subregion' for the lowland or highland part of Madidi, and 'site' for single study sites (each with 6–14 plots and inter-plot distances of 0.5–13 km). The term 'area' is used to refer to these geographic scales collectively.

METHODS

Vegetation sampling and plant identification

A total of 69 non-permanent 0.1-ha (50 × 20 m) plots, 25 in Yasuní and 44 in Madidi were inventoried (see Appendix 1 for their geographical coordinates and elevation). The plots were placed in three different broad habitat types: (1) well-drained upland (*terra firme*) forests never flooded by rivers, (2) well-drained floodplains periodically flooded by rivers or streams and (3) permanently inundated, poorly drained swamps (only in Yasuní). Plots were placed to span the available topographic and other habitat heterogeneity at each site, with their locations being based on satellite imagery and aerial photographs, and in the rugged Madidi region also according to accessibility. All plots were located in well-developed forest of a single type (*terra firme*, floodplain, or swamp) with no signs of recent anthropogenic disturbance and excluding big canopy gaps. All woody plant individuals ≥ 2.5 cm dbh (diameter measured at 1.3 m above ground) were inventoried, and identified to species or morphospecies (taxonomic units that could not be assigned to named species) in the field if possible or



Figure 1. Map of the study area. Shaded areas indicate the locations of the two study regions: Yasuní (in Ecuador, two sites) and Madidi (in Bolivia, five sites).

otherwise collected. Voucher specimens (MJM 301-3866 and APY 2023-2525 from Ecuador, and MJM 3876-7051 from Bolivia) were sorted to species level and distributed to taxonomic specialists (see Acknowledgements) or matched with vouchers identified by specialists. Vouchers from Yasuní or Madidi were deposited in the AAU, MA, MO, QCA, and QCNE or the LPB, MA, and MO herbarium, respectively (acronyms according to Holmgren *et al.* 1990). We included morphospecies in the analyses reported here.

Data analysis

We assessed the general floristic patterns by computing a Non-metric Multidimensional Scaling (NMS) ordination using Steinhaus (Sørensen with cover) distance measure and run using PC-ORD's autopilot procedure with the slow and thorough setting (McCune & Grace 2002). To further assess the extent to which the different topographic habitats produce relatively similar plant communities in the two regions, we computed the

average floristic similarity between plots located in separate regions, but in specific topographic habitats using the Steinhaus coefficient (= Sørensen coefficient for abundance data; Legendre & Legendre 1998).

For the subsequent analyses, plots were grouped according to various site combinations: Yasuní region (two sites), Madidi region (five sites), the Madidi lowland subregion (three sites: Aguapolo, Yariapo and Tequeje), the Madidi submontane subregion (two sites: Tumupasa and Ruins), or each site separately.

We described and quantified the degree of dominance in Yasuní and Madidi regions by identifying the 10 most common families, genera and species (the dominant taxa) in each region and computing the proportion of the stems in the region they accounted for. We assessed the extent to which these dominant taxa were shared between the two regions and the individual sites.

Following the approach of Pitman *et al.* (2001), we tested the consistency of species, genus and family relative abundances between areas of a similar spatial extent (regions, subregions or sites) as well as across spatial

Table 1. Mean density (number of stems) and diversity (number of species) for the 0.1-ha study plots in the Madidi National Park, Bolivia (n = 44) and the Yasuní National Park, Ecuador (n = 25) for large trees (≥ 10 cm dbh), small trees (< 10 cm dbh) and lianas (≥ 2.5 cm dbh). The range is given in parentheses. Common species are defined as species having > 1 individual ha^{-1} in a given region.

	Madidi			Yasuní		
	Large trees	Small trees	Lianas	Large trees	Small trees	Lianas
All species						
Density	73 (47–119)	190 (78–363)	24 (1–84)	61 (40–101)	180 (36–304)	19 (1–48)
Diversity	31 (18–55)	58 (32–89)	10 (1–22)	37 (6–66)	87 (19–146)	11 (1–24)
Common species						
Density	62 (32–104)	176 (70–335)	18 (1–78)	45 (26–71)	160 (33–278)	14 (1–34)
Diversity	24 (10–33)	47 (29–63)	6 (1–14)	21 (5–39)	69 (16–118)	6 (1–13)

scales, comparing the frequencies (% plots occupied) and mean densities within occupied plots of a given area, using Spearman rank correlations (r_s). To address the importance of location and spatial scale for the between-area consistency of species relative abundance, we repeated the correlation analyses for all regions, subregions and sites. We addressed the importance of habitat type by repeating some of the correlation analyses using only *terra firme* plots rather than all plots. We assessed whether the between-area and cross-scale consistency of the relative abundance patterns depended on taxonomic rank by repeating the correlation analyses at the genus and family levels. Furthermore, we carried out similar correlation analyses for trees and lianas, separately, as well as for trees ≥ 10 cm dbh and < 10 cm dbh to evaluate the importance of life form and plant size, respectively. Hemi-epiphytes could not be used in the life form-specific analyses due to their poor representation. Species recorded with more than a single life form were removed from the life form-specific analyses. Finally, we repeated the correlation analyses for just the species belonging to the families which constitute the 10 most common families in either Madidi or Yasuní (sum total is 13 families because only 7 families are coincident in both regions) and for the remaining species, separately, to assess whether the between-area consistency of the relative abundance patterns are similar for abundant and rare families.

Steinhaus similarities were computed in the R-Package 4.0d6 (Département de sciences biologiques, Université de Montréal, Montréal, Canada), while the NMS was computed in PC-ORD 4.10 (McCune & Mefford 1999). Correlations were computed in JMP 4.04 (SAS Institute Inc., Cary North Carolina, USA).

RESULTS

Inventory data

The 44 Bolivian plots contained 12 822 individuals ≥ 2.5 cm dbh, representing 94 families, 359 genera and 874 species, the latter including 217 morphospecies

(24.8% of all species) of which 185 were determined down to genus and another 32 down to family. There were 11 625 individuals of free-standing trees, including 3252 individuals ≥ 10 cm dbh, 1164 liana individuals (9.1% of all stems) and 33 hemi-epiphyte individuals (0.3% of all stems). The 25 Ecuadorian plots contained 6953 individuals ≥ 2.5 cm dbh, representing 86 families, 370 genera and 1075 species, including 273 morphospecies (25.4% of all species) of which 227 were identified to genus plus an additional 46 to family (see species list annexed to Macía *et al.* 2001). There were 6159 individuals of free-standing trees, including 1568 individuals ≥ 10 cm dbh, 747 liana individuals (10.8% of all stems) and 47 hemi-epiphyte individuals (0.7% of all stems). Stem density was higher in Madidi than in Yasuní for trees ≥ 10 cm dbh, but not for trees < 10 cm dbh or lianas (Table 1). Species richness per plot of trees ≥ 10 cm dbh and lianas was similar in the two regions, whereas Yasuní had 50% more species of trees < 10 cm dbh per plot compared with Madidi (Table 1).

Floristic patterns

The NMS ordination analysis produced a three-dimensional solution with stress = 13.56, instability = 0.00008 after 400 iterations ($P = 0.0196$, $n = 50$ Monte Carlo runs). The ordination indicated clear differences in species composition between the Madidi and Yasuní regions and between topographic habitats within regions (Figure 2). However, neither the ordination (Figure 2) nor the comparison of plots from specific habitats in Yasuní and Madidi (Table 2) indicated any clear tendency for similar topographic habitats in the two regions to be floristically similar (Table 2).

Dominance patterns

Both regions exhibited pronounced dominance by limited sets of taxa at all taxonomic levels. The 10 most common families in Madidi were, decreasing in importance, Violaceae, Arecaceae, Moraceae, Meliaceae, Rubiaceae, Fabaceae, Euphorbiaceae, Flacourtiaceae,

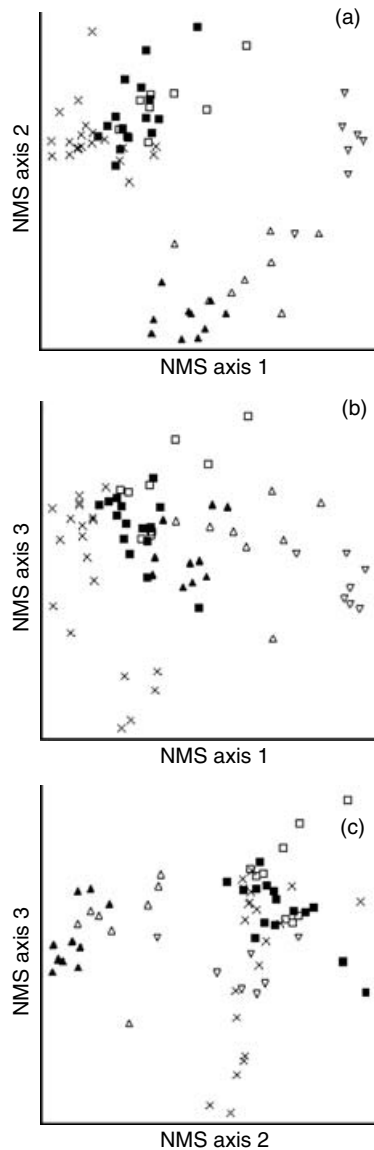


Figure 2. NMS ordination of sixty-nine 0.1-ha plots in Yasuní and Madidi according to the species composition of woody plants ≥ 2.5 cm dbh (see Results for further details): (a) axes 1 and 2; (b) axes 1 and 3; (c) axes 2 and 3. Habitat symbols are represented as follows: lowland *terra firme* (Madidi: ■, Yasuní: ▲), floodplains (Madidi: □, Yasuní: △), swamps (Yasuní: ▽), and submontane *terra firme* (Madidi: X).

Chrysobalanaceae and Piperaceae, and in Yasuní were Fabaceae, Arecaceae, Rubiaceae, Bombacaceae, Euphorbiaceae, Meliaceae, Moraceae, Lauraceae, Annonaceae and Violaceae (percentages of stems per family within a region in Table 3). The 10 most abundant families within each region had more than half of the individuals (Madidi: 51.4%, Yasuní: 56.7%) and a large fraction of the species (Madidi: 32.8%, Yasuní: 43.6%).

The 10 most common genera in Madidi were *Rinorea* (8.3% of all stems within the region), *Iriartea* (5.7%), *Guarea* (3.8%), *Pseudolmedia* (3.5%), *Piper* (2.8%),

Table 2. Mean Steinhaus similarity for woody plant (dbh ≥ 2.5 cm) species composition of various groups of Madidi (Bolivia) and Yasuní (Ecuador) 0.1-ha plots. For group sample sizes, see Appendix 1.

	Madidi <i>terra firme</i> lowlands	Madidi <i>terra firme</i> submontane	Madidi floodplain
Yasuní <i>terra firme</i>	5.4%	4.6%	5.0%
Yasuní floodplain	6.2%	4.4%	5.7%
Yasuní swamp	3.8%	1.2%	3.9%

Styloceras (2.1%), *Siparuna* (2.0%), *Hirtella* (1.8%), *Trichilia* (1.8%), and *Protium* (1.7%), and in Yasuní were *Inga* (4.3% of all stems within the region), *Matisia* (3.9%), *Guarea* (3.0%), *Zygia* (2.4%), *Rinorea* (2.2%), *Mauritia* (2.1%), *Miconia* (2.0%), *Coussarea* (1.9%) *Machaerium* (1.9%) and *Bauhinia* (1.8%). The 10 most abundant genera within each region had around a third of the individuals (Madidi: 33.5%, Yasuní: 25.5%), but only a small fraction of the species (Madidi: 10.8%, Yasuní: 7.1%) in that region.

The 10 most common species in Madidi were *Rinorea viridifolia* Rusby (6.1% of all stems within the region), *Iriartea deltoidea* Ruiz & Pav. (5.7%), *Rinorea guianensis* Aubl. (2.2%), *Styloceras brokawii* A. H. Gentry & R. B. Foster (2.1%), *Pseudolmedia laevis* (Ruiz & Pav.) J. F. Macbr. (1.8%), *Amaioua guianensis* Aubl. (1.6%), *Pseudolmedia laevigata* Trécul. (1.5%), *Hasseltia floribunda* Kunth (1.3%), *Lunania parviflora* Spruce ex Benth. (1.2%) and *Quararibea wittii* K. Schum. & Ulbr. (1.2%) (see also Figure 3). In Yasuní the 10 most common species were *Mauritia flexuosa* L. f. (2.0% of all stems), *Rinorea lindeniana* (Tul.) Kuntze (1.6%), *Machaerium cuspidatum* Kuhl. & Hoehne (1.5%), *Phytelephas tenuicaulis* (Barfod) An. Hend. (1.2%), *Sorocea steinbachii* C. C. Berg (1.2%), *Coussarea macrophylla* Müll. Arg. (1.1%), *Euterpe precatoria* Mart. (1.1%), *Iriartea deltoidea* (1.1%), *Matisia oblongifolia* Poepp. & Endl. (1.1%) and *Quararibea wittii* (1.1%) (see also Figure 3). The 10 most abundant species within each region had near a fifth of the individuals (Madidi: 24.7%, Yasuní: 13.0%).

Considering the five Madidi sites separately there were differences among the top 10 dominants, although more than half of them (52.8%) were present in at least three different sites (Table 4). Some species were highly abundant at a single site, but were not found elsewhere, e.g. *Amaioua guianensis* in Madidi Ruins, *Rinorea guianensis* in Madidi Tumupasa and *Hirtella racemosa* Lam. in Madidi Aguapolo (Table 4). The Madidi Ruins site was characterized by its specific suite of dominants, with 8 out of the top 10 dominant species being generally absent or scarce at the other sites, notably *Amaioua guianensis*, *Aparisthmium cordatum* (A. Juss.) Baill., *Bathysa peruviana* K. Krause, *Helicostylis tomentosa* (Poepp. & Endl.) Rusby, *Pourouma guianensis* Aubl. and *Protium spruceanum* (Benth.) Engl. Considering the species which were among the top 10 most common at either of the two Yasuní sites most (87.1%) were present at both

Table 3. Results for the 13 families that constitute the 10 most common families in the Madidi National Park (Bolivia) or the Yasuní National Park (Ecuador). To the left, percentages of stems by family per region. The two columns to the right, cross-scale consistency in relative abundances within families: Intra-site Spearman rank correlations between frequency (% of plots occupied in a given area) and density (mean number of individuals ha⁻¹) for those 13 families. * P = < 0.05, ** P < 0.01, *** P < 0.001, **** P < 0.0001. The number of species is given in parentheses. Bold face indicates the 10 most abundant families in a given region.

Family	Percentages of stems in		
	Madidi (M) and Yasuní (Y)	Madidi total	Yasuní total
Annonaceae	M: 2.5, Y: 3.6	0.37 (26)	0.37* (42)
Arecaceae	M: 8.3, Y: 7.6	0.22 (11)	0.62** (24)
Bombacaceae	M: 1.6, Y: 5.3	0.94**** (10)	0.77*** (17)
Chrysobalanaceae	M: 2.8, Y: 0.8	0.58** (20)	0.41 (20)
Euphorbiaceae	M: 3.4, Y: 4.5	0.51* (24)	0.51** (37)
Fabaceae	M: 4.2, Y: 15.1	0.25* (94)	0.57**** (125)
Flacourtiaceae	M: 3.2, Y: 1.3	0.77** (14)	0.62** (20)
Lauraceae	M: 2.4, Y: 3.8	0.42** (46)	0.35** (75)
Meliaceae	M: 5.8, Y: 4.4	0.76**** (20)	0.80**** (33)
Moraceae	M: 6.3, Y: 4.4	0.72**** (31)	0.59**** (44)
Piperaceae	M: 2.8, Y: 0.4	0.48 (13)	0.69 (5)
Rubiaceae	M: 5.7, Y: 5.4	0.30* (55)	0.44*** (64)
Violaceae	M: 9.4, Y: 3.6	0.70 (5)	0.10 (8)

sites. However, *Attalea butyracea* (Mutis ex L. f.) Wess. Boer and *Coussarea macrophylla* were only found at Yasuní Guiyero.

Twenty (42.5%) of the species which were among the top 10 dominants at at least one site were shared between Madidi and Yasuní (Table 4), with *Guarea kunthiana* Adr. Juss., *Iriartea deltoidea*, *Otoba parvifolia* (Markgr.) A. H. Gentry, *Pseudolmedia laevis*, *Rinorea viridifolia* and *Socratea exorrhiza* (Mart.) H. Wendl. being present at all seven study sites.

Between-area and cross-scale consistency in relative abundances

With respect to between-area consistency in relative abundances, the densities of shared species were moderately correlated among the two regions ($r_s = 0.31$, $P < 0.0001$; Table 5; Figure 3). If densities were based only on *terra firme* plots, instead of on all plots, the correlation declined to $r_s = 0.20$ ($P = 0.01$). The correlation (again considering plots in all habitats) was similar when Yasuní was compared with Madidi or just the Madidi lowland plots, but clearly lower if Yasuní was compared only to the Madidi submontane plots (Table 5). Again both correlations were lower if only *terra firme* plots were considered ($r_s = 0.19$, $P = 0.04$ for Madidi lowland and $r_s = 0.17$, $P = 0.07$ for Madidi submontane plots). The densities of shared species were more highly correlated among sites within regions than between regions, except that densities in Madidi Ruins were uncorrelated with densities in the other Madidi sites (Table 5).

Concerning cross-scale consistency in species relative abundance, the correlations between frequencies (% plots

occupied) and mean densities within occupied plots were quite high and apparently did not depend on the spatial extent (site, subregion, region) of the area considered (Table 6, Figure 4). At the regional scale the frequency–density correlation was somewhat stronger for Yasuní than Madidi, although not so apparent at the site scale (Table 6). Reflecting the higher stem density, but lower diversity (Table 1), species in Madidi had higher local abundances than species of similar frequency in Yasuní (Figure 4).

The consistency of the between-area and cross-scale relative abundances increased with taxonomic level and did so for sites, subregions, as well as regions (Tables 5 and 6). Notably, family-level correlations often exceeded 0.80.

Comparing the species belonging to the 13 families which comprise the top 10 most common families in either region with those exhibited by species belonging to the other, more rare families (Tables 5 and 6), the consistency of the relative abundances was more pronounced in the first group, particularly in terms of the cross-scale correlations (Table 6). However, considering these 13 families separately, the species-level cross-scale correlations in relative abundance were quite variable (Table 3), e.g. relatively low in Annonaceae and Rubiaceae and relatively high in Bombacaceae and Meliaceae.

Considering the tree and liana life forms separately, trees (both small and large) exhibited relative abundance correlations similar to those reported above for all life forms combined (Tables 7 and 8). Lianas, however, showed rather contrasting patterns. Densities of liana species were generally at most weakly correlated between areas, except for a rather strong correlation between

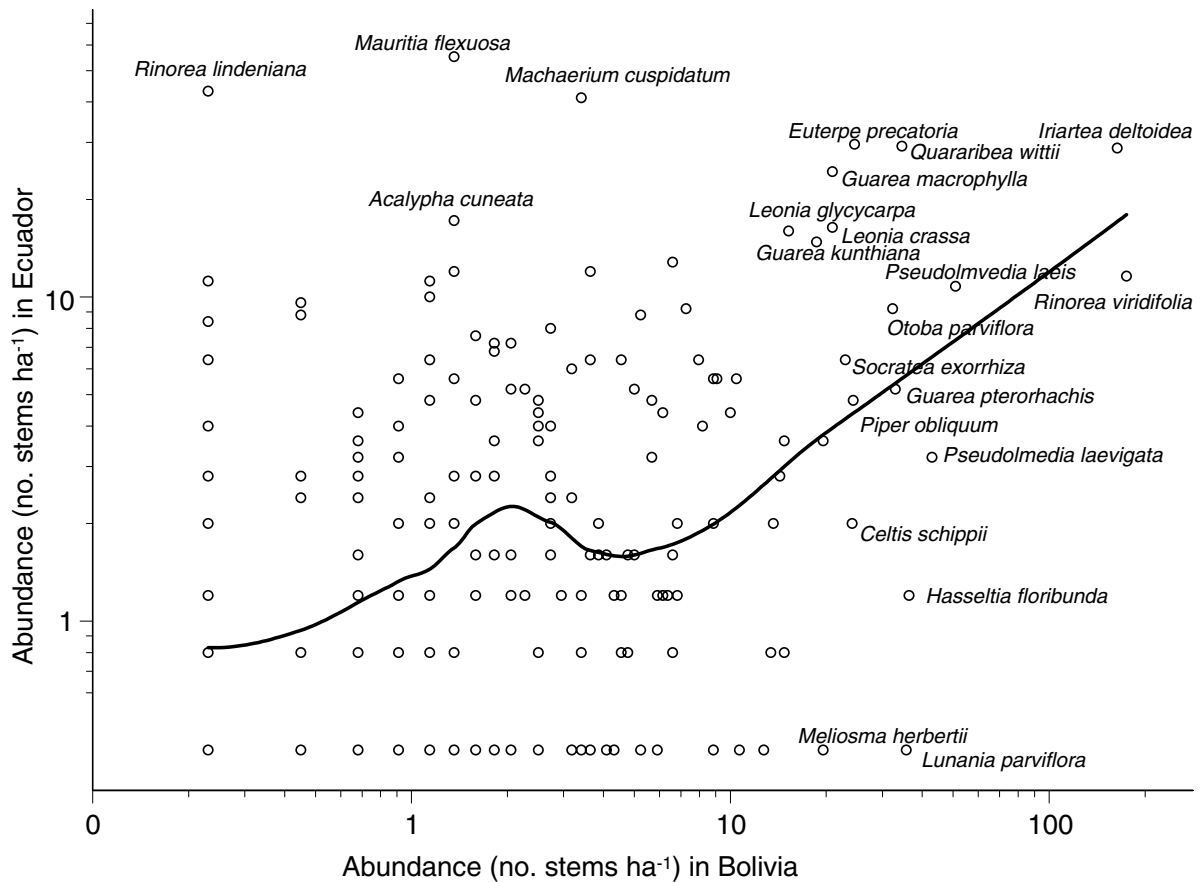


Figure 3. The average density (stems ha^{-1}) in Madidi and Yasuni for the species shared between the two regions ($n = 220$ species). For illustration a quadratic symmetric local regression fit of the density in Yasuni on the density in Madidi is shown.

the two regions (Table 7). Likewise the cross-scale correlations were lower for lianas than for trees, and in Madidi often not statistically significant at the site-level (Table 8).

DISCUSSION

Our results largely confirm the oligarchy hypothesis of Pitman *et al.* (2001). We found pronounced dominance by limited sets of species, genera and families at all the spatial scales investigated both within and among the Yasuni and Madidi regions. We also found that relative abundance ranks were moderately to highly consistent between sites and across spatial scales.

While the rank correlations in relative abundance between areas were stronger within regions, even the abundance rank correlation between the two regions, ~ 1900 km apart, was not negligible and in fact not much smaller than found by Pitman *et al.* (2001) for trees (≥ 10 cm dbh) in the less distant (~ 1400 km) Yasuni and Manu (Peru) regions (Table 5). Furthermore, across-scale rank correlations were quite high within sites as

well as subregions and regions (Table 6). Hence, the same species which dominate at the smallest scale studied (single plots; 0.1 ha) also tend to dominate across wide geographic areas. When considering dominant species, it is striking how many are shared between Madidi and Yasuni sites, with the species *Guarea kunthiana*, *Iriartea deltoidea*, *Otoba parvifolia*, *Pseudolmedia laevis*, *Rinorea viridifolia* and *Socratea exorrhiza* occurring at all sites (Table 4). We note that our results add to the many studies demonstrating the extraordinary abundance of the large palm *Iriartea deltoidea* in western Amazonian (Pitman *et al.* 2001, Valencia *et al.* 2004, Vormisto *et al.* 2004a) and other wet Neotropical forests (Borchsenius 1997, Clark *et al.* 1999). Hence, our results provide qualified support for the conclusion by Pitman *et al.* (2001) that Western Amazonian forests close to the Andes tend to be dominated by the same limited set of species across large regions. The correspondence between the Yasuni and Madidi plant communities is even more remarkable when considering the divergent climatic and topographic setting of the two regions. The Yasuni landscape is composed of gently rolling hills and the climate does not have a regular or pronounced dry season. In contrast Madidi has a sharply

Table 4. Comparison of density (mean number of individuals ha⁻¹) for the 10 most common species (in bold) in the seven study sites in the Madidi National Park (Bolivia: MA, Aguapolo; MI, Yariapo; MR, Ruins; MQ, Tequeje; MU, Tumupasa) and the Yasuni National Park (Ecuador: YD, Dicaro; YG, Guiyero). The species with the symbol * are lianas.

Species	MA	MI	MR	MQ	MU	YD	YG
Annonaceae							
<i>Oxandra cf. acuminata</i>				130			
<i>Unonopsis floribunda</i>	83	13	6	43	6		
Arecaceae							
<i>Attalea butyracea</i>							35
<i>Euterpe precatoria</i>	66	15	23	45		28	31
<i>Iriartea deltoidea</i>	57	182	101	287	189	30	28
<i>Mauritia flexuosa</i>		5				65	47
<i>Phytelephas temuicaulis</i>						15	45
<i>Socratea exorrhiza</i>	19	29	18	65	3	6	6
Bombacaceae							
<i>Matisia malacocalyx</i>						30	17
<i>Matisia oblongifolia</i>						2	51
<i>Quararibea wittii</i>		46	33	25	50	3	50
Burseraceae							
<i>Protium spruceanum</i>			98		1		
Buxaceae							
<i>Styloceras brokawii</i>		145	24	32	58		
Cecropiaceae							
<i>Pourouma guianensis</i>			108			1	6
Chrysobalanaceae							
<i>Hirtella racemosa</i>	213						
Euphorbiaceae							
<i>Acalypha cuneata</i>						36	2
<i>Aparisthium cordatum</i>			76		3	8	
<i>Drypetes</i> sp. 1		2		112	18		
Fabaceae							
<i>Brownea grandiceps</i>						34	21
<i>Machaerium cuspidatum*</i>				25		45	38
Flacourtiaceae							
<i>Hasseltia floribunda</i>	10	20	21	60	65		2
<i>Lunania parviflora</i>	27	48		68	37		
Hippocrateaceae							
<i>Cheilochlinium cognatum*</i>	57					7	4
Lecythidaceae							
<i>Gustavia longifolia</i>						34	9
Meliaceae							
<i>Guarea kunthiana</i>	7	17	3	2	46	17	13
<i>Guarea macrophylla</i>		26		88	8	40	12
<i>Guarea pterorhachis</i>		38	5	70	48	11	1
Monimiaceae							
<i>Mollinedia ovata</i>		59				1	1
Moraceae							
<i>Helicostylis tomentosa</i>			75			2	2
<i>Pseudolmedia laevigata</i>			164	13	42	2	4
<i>Pseudolmedia laevis</i>	56	62	1	87	53	9	12
<i>Sorocea steinbachii</i>						6	51
Myristicaceae							
<i>Iryanthera hostmammii</i>						30	16
<i>Otoba parvifolia</i>	44	52	1	23	33	7	11
Nyctaginaceae							
<i>Neea</i> sp. 1						14	32
Piperaceae							
<i>Piper heterophyllum</i>		20			58		
Rubiaceae							
<i>Amaioua guianensis</i>			250				
<i>Bathysa peruviana</i>			118		4		
<i>Coussarea macrophylla</i>							51
Siparunaceae							
<i>Siparuna bifida</i>	1	40	4	132	2		
<i>Siparuna guianensis</i>	104		1		7		

Table 4. Continued.

Species	MA	MI	MR	MQ	MU	YD	YG
Sterculiaceae							
<i>Byttneria pescapraefolia</i> *		39		2			
Tiliaceae							
<i>Pentaplaris davidsmithii</i>	70	12		7	10		
Violaceae							
<i>Leonia glycyarpa</i>		1	83			9	21
<i>Rinorea guianensis</i>					228		
<i>Rinorea lindeniana</i>						68	24
<i>Rinorea viridifolia</i>	379	44	133	230	178	11	12

dissected Andean foothill landscape and the climate has a 3–4-mo dry period during which periodic cold spells down to 4.5 °C occur.

We note that cross-scale rank correlations were more consistent in the Yasuní region than in the Madidi region, but not so apparent within single sites (Table 6). This most likely reflects greater environmental heterogeneity in the rugged Madidi region compared with the rather flat Yasuní region (cf. Pitman *et al.* 2001). Similarly, Vormisto *et al.* (2004a) found less-dominant

oligarchy in palm communities in the edaphically heterogeneous Iquitos–Pebas region in north-eastern Peru compared with Yasuní. While between-site abundance correlations in Madidi are generally lower than in Yasuní, those involving one particular site, Madidi Ruins, appear anomalously low (Tables 5 and 7), although the frequency–density dominance correlations within this site are not particularly low (Tables 6 and 8). We believe the explanation might be that this site has experienced anthropogenic disturbance in the past

Table 5. Between-area consistency in relative abundances. Intersite Spearman rank correlations in density (mean number of individuals ha⁻¹) for shared species, genera, families, species belonging to the 13 families which constitute the top 10 most common families in either Madidi or Yasuní, or all other species. *P < 0.05, **P < 0.01, ***P < 0.001, ****P < 0.0001. The number of shared taxa is given in parentheses.

Site 1	Site 2	Species	Genera	Family	13 dominant families	All other families
Madidi total	Yasuní total	0.31**** (220)	0.47**** (234)	0.81**** (78)	0.36*** (107)	0.25** (113)
Madidi lowlands	Yasuní total	0.32**** (184)	0.46**** (208)	0.79**** (72)	0.34*** (93)	0.29** (91)
Madidi submontane	Yasuní total	0.22** (156)	0.40**** (190)	0.78**** (75)	0.24* (75)	0.19 (81)
Madidi lowlands	Madidi submontane	0.40**** (322)	0.57**** (211)	0.77**** (75)	0.44**** (149)	0.35**** (173)
Madidi Aguapolo	Madidi Yariapo	0.49**** (131)	0.50**** (131)	0.57**** (53)	0.58**** (61)	0.40**** (70)
Madidi Aguapolo	Madidi Tequeje	0.49**** (116)	0.63**** (121)	0.72**** (54)	0.62**** (55)	0.37** (61)
Madidi Aguapolo	Madidi Ruins	0.09 (99)	0.27** (103)	0.39** (49)	0.17 (43)	0.02 (56)
Madidi Aguapolo	Madidi Tumupasa	0.40**** (133)	0.42**** (130)	0.73**** (56)	0.44*** (58)	0.36** (75)
Madidi Yariapo	Madidi Tequeje	0.51**** (149)	0.51**** (134)	0.71**** (61)	0.48**** (77)	0.54**** (72)
Madidi Yariapo	Madidi Ruins	0.06 (99)	0.27** (111)	0.57**** (53)	0.16 (49)	–0.06 (50)
Madidi Yariapo	Madidi Tumupasa	0.37**** (181)	0.47**** (151)	0.79**** (61)	0.37*** (88)	0.37**** (93)
Madidi Tequeje	Madidi Ruins	0.17 (99)	0.25** (117)	0.44*** (56)	0.45** (50)	–0.15 (49)
Madidi Tequeje	Madidi Tumupasa	0.42**** (149)	0.56**** (135)	0.80**** (64)	0.45**** (73)	0.40**** (76)
Madidi Ruins	Madidi Tumupasa	0.09 (130)	0.21* (130)	0.59**** (57)	0.22 (59)	–0.03 (71)
Yasuní Dicaro	Yasuní Guiyero	0.50**** (442)	0.68**** (248)	0.92**** (73)	0.46**** (226)	0.54**** (216)

Table 6. Cross-scale consistency in relative abundances. Spearman rank correlations between frequency (% of plots occupied in a given area) and density (mean number of individuals ha⁻¹ in the occupied plots) for different taxonomic levels or species groups (species belonging to the 13 families which constitute the top 10 most common families in either Madidi or Yasuní, or all other species) in a given region (Yasuní, Madidi), subregion (Madidi lowlands and submontane) or site. P < 0.0001 in all cases. The number of taxa is given in parentheses.

Site	Species	Genera	Family	13 dominant families	All other families
Madidi total	0.40 (874)	0.49 (357)	0.70 (94)	0.49 (369)	0.34 (505)
Madidi lowlands	0.43 (605)	0.50 (289)	0.70 (83)	0.53 (261)	0.33 (344)
Madidi submontane	0.42 (591)	0.53 (279)	0.81 (86)	0.49 (257)	0.36 (334)
Madidi Aguapolo	0.46 (281)	0.55 (182)	0.64 (62)	0.59 (118)	0.39 (163)
Madidi Yariapo	0.48 (330)	0.51 (203)	0.83 (66)	0.55 (161)	0.40 (169)
Madidi Tequeje	0.53 (307)	0.58 (187)	0.68 (72)	0.64 (134)	0.45 (173)
Madidi Tumupasa	0.37 (410)	0.43 (229)	0.80 (77)	0.49 (186)	0.27 (224)
Madidi Ruins	0.47 (311)	0.52 (180)	0.63 (66)	0.51 (130)	0.43 (181)
Yasuní total	0.50 (1075)	0.58 (362)	0.85 (84)	0.51 (514)	0.48 (557)
Yasuní Dicaro	0.44 (743)	0.53 (296)	0.86 (76)	0.46 (365)	0.41 (376)
Yasuní Guiyero	0.45 (774)	0.54 (314)	0.82 (81)	0.49 (375)	0.41 (397)

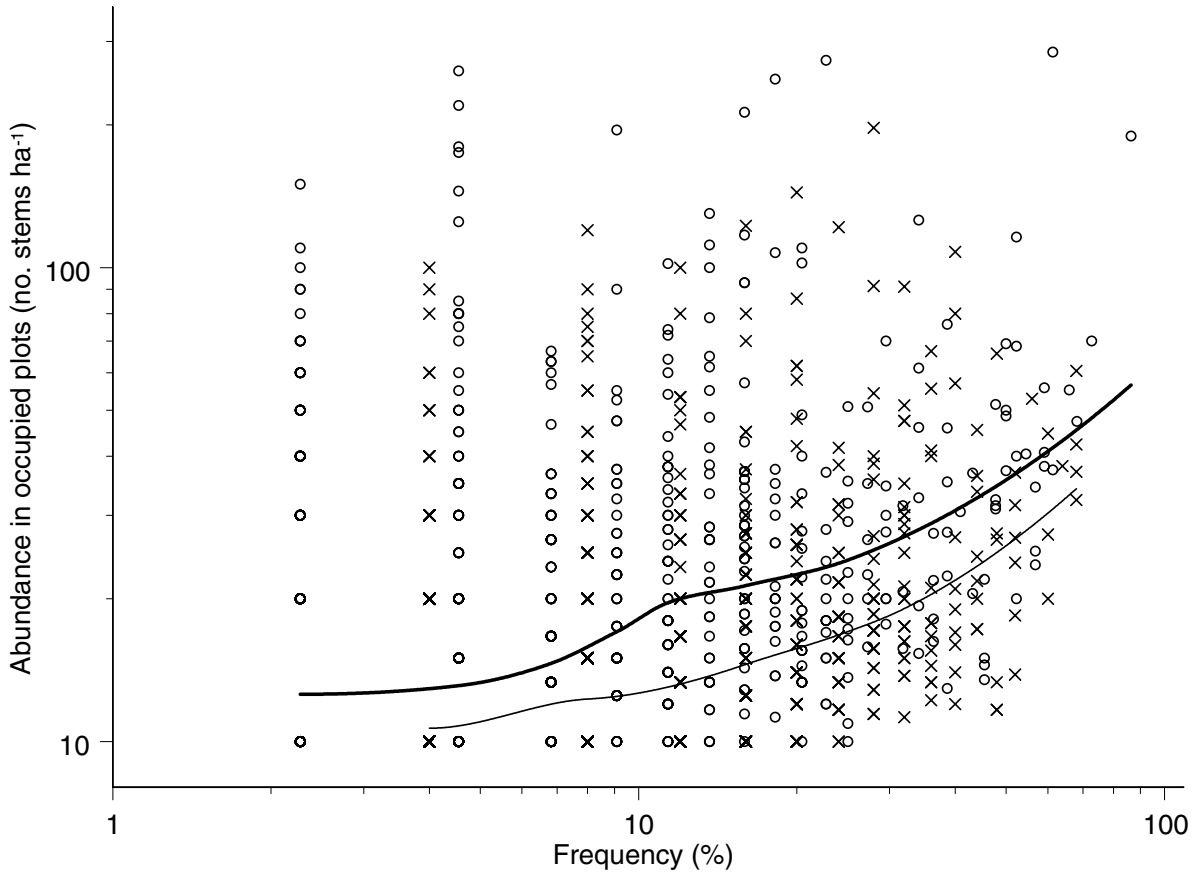


Figure 4. Abundance (average density, stems ha⁻¹) in the occupied plots as a function of frequency (% of plots occupied) is shown for all species present in given region (crosses = Yasuní [n = 1075 species]; circles = Madidi [n = 874 species]). For illustration quadratic symmetric local regression fits of abundance on frequency are shown for each region (Yasuní: thin line; Madidi: thick line).

(>100 y ago according to local informants). Among the species dominant exclusively at this site are several well-known pioneer taxa, notably *Aparisthmium cordatum* and *Pourouma* (here, *P. guianensis*) (Gentry 1993). No

similar disturbance indicators are apparent among the dominants at the other sites. It is well-known that past human disturbance may have long-lasting (>100 y) effects on plant community structure in Neotropical

Table 7. Between-area consistency in relative abundances. Intersite Spearman rank correlations in density (mean number of individuals ha⁻¹) for different plant size and life form groupings at Madidi and Yasuní. * P < 0.05, ** P < 0.01, *** P < 0.001, **** P < 0.0001. The number of shared taxa is given in parentheses.

Site 1	Site 2	Trees ≥ 2.5 cm dbh	Trees ≥ 10 cm dbh	Trees < 10 cm dbh	Lianas ≥ 2.5 cm dbh
Madidi total	Yasuní total	0.30**** (174)	0.20 (82)	0.27*** (146)	0.43* (29)
Madidi lowlands	Yasuní total	0.31*** (143)	0.25 (62)	0.34*** (117)	0.38 (26)
Madidi submontane	Yasuní total	0.23** (130)	0.19 (61)	0.29** (106)	-0.02 (17)
Madidi lowlands	Madidi submontane	0.43**** (255)	0.36**** (131)	0.42**** (204)	-0.03 (56)
Madidi Aguapolo	Madidi Yariapo	0.44**** (110)	0.48*** (58)	0.31** (86)	0.64** (19)
Madidi Aguapolo	Madidi Tequeje	0.50**** (99)	0.38** (50)	0.49**** (80)	0.29 (14)
Madidi Aguapolo	Madidi Ruins	0.09 (86)	0.11 (28)	0.06 (66)	0.17 (10)
Madidi Aguapolo	Madidi Tumupasa	0.40**** (109)	0.45*** (54)	0.41*** (84)	0.26 (20)
Madidi Yariapo	Madidi Tequeje	0.52**** (130)	0.20 (64)	0.56**** (107)	0.31 (17)
Madidi Yariapo	Madidi Ruins	0.04 (84)	0.46** (31)	0.06 (67)	0.36 (11)
Madidi Yariapo	Madidi Tumupasa	0.36**** (150)	0.46**** (78)	0.36**** (123)	0.20 (28)
Madidi Tequeje	Madidi Ruins	0.25* (86)	0.19 (28)	0.33** (70)	-0.84** (9)
Madidi Tequeje	Madidi Tumupasa	0.40**** (126)	0.28* (66)	0.37*** (100)	0.25 (20)
Madidi Ruins	Madidi Tumupasa	0.11 (112)	0.20 (47)	0.13 (92)	-0.24 (15)
Yasuní Dicaro	Yasuní Guiyero	0.52**** (388)	0.49**** (131)	0.53**** (324)	0.32 (31)

Table 8. Cross-scale consistency in relative abundances. Spearman rank correlations between the frequency (% of plots occupied in a given area) and density (mean number of individuals ha⁻¹ in the occupied plots) for different plant size and life form groupings in Madidi and Yasuní. *P < 0.05, **P < 0.01, ***P < 0.0001. The number of taxa is given in parentheses.

Site	Trees ≥ 2.5 cm dbh	Trees ≥ 10 cm dbh	Trees < 10 cm dbh	Lianas ≥ 2.5 cm dbh
Madidi total	0.46*** (660)	0.45*** (408)	0.48*** (582)	0.23** (187)
Madidi lowlands	0.50*** (446)	0.46*** (239)	0.48*** (385)	0.19* (139)
Madidi submontane	0.47*** (469)	0.44*** (300)	0.52*** (401)	0.20* (104)
Madidi Aguapolo	0.57*** (215)	0.58*** (116)	0.54*** (171)	0.19 (59)
Madidi Yariapo	0.49*** (253)	0.47*** (136)	0.42*** (216)	0.37** (69)
Madidi Tequeje	0.60*** (241)	0.42*** (121)	0.60*** (209)	0.23 (55)
Madidi Tumupasa	0.42*** (330)	0.38*** (201)	0.43*** (278)	0.12 (72)
Madidi Ruins	0.52*** (251)	0.52*** (146)	0.57*** (215)	0.13 (47)
Yasuní total	0.51*** (877)	0.44*** (471)	0.50*** (759)	0.38*** (147)
Yasuní Dicaro	0.44*** (626)	0.37*** (287)	0.44*** (548)	0.30** (87)
Yasuní Guiyero	0.47*** (639)	0.43*** (315)	0.49*** (535)	0.31** (91)

forests (Balée & Campbell 1990, Heckenberger *et al.* 2003, Svenning *et al.* 2004).

We found dominance to increase with taxonomic rank with family-level oligarchic dominance being particularly pronounced, both in terms of proportion of stems accounted for by the dominant taxa and in terms of between-area and cross-scale consistency in relative abundance ranks (Tables 5 and 6). Hence, our results confirm observations that family-level composition is highly predictable in tropical forests (Gentry 1988b, Richards 1996). Comparing the most dominant families (those among the top 10 dominants in either Madidi or Yasuní) with the rarer families we found consistent between-area and cross-scale relative abundance ranks in both groups, albeit more strongly so within the group of dominant families (Tables 5 and 6).

Hence, oligarchic dominance is not the result of a process which acts dichotomously causing some species to be dominant and others to be rare, but rather a process which affects species' abundances in a more continuous fashion. While our data do not allow us to identify this process more directly, we note that differential shade tolerance is a strong candidate (Svenning *et al.* 2004). Recent evidence suggests that shade tolerance varies in a continuous fashion among Neotropical tree species (Wright *et al.* 2003).

Our study shows that oligarchic dominance is not a phenomenon limited to certain plant life forms such as large canopy trees. Considering plant life form, the relative abundance ranks were less consistent for lianas than for trees (Tables 7 and 8). While this result may seem to contradict Burnham's finding of strong oligarchic dominance among lianas in Yasuní (Burnham 2002, 2004), we in fact also found rather strong oligarchic dominance among lianas in Yasuní, but not in Madidi (Table 8). Both studies found the legume *Machaerium cuspidatum* to be the most abundant liana in Yasuní (Table 4). We also note that it is possible that the different dominance patterns documented for trees and lianas may reflect the much sparser sampling of lianas, most of which

have diameters < 2.5 cm (also cf. Mascaro *et al.* 2004, Nabe-Nielsen 2001). While findings that range size of Amazonian trees increases with tree height (Ruokolainen *et al.* 2002, Ruokolainen & Vormisto 2000) would cause one to expect oligarchic dominance to likewise be stronger among large trees at larger spatial scales, we found that oligarchic dominance was similar for trees < 10 cm dbh and trees ≥ 10 cm dbh, and even slightly stronger for the first group. We note that the two groups separate individuals according to their size and not the potential maximum size of their species (which we currently have not been able to estimate for a sufficient number of species to allow such an analysis). Hence, it is still possible that a comparison of understorey treelet and canopy tree species would show oligarchic dominance to be stronger among the latter. However, we find no indication of this in our data. Notably, a number of treelet species (e.g. *Rinorea viridifolia*, *Styloceras brokawii*, *Siparuna bifida*, *Piper heterophyllum*) are found among the dominant species (Table 4).

Our study supports the suggestion that western Amazonian forests, despite pronounced geographic floristic differences, tend to be dominated over wide areas by limited sets of plant species, genera and families. An important avenue for future research will be to provide an understanding of ecological mechanisms creating such a predictable large-scale community structure.

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Appendix 1. Location and characteristics of the sixty-nine 0.1-ha vegetation plots inventoried in the Madidi National Park (Bolivia: MA, Aguapolo; MI, Yariapo; MR, Ruins; MQ, Tequeje; MU, Tumupasa) and the Yasuní National Park (Ecuador: YD, Dicaro; YG, Guiyero).

Plot number-locality	Habitat description	Elevation (m)	Geographic coordinates	Number of stems	Number of species
1-MI	Floodplain	460	14° 12' 59.7" S; 67° 57' 16.5" W	248	81
2-MI	Terra firme	560	14° 12' 47.8" S; 67° 56' 94.5" W	264	102
3-MI	Floodplain	610	14° 11' 43.2" S; 67° 58' 19.2" W	271	64
4-MI	Terra firme	530	14° 12' 33.3" S; 67° 57' 38.5" W	249	92
5-MI	Floodplain	530	14° 13' 32.2" S; 67° 56' 37.4" W	207	80
6-MI	Terra firme	540	14° 13' 28.5" S; 67° 56' 28.6" W	183	52
7-MI	Terra firme	515	14° 14' 01.4" S; 67° 56' 33.1" W	295	90
8-MI	Terra firme	480	14° 15' 45.8" S; 67° 56' 28.5" W	275	87
9-MI	Floodplain	535	14° 12' 40.3" S; 67° 56' 34.1" W	157	71
10-MI	Floodplain	500	14° 13' 01.9" S; 67° 56' 45.2" W	251	55
11-MI	Terra firme	580	14° 13' 29.6" S; 67° 57' 00.9" W	226	64
12-MU	Terra firme	945	14° 10' 17.2" S; 67° 54' 28.8" W	220	76
13-MU	Terra firme	820	14° 10' 35.1" S; 67° 54' 39.8" W	261	83
14-MU	Terra firme	820	14° 10' 37.0" S; 67° 55' 16.3" W	261	87
15-MU	Terra firme	810	14° 10' 32.0" S; 67° 55' 07.4" W	250	100
16-MU	Terra firme	805	14° 10' 25.2" S; 67° 54' 56.1" W	251	77
17-MU	Terra firme	840	14° 11' 00.2" S; 67° 55' 22.3" W	471	119
18-MU	Terra firme	950	14° 10' 24.8" S; 67° 55' 10.7" W	335	72
19-MU	Terra firme	1070	14° 09' 35.5" S; 67° 55' 19.8" W	366	106
20-MU	Terra firme	930	14° 10' 07.9" S; 67° 55' 16.9" W	256	75
21-MU	Terra firme	840	14° 10' 14.2" S; 67° 54' 44.2" W	232	71
22-MU	Terra firme	800	14° 10' 20.4" S; 67° 54' 47.8" W	263	78

Appendix 1. Continued.

Plot number-locality	Habitat description	Elevation (m)	Geographic coordinates	Number of stems	Number of species
23-MU	Terra firme	925	14°10'13.6"S; 67°54'39.2"W	208	57
24-MQ	Terra firme	470	13°55'29.6"S; 68°12'01.4"W	332	99
25-MQ	Terra firme	450	13°54'59.1"S; 68°12'32.8"W	310	87
26-MQ	Terra firme	515	13°56'11.8"S; 68°12'00.7"W	346	110
27-MQ	Terra firme	550	13°55'39.8"S; 68°12'18.7"W	416	136
28-MQ	Floodplain	425	13°55'14.0"S; 68°12'33.5"W	277	78
29-MQ	Terra firme	455	13°55'45.5"S; 68°12'05.6"W	394	109
30-MR	Terra firme	780	13°53'50.1"S; 68°09'54.2"W	258	92
31-MR	Terra firme	735	13°53'34.6"S; 68°09'56.5"W	209	61
32-MR	Terra firme	925	13°53'36.7"S; 68°09'36.2"W	417	62
33-MR	Terra firme	1045	13°54'01.7"S; 68°09'55.9"W	441	89
34-MR	Terra firme	1015	13°53'49.6"S; 68°09'43.1"W	384	85
35-MR	Terra firme	950	13°53'36.4"S; 68°09'23.9"W	503	84
36-MR	Terra firme	905	13°54'16.8"S; 68°09'22.6"W	314	97
37-MA	Terra firme	420	14°33'25.2"S; 67°40'05.6"W	349	99
38-MA	Terra firme	400	14°33'13.5"S; 67°40'22.6"W	294	94
39-MA	Terra firme	380	14°33'22.4"S; 67°40'34.1"W	296	93
40-MA	Floodplain	260	14°33'51.9"S; 67°40'24.3"W	228	74
41-MA	Floodplain	270	14°33'39.8"S; 67°40'39.6"W	259	91
42-MA	Terra firme	320	14°33'33.4"S; 67°40'23.4"W	268	77
43-MA	Floodplain	260	14°33'31.8"S; 67°40'41.4"W	242	69
44-MR	Terra firme	950	13°53'54.3"S; 68°09'39.6"W	285	78
1-YG	Floodplain	250–300	0°39'51.1"S; 76°25'41.3"W	233	60
2-YG	Terra firme	250–300	0°39'57.2"S; 76°25'46.0"W	436	184
3-YG	Floodplain	250–300	0°40'10.1"S; 76°25'53.6"W	295	68
4-YG	Terra firme	250–300	0°40'13.3"S; 76°26'16.2"W	347	149
5-YG	Terra firme	250–300	0°37'34.0"S; 76°27'39.4"W	289	170
6-YG	Terra firme	250–300	0°37'38.2"S; 76°27'44.2"W	408	184
7-YG	Terra firme	250–300	0°38'33.3"S; 76°27'52.5"W	372	163
8-YG	Swamp	250–300	0°36'42.6"S; 76°27'40.8"W	164	60
9-YG	Swamp	250–300	0°41'04.7"S; 76°25'53.9"W	191	98
10-YG	Floodplain	250–300	0°36'17.8"S; 76°27'28.6"W	244	118
11-YG	Floodplain	250–300	0°36'07.3"S; 76°27'31.0"W	219	91
12-YG	Floodplain	250–300	0°36'00.5"S; 76°27'21.5"W	298	149
13-YG	Swamp	250–300	0°36'30.5"S; 76°27'26.7"W	81	24
14-YG	Swamp	250–300	0°36'40.5"S; 76°27'34.3"W	127	41
15-YD	Terra firme	250–300	1°01'20.7"S; 76°11'24.4"W	393	211
16-YD	Terra firme	250–300	1°01'16.5"S; 76°11'21.3"W	332	179
17-YD	Terra firme	250–300	0°58'25.4"S; 76°13'16.9"W	327	178
18-YD	Terra firme	250–300	0°58'31.1"S; 76°13'22.4"W	331	160
19-YD	Floodplain	250–300	0°52'34.6"S; 76°14'38.8"W	371	169
20-YD	Terra firme	250–300	0°52'21.4"S; 76°14'34.3"W	361	172
21-YD	Floodplain	250–300	0°51'51.5"S; 76°16'43.4"W	344	156
22-YD	Floodplain	250–300	0°52'00.5"S; 76°14'00.2"W	352	165
23-YD	Swamp	250–300	0°51'50.6"S; 76°16'46.9"W	165	45
24-YD	Swamp	250–300	0°53'22.2"S; 76°13'31.2"W	112	39
25-YD	Swamp	250–300	0°54'07.5"S; 76°13'15.4"W	114	40