Floristic composition, structure, and diversity of four forest plots in the Sierra Maigualida, Venezuelan Guayana

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Abstract. A phytosociological study was carried out in four 1-ha forest plots in the Sierra Maigualida region, Venezuelan Guayana. Density, dominance, and frequency values were calculated as well as the species and family importance values (FIVs) in each plot. A total of 65 families, 232 genera and 533 species were represented in the 4 ha of forest. The number of stems $\geq 10\,cm\,dbh$ varied from 355 to 563, the number of species from 133 to 191, the genera from 76 to 120, the families from 38 to 51, and the basal area from 20.56 to $40.83\,m^2$ per hectare. Overall the most species rich family was Fabaceae (38 species), the most numerous in total stems was Burseraceae (165 individuals), and the most dominant in terms of basal area was Sapotaceae ($1367.13\,cm^2$). The most conspicuous families, as represented among the top five FIV, include Burseraceae in all four plots, Moraceae in three of the plots, and Sapotaceae in two plots. Less than 20% of the total inventory of species are represented in two or more plots. The percentages of species which are unique to a single plot range from 56 to 67%. The within-plot diversities recorded in the present study indicate that the Sierra Maiguailida harbors the richest forests thus far documented in Venezuelan Guayana. Meanwhile, the low between-plot similarity indices reinforce the notion that the species richness of this region is unusually high and suggest the need to extend collections and inventory studies.

Introduction

In the last two decades the number, area, and spatial distribution of quantitative botanical plot inventories in the Amazon-Guayana rainforest region have expanded considerably, thus permitting the mapping and modeling of large-scale geographical patterns of plant diversity and density and leading to advances in the identification of conditioning environmental factors (Terborgh and Andresen 1998; ter Steege et al. 2000, 2003). However, significant gaps in the data coverage still remain, especially with regard to some of the more remote interfluvial and upland regions. Filling in some of these blank spaces could possibly alter prevailing notions about the emerging patterns and in turn hypotheses about their causes (Mori and Boom 1987; Milliken 1998). The Venezuelan Guayana is precisely one of the areas where relatively sparse and scattered plot-based studies have been carried out thus far. The overall floristic

content of this region is described extensively in the encyclopedic *Flora of the Venezuelan Guayana* (Berry et al. 1995) and the major vegetation types have been mapped at a large scale (Huber and Alarcón 1988; Huber 1995d). But our understanding of the composition, structure and diversity at the local level as well as the range and variation among localities within this vast region is still incipient (Huber 1995b), mainly because there have been too few quantitative transect or plot-based studies overall and those that have been done are too concentrated in a few selected ecogeographic zones (Catalan Castillo et al. 1980; Uhl and Murphy 1981; Gentry 1988b; Aymard et al. 1989, 1998; Boom 1990; Stergios et al. 1993; Marín and Chaviel 1996; Rosales 1996; Dezzeo and Briceño 1997; Castellanos 1998; Knab-Vispo et al. 1999; Dezzeo et al. 2000). More site-specific inventories and censuses are therefore needed to obtain a better resolution of the vegetation picture. One compelling reason for extending the coverage of fine-grained studies is that Guayana shield forests have been generally characterized as being species poor in comparison to Amazonian forests, yet considerable variation in the richness of forest sites within the Guayana shield has also been found (ter Steege et al. 2003; cf. Mori and Boom 1987), thus raising the question whether the low diversity rating may to some extent be an artifact of inadequate sampling.

One of the previously unexplored areas in the Venezuelan Guayana is the Sierra Maigualida, where the present study took place. The scientific literature contains almost no references to the floristic composition of this area, a rare exception being the vegetation map of Venezuela produced by Huber and Alarcón (1988), who nevertheless acknowledge that it 'has been little explored'. Huber et al. (1997) provide a sketch of the floristic component of the high mountain zone ($>1500\,\text{m asl}$) but lower elevation areas were not studied. The virtual absence of previous scientific information and obvious need for empirical botanical documentation provided a main stimulus for the present study.

The data presented here was gathered and recorded between May 1996 and October 1999 and formed an auxiliary component of a general ethnobotanical field study of the Hotï people, who are the indigenous inhabitants of the Sierra Maigualida region. One of our research objectives was to provide a quantitative assessment of Hotï knowledge and use of local plant diversity, so we adopted the ethnobotanical plot survey technique that has been used successfully in other quantitative ethnobotanical studies (Boom 1986, 1989; Prance et al. 1987; Baleé 1994). The ethnobotanical results of our study are presented in other documents or publications, the main concern here being to describe the floristic composition of the four 1-ha forest plots.

Sierra Maigualida

The Sierra Maigualida is the largest continuous mountain system in the Guayana shield, extending $>200\,\text{km}$ from north to south with an average
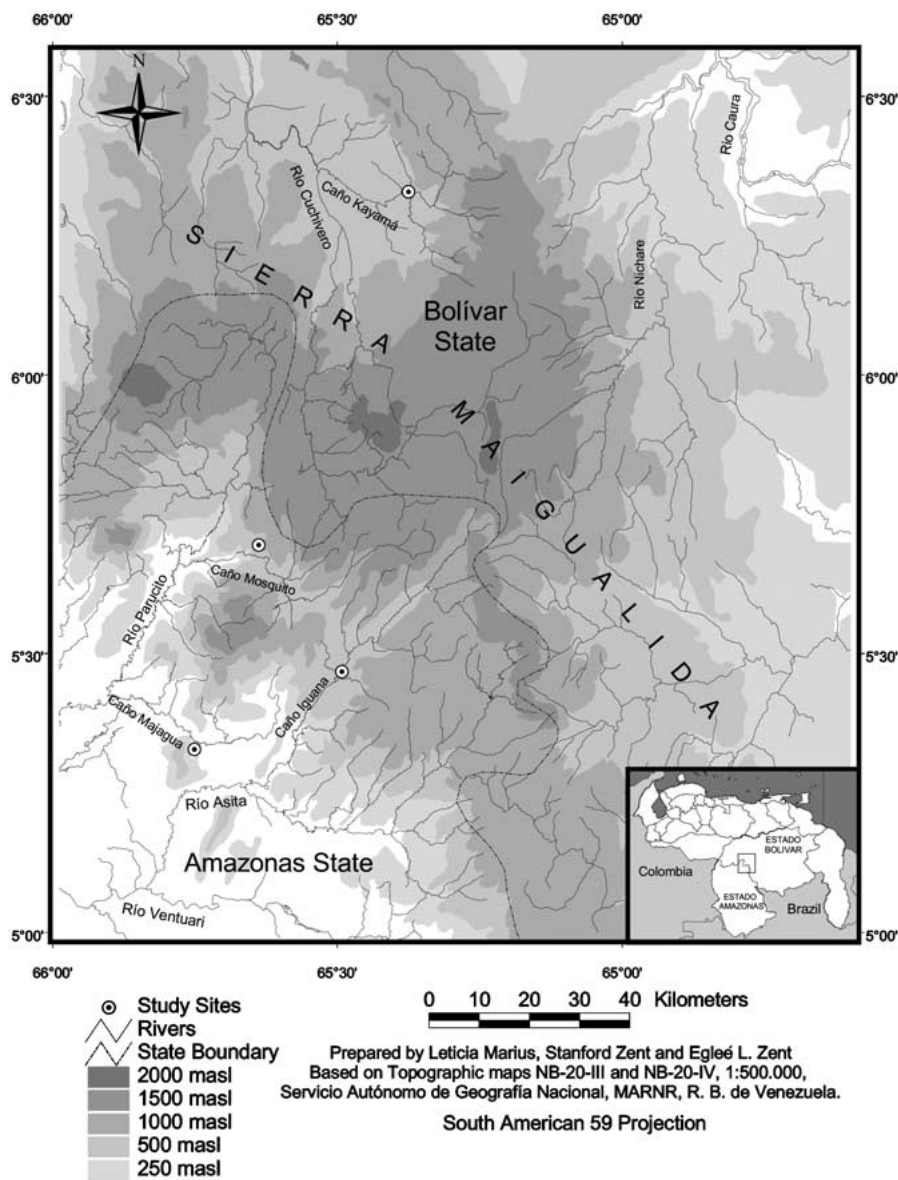
Figure 1. Central sector of the Sierra Maigualida.

width of 20–40 km, for a total area of 7000 km^2, between 4° and 7° N and 65° and 66° W (Huber 1995a). This range forms the watershed between the Caura river basin in Bolívar State toward the east and the Ventuari river valley in Amazonas State on the western side (Figure 1). In contrast to the more

well-known and distinctively shaped tepuis (steep cliff, tabletop sandstone mountains), the Maigualida is characterized by a sharply dissected, variably steep topography and a predominantly granitic bedrock, with elevations ranging from 150 to 2400 m asl. According to remote and spot land surveys (Garcia 1987; MARNR-ORSTOM 1988), the region as a whole displays considerable geological, geomorphological, edaphic, and climatic variation, factors which should predict a mosaic of diverse floristic communities (Huber, personal communication), but in-depth ecological studies are lacking. Most of this area is covered by dense, tall forests, the main exceptions being the high altitude zones above 2000 m asl where tepui-like meadows and scrub predominate (Huber 1995a).

The prior state of scientific knowledge about the floristic composition of the lower mountain zones of the Sierra Maigualida is confined to macro-scale inferential descriptions based mainly on altitudinal zonation, rainfall amounts, and extrapolation of botanical information from ecologically similar surrounding areas (Huber and Alarcón 1988). Huber (1995b) sketches the main forest types that are clearly observable from aerial reconnaissance: (i) ascending the east-facing slopes up to 600 m asl, one finds dense, tall, evergreen, basimontane forests, (ii) on steeper slopes, between 600 and 1500 m asl, there are medium-sized, evergreen montane to lower montane forests, characterized by an irregular, open canopy structure, (iii) between 1500 and 2000 m asl, a poorly differentiated mosaic of montane and upper montane cloud forests consisting of low to medium-tall (4–12 m) trees commonly covered by mosses and other epiphytes, and (iv) on the western slopes, there are somewhat drier montane forests, some of which are semi-deciduous while others are interspersed with open areas of bracken ferns, the latter being indicative of a history of fire disturbance.

Study sites

One hectare forest plots were established at four sites in or around the Sierra Maigualida: Caño Iguana (IG), Kayamá (KA), Caño Majagua (MA), and Caño Mosquito (MO) (Figure 1). All of the plots are located within the vicinity of a Hotï Indian settlement. The sample of different sites was selected with the aim of encompassing a wide range of ecoregional diversity.

The forest plot at IG is located about 15 min walk to the southeast of a Hotï village and New Tribes Mission base consisting of about 175 people along the left bank of the Caño Iguana at approximately 5°28.17 N, 65°29.87 W. The community is nestled within a deep and narrow river valley surrounded on both sides by peaks rising to 1000 m altitude or more. It can be reached by small airplane, in which case it is a 1 h flight from Puerto Ayacucho, the main urban center and political seat of Amazonas state, or by dugout canoe and foot travel (3 days) from the town of San Juan de Manapiare (SJM), the provincial capital. The plot was set up in a patch of trail-less high forest identified by local residents as primary vegetation in which there were no visible signs of human-

induced disturbance, such as felled tree trunks or stumps. However, given the close proximity to the settlement, it is likely that low-intensity extractions of edible fruits, leaves (for house-thatch, wrapping material), and honey (involving the felling of single trees) do occur periodically. Furthermore, the typical animal populations of such forest have been depleted by many years of intensive hunting. The layout of the plot is such that it runs almost vertically up the slope of a mountain and therefore encompasses a considerable altitudinal and topographic gradient, extending between 250 and 420 m asl from one end to the other with an average slope of 20° and a range of 3–48° per 20 m of distance. The general appearance of the forest from the ground is tall and dense, displaying a mostly unbroken canopy between 18 and 30 m tall and the common appearance of forest giants (> 1 m dbh) standing 35 m tall or more, the main exception being a sizeable stretch of very steep, rocky terrain where several light gaps are noticeable. The understory is easily distinguished and relatively dense, consisting of juvenile trees and individuals of the Marantaceae, Heliconaceae, and Poaceae. The soils located in this area are classified as well-drained, highly weathered, mineral-poor, iron- and aluminum-oxide hardened oxisols (MARNR-ORSTOM 1988).

The forest plot at KA is about 2.8 km southeast (40 min walk away) of the mission settlement of San José de Kayamá, which is populated by approximately 600 Hotï and Eñepa Indians and a small contingent of Roman Catholic nuns, situated near the confluence of the Kayamá and Moya Rivers, right bank tributaries of the Cuchivero River, at 6°19.66 N, 65°22.69 W. The community is accessed by small aircraft, which takes 2 h from Ciudad Bolívar, the capital of Bolívar State. The area presents a variegated mosaic of rock outcrops, open savanna, woody savanna, gallery forest along streams, low forests on domed hills, and high, dense forests on mountain slopes and summits. Therefore the survey plot had to be placed at some distance from the settlement center, dictated essentially by the constraint of finding a relatively close continuous block of undisturbed forest vegetation. The altitudinal range of the plot fluctuates between 335 and 400 m asl, the slope angle per 20 m of distance ranging between 1–39° with an average of 15°. The forest at this site is primarily medium to tall (15–25 m), dense, with a clearly visible lower arboreal strata and a moderately dense understorey. However, also included within the plot, there is one granitic dome hilltop (or unexposed inselberg) that is covered by an obviously divergent vegetation type consisting of smaller, shorter, more twisted trees, 8–12 m tall, and a thicker grassy and shrubby understory, which may represent a transitional belt between savanna and high dense forest communities. Thus the forest plot we staked out appears to encompass heterogeneous or overlapping floras and vegetation types and as such is consistent with the prevailing mixed landscape. Soils in this area correspond to well-drained, acidic, low-base, clayish ultisols (CVG-TECMIN, in press).

The plot at MA is relatively close (5 min walk) to a semi-nomadic Hotï settlement of 25 people located on the left (south) bank of the Caño Majagua, about 30 km southeast of the mouth where it flows into the Río Parucito, at

5°21.00 N, 65°45.74 W. Access to the community is by fluvial transport from SJM, a trip that takes from 1 (wet season) to 3 days (dry season) depending on hydrographic conditions. The plot runs perpendicular to the river channel and encompasses a forest area which at the time it was laid out showed no apparent signs of anthropogenic habitat alteration other than low-impact fruit and leaf harvesting and was considered by local inhabitants to be primary forest. The local topography varies little, recorded altitudes within the plot ranging between 140 and 170 m asl, with the steepest slope angles being less than 20% and an average displacement of 8° per 20 m of distance. The forests within this plot display a continuously dense, 15–25 m tall canopy, with only a couple of very large, emergent trees, a striking abundance of palms, and a fairly dense understory. About 35% of the plot area is very flat and low-lying, and thus is sporadically and seasonally flooded with up to 15–20 cm of standing water. The remaining area is higher, moderately sloping and not subject to flooding. The different ground slope/flooding conditions partition the local plant community somewhat, such that there appear to be two distinct communities present here: periodically waterlogged and well-drained forests. Several species of the inventory were present exclusively in one or the other forest type (see below). The main soil type found here is seasonally wet, organic matter-enriched, plinthitic inceptisol (MARNR-ORSTOM 1988).

The plot at MO was laid out in a stretch of undisturbed forest about 250 m north-northeast of a small semi-nomadic Hotï settlement of 10 people on the northern side of the Caño Mosquito, about 40 km east of the mouth, at 5°41.61 N, 65°38.24 W. The community is situated within an upriver, interfluvial zone and therefore it can be reached only by a combination of foot and river travel, 3–5 days travel time from SJM depending on local weather and fluvial conditions. The local topography is invariably steep and hilly. The elevation of the plot varies from 400 to 480 m asl with an average slope change of 15° and a range of 0–45° per 20 m of distance. The forest cover was uniformly dense and tall (20–35 m), the only exception being a small gap which corresponds to a ravine where a stream flows and crosscuts the plot trajectory. Lianas, epiphytes, and herbaceous climbers are common on the trunks and branches of trees. The understory vegetation is dense and tangled. The soils of this area are well drained, very weathered, mineral-poor, plinthite-hardened oxisols (MARNR-ORSTOM 1988).

There are no meteorological stations located directly within the Sierra Maigualida, so the climatic parameters can only be approximated on the basis of data collected personally or recorded in nearby areas. Between January 1997 and February 1999, we took daily readings of rainfall, temperature and humidity, but since we did not stay at any one site for a continuous 12-month period, our data permits only a projected estimate of the site-specific annual ranges. From our data, we calculate that annual rainfall ranged between 2389 and 2724 mm at the four field sites during this time period, with May–August being the wettest months (> 300 mm) and December–March the driest months (< 100 mm). By comparison, at SJM, approximately 32 km west of the MA

study site, precipitation averaged 2633 ($\pm$315) mm/year from 1984 to 1998 (unpublished data, Ministerio del Ambiente), while at Pie de Salto on the Caura River, approximately 97 km east of the KA study site, the recorded rainfall was 2974 mm/year between 1969 and 1991 (Castellanos 1998). Temperatures throughout the region oscillate between a daily maximum of 30.8 ($\pm$2.4) and a daily minimum of 21.7 ($\pm$0.5) °C (range of 18–44 °C). By contrast, at SJM maximum daily temperatures average 33.7 °C and minimum daily temperatures average 19.5 °C. Relative humidity was quite variable according to the season, but the average daily maximum value was 92.6 ($\pm$1)% and the average daily minimum value was 63.7 ($\pm$11.9)% (Zent 1999).

Methodology

The quantitative forest inventories carried out at all four sites were characterized by the same plot size (1 ha) and shape (20 m × 500 m) and same plant size selection criteria ($\geq$10 cm dbh). This sample design conforms with that commonly used in other quantitative ecological and ethnobotanical studies within the Amazonian region, thus permitting comparison of the results across sites (Mori et al. 1983; Campbell et al. 1986; Prance et al. 1987). Placement of the study plots at the respective study sites was performed using a semi-random method. First, the general area to be surveyed was selected with the aid of local residents who pointed out where relatively large patches of human-undisturbed forest could be found in the vicinity of their villages. Second, the specific plot location was chosen using a variation of the random walk method (Greig-Smith 1983) such that numbers were randomly selected to determine: (a) the starting point of the plot, and (b) the compass bearing for laying out the central transect of the plot.

The plots were laid out by first measuring a straight 500 m-long transect using a Suunto compass and measuring tape. Vinyl stake flags were placed at 20 m intervals along the transect and also at a distance of 10 m on both sides of these measured at right angles from the transect angle, thus marking off twenty-five 20 m × 20 m quadrats. Plot topography was determined using a Suunto clinometer and measuring adjustments were made in accordance with slope changes (Peters 1996). Within each quadrat, all stems (tree, vine, palm, strangler, tree-like herb with pseudostem) $\geq$10 cm diameter were measured using a diameter tape at 1.3 m height or above the buttress roots, the tree heights were recorded using the clinometer, and their relative positions were drawn. Numbered aluminum tags were nailed to each stem $\geq$10 cm dbh and red vinyl ribbons were tied around them to enhance visibility. Voucher specimens of most of the tagged individuals were collected, pressed and preserved in the field with alcohol (90%). The quality of the specimen collections was optimized by making collections at several times in different seasons over a 3-year span in all of the plots, with an eye toward collecting fertile material if and when available. In the case of individuals that could be identified unambiguously as being the same species as individuals previously collected, no specimen was

collected and it was recorded as being equal to the previous collection. Thus a total of 1456 voucher numbers (72% of the total number of stems) were collected and complete sets were deposited at the Manuel Ovalles Herbarium (MYF) and National Herbarium (VEN). Large portions of the collection have also been sent to the National University of the Llanos 'Ezequiel Zamora' (UNELLEZ) and the Missouri Botanical Garden (MO). Identifications were made by botanists Angel Fernandez (VEN), Carlos Reyes (VEN), Reyna Gonto (VEN), Gerardo Aymard (UNELLEZ), Ronald Leisner (MO), and various others. In the case of more than one individual being identified as a morphospecies but belonging to the same generic or family group, we treated these as distinct only when the botanist could clearly establish their difference, thus possibly underestimating species richness.

A number of the quantitative measures typically employed in biodiversity plot studies were calculated for each forest plot. These include: stem density, basal area, diameter class frequency distribution, species area curve, percentage of buttressed stems, percentage of individuals with exudates, relative density, relative dominance, relative frequency, importance value (IVI), and family importance value (FIV) (Mori et al. 1983; Boom 1986; Milliken 1998). Plot heterogeneity (diversity plus evenness of species) was measured using Margalef's index, Fischer's alpha, Simpson's concentration index, Shannon-Wiener's information index, and Pielou's measure of evenness (Greig-Smith 1983; Magurran 1988). Additionally, the species-abundance patterns (also known as the Whittaker plot) in each plant community were plotted (Whittaker 1965). Similarity between the plots was assessed using Jaccard's coefficient of similarity with respect to the proportion of occurrence of shared species and Sorenson's coefficient of similarity in reference to the density of shared species (Greig-Smith 1983; Magurran 1988; Comiskey et al. 1998).

Results

Community structure

The general structural characteristics of each plot, including the number of stems, species, genera, families, basal area, and average tree size are presented in Table 1.

The plot at IG had an absolute density of 355 stems, consisting of 342 trees, 11 palms, and 2 lianas. A total of 133 species, 76 genera, and 38 families were represented in this inventory (Table 1). Despite the fact that the absolute density of stems was significantly lower than in the other plots studied here and is in fact below the normal range exhibited for most other Amazonian forest plots (cf. Campbell et al. 1986; Gentry 1988a; Knab-Vispo et al. 1999), the total basal area is the second highest ($33.65\,m^2$) and the average dbh is the highest (27.71 cm). In view of the relatively low stem density, the considerable presence of medium to large-sized trees, including several very large ($>1\,m\,dbh$)

Table 1. Structural characteristics of trees $\geq 10\,cm\,dbh$ in four forest plots of the Sierra Maigualida, Venezuela.

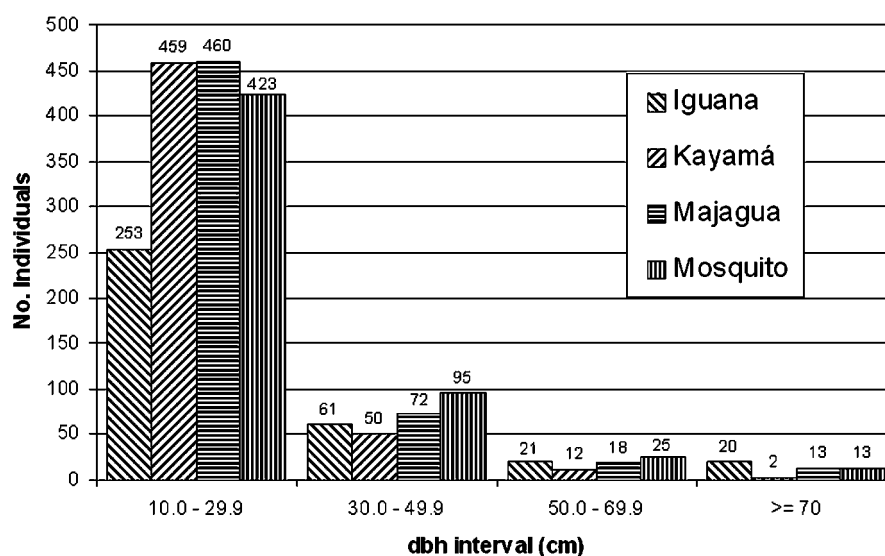| Site	Stem density	Species	Genera	Families	Basal area (m^2)	Average dbh (cm)	Largest tree (cm dbh)
IG	355	133	76	38	33.65	27.71	*Micropholis egensis* (A.DC) Pierre (124.14)
KA	538	191	120	51	20.56	19.50	*Sterculia pruriens* (Aublet) K. Schum. (73.5)
MA	563	182	102	42	31.22	21.91	*Ceiba pentandra* (L.) Gaertn. (118.3)
MO	556	187	110	45	40.83	24.32	*Micropholis egensis* (A.DC) Pierre (197.5)

Figure 2. Frequency distribution of stems according to diameter interval class.

emergents, accounts for the basal area actually being above the average ($<30\,m^2$) observed throughout the neotropics (see for example Campbell et al. 1986; Knab-Vispo et al. 1999). However, the basal area also showed a rather patchy distribution across the different quadrats (variance to mean ratio $s/\bar{x} = 1822/3303 = 0.55$), a feature that may be associated with the occasionally rugged terrain. The distribution of stems according to diameter size classes in this plot as well as all the other plots displays the negative exponential curve characteristic of mature tropical forest (Figure 2). The most significant result in this data set is the relatively high proportion (5.6%) of trees corresponding to the largest diametric class ($\geq 70\,cm$). This amount is well above the level usually observed (1–2%) in terra firme forest (Mori et al. 1983; Campbell et al. 1986;

Clark and Clark 1996) and indeed is one of the highest proportions of large-size trees ever recorded for neotropical lowland wet forests (cf. Mori and Boom 1987). This size class included individuals of the following species: *Brosimum alicastrum*, *Micropholis egensis*, *M. melinoniana*, *Erisma uncinatum*, *E.* sp. 1, *Apeiba intermedia*, *Coccoloba fallax*, *Trichilia pleeana*, and *Sterculia* sp. 1. The Uhl and Murphy index (ratio of stems ≥ 10 cm dbh/stems ≥ 20 cm dbh) was calculated as 2.04, also confirming the physiognomic depiction of this forest as one dominated by big trees. Consistent with the result that IG has a higher percentage of trees in the highest diameter class, we also find there the highest percentage (43%) of buttressed trees, which may also represent a mechanical adaptation to the steep slopes (cf. Crook et al. 1997). 28.5% of the trees at IG exhibited exudations from the stems in the form of latexes, resins and saps, mostly attributed to various species of the Moraceae (*Brosimum* spp., *Pseudolmedia* spp.) and Sapotaceae (*Micropholis* spp.).

The KA plot was characterized by 538 stems, of which there were 480 trees, 24 palms, 21 stranglers, nine lianas, and four tree-like herbs (all of the latter being *Phenakospermum guyannense*). The greatest amount of local floristic diversity was recorded here, including 191 species, 120 genera, and 51 families. However, this result may partly be the product of an ecotone or edge effect (Odum 1993), involving the mixing or close juxtaposition of species and families normally belonging to different plant associations, given that the general landscape surrounding the plot is characterized by a mosaic of diverse eco-vegetational zones ranging from savanna to high forest communities. Thus in quadrats 1–16 (starting from the northern end of the plot), there was a numerous representation of taxonomic groups that could also be found in the other plots studied here and therefore might be considered typical inhabitants of high forest habitats of the Maigualida, such as: *Iryanthera* spp., *Eschweilera* spp., *Lecythis* spp., *Coccoloba* spp., *Protium* spp., and *Trichilia* spp. By contrast, quadrats 17–21 were covered by a distinctively thinner, shorter, smaller, more twisted vegetation type, apparently transitional between forest and savanna, consisting partially of species which could also be spotted occasionally on the more open savanna, such as *Clusia microstemon*, *C. rosea*, *C. brachystyla*, *Curatella americana*, *Piptocoma schomburgkii*, *Ficus guianensis*, *Bathysa* sp., *Vochysia* spp., and *Byrsonima* spp. Another piece of evidence suggesting a possible edge effect is the relatively high number of families, which compares favorably or closely with other plots that are much richer in species (Gentry 1988a; Faber-Langendoen and Gentry 1991; Valencia et al. 1994; see also Johnston and Gillman 1995). Despite the relatively high stem density, the basal area was the lowest (20.56 m^2) of the four plots. Although this figure is substantially lower than any of the other plots and also appears to be rather low in comparison to the basal areas recorded in other neotropical lowland rain forests (Galeano et al. 1998), it is only slightly lower than the basal area (average of 22.3 m^2 ha^{-1}) obtained for terra firme forest in the Caura watershed (Knab-Vispo et al. 1999), about 67 km northwest of the KA plot. Consistent with this result, the KA plot also had the highest fraction of individuals (88%) in the smallest stem diameter class ($<$ 30 cm dbh) (Figure 2),

which is slightly less than the 90–92% breakdown observed in other Amazonian terra firme forests (Boom 1986; Campbell et al. 1986; Ferreira and Prance 1998). Only two trees, *Caraipa densifolia* and *Sterculia* sp., were found with dbh >70 cm. The Uhl and Murphy index was 3.06, which is somewhat higher than the value produced at IG and therefore indicates a forest populated by generally smaller trees. The comparatively lower woody biomass, besides being an outcome of the ecotonal conditions, may be influenced by a higher rate of natural disturbances which act to bring down trees, create gaps, and trigger recruitment by younger individuals (cf. Hartshorn 1978). The frequent disturbance regime might also help to explain why, despite the generally small size of most stems, 27% of trees were observed as having buttresses. KA also has the smallest proportion of exudating trees (27%), mostly accounted for by various members of the *Burseraceae*, including *Protium* spp., *Crepidospermum* spp., and *Tetragastris altissima*.

The plot at MA contained 563 stems, which was the highest absolute density recorded in the present study. This total included 425 trees, 119 palms, nine lianas, two stranglers, and eight tree-like herbs. The plot composition was less diverse than in KA but more diverse than in IG, with 182 species grouped into 102 genera and 42 families. Some portion of this diversity can be attributed to niche or community partitioning associated with differences in soil moisture, such that somewhat different forest formations appear on flooded versus non-flooded sections of the plot. During the height of the dry season some species experience hydric stress, shedding some or most of their leaves and in some cases becoming inflammable. Thus, similar to the KA sample, the MA plot appears to encompass a mix of distinct communities which includes on the one hand an assemblage of species that are tolerant of seasonal or sporadic flooding and on the other hand species that are adapted to water shortage through deciduous foliation or fire resistance. Some of the distinctive species found only on the flooded portion of the plot included: *Astrocaryum gynacanthum*, *Euterpe precatoria*, *Attalea* sp., *Ceiba* sp., *Licania apetala*, *L. heteromorpha*, *Calycolpus calophyllus*, *Hirtella elongata*, *Brosimum guianense*, *B. lactescens*, *Trichilia inaequilatera*, and *T. mazanensis*. By contrast, most of the deciduous species, such as *Couma macrocarpa*, *Spondias mombin*, *Enterolobium schomburgkii*, *Pterocarpus rohrii*, *Platymiscium pinnatum*, and *Machaerium* spp., were observed to be growing on the higher and drier portions of the plot. Fire resistant species, like the locally dominant palms, *Oenocarpus bacaba* and *Attalea maripa*, were also encountered exclusively on elevated ground. The total basal area of the plot is 31.22 m^2, the third highest in this study and within the normal neotropical range (Galeano et al. 1998), a result sustained more by the higher density than by the average stem size (21.9 cm dbh). The largest trees comprised 2.3% of the stem total and included: *Ceiba pentandra*, *Aspidosperma excelsum*, *Calophyllum brasilensis*, *Caryocar microcarpum*, *E. uncinatum*, and *M. egensis* (Figure 2). Basal area is more evenly distributed by quadrat (variance to mean ratio $s/\bar{x} = 1427/3122 = 0.46$) in comparison to the IG forest, a not unexpected result given the relative lack of slope deviation. The lowest percentage of trees with

buttresses (21%) was also recorded in this plot, an outcome that may be related to the small tree size as well as the flat topography. Stems totalling 30.6% had exudates, including several species of the Moraceae (*Pseudolmedia* spp., *Helicostylis tomentosa*) and Cecropiaceae (*Pourouma* spp.).

The plot at MO registered a population of 556 large stems, comprised of 515 trees, 22 palms, 10 lianas, seven stranglers, and two tree-like herbs. The composition included 187 species, 110 genera, and 45 families. In comparison with the other sites studied here, this plot is characterized by the second highest values for density as well as species richness. Even though the number of species at this site came close to the top number recorded at KA, the latter still had 10 more genera and six more families, thus indicating that MO is characterized by a richer stand of congeneric species. The MO forest presents the highest basal area (40.83 m^2) recorded in this study and may also be considered one of the highest recorded anywhere in the neotropics (see Knab-Vispo et al. 1999). However, the basal area is unevenly distributed over the plot (variance to mean ratio $s/\bar{x} = 2786/4083 = 0.68$), even more so than at IG, which may also be influenced by the considerable slope variation. The largest size class, representing 2.3% of the stem total (Figure 2), is represented by *M. egensis*, *E. uncinatum*, *Parkia pendula*, *Apuleia mollaris*, *Piptadenia psilostachya*, and *Pterocarpus rohrii*. The Uhl and Murphy index was 2.24, thus confirming the impression of a forest dominated by trees of large girth. Twenty-nine percent of stems were observed as having buttresses, the second highest figure in that category, which may be related to the slope variation as well as the larger number of trees in the middle and larger size classes. The MO plot also had the highest number of exudating stems (40.5%), one reason being the abundance of individuals of *Micandra siphinoides* (Euphorbiaceae) as well as member species of the Moraceae.

In sum, the results show that there are no simple correlations between stem density, species diversity, and basal area. Stem densities fall within the previously observed range for neotropical lowland rain forests (423–859 individuals ha^{-1} according to Galeano et al. 1998) with the possible exception of the lower density observed at IG (but see Knab-Vispo 1999). Species richness compares favorably with other neotropical lowland terra firme forests in general and with Guayanan forests in particular (Boom 1990; Johnston and Gillman 1995; Knab-Vispo 1999). In the case of KA and MA, the recorded alpha diversity may be an artifact of within-plot beta diversity (cf. Comiskey et al. 1998). All of the plots display the reverse J-shaped size distribution curve typical of mature tropical forest, but the significantly larger basal area at MO and larger average tree size at IG suggest that these stands may reflect greater age and/or are less exposed to disturbances (cf. Mori and Boom 1987).

Floristic composition

The 25 most important species occurring in the respective plots are listed in Table 2. Generally speaking, the floristic composition data from the plots

Table 2. Comparison of relative density (RDe), relative dominance (RDo), relative frequency (RF), and importance values (IVI) of the 25 most important species in four forest plots, Sierra Maigualida, Venezuela.

Site	Latin name	RDe	RDo	RF	IVI
IG	*Brosimum alicastrum* Sw. subsp. *bolivarense* (Pittier) Berg	16.92	5.35	2.75	25.02
	Micropholis egensis (A.DC.) Pierre	16.49	2.54	2.75	21.77
	Trichilia pleeana (Juss.) C.DC.	4.21	4.23	3.09	11.53
	Coccoloba fallax Lindau	4.70	3.94	2.41	11.04
	Sloanea laxiflora Spruce ex Benth.	1.66	3.94	2.41	8.00
	Pseudolmedia laevis (R. and P.) Macbr.	1.40	3.66	2.75	7.81
	Urera caracasana Griseb.	1.47	3.66	2.41	7.54
	Micropholis melinoniana Pierre	5.97	0.85	0.69	7.50
	Pouteria venosa (Mart.) Baehni	0.75	2.54	2.41	5.69
	Bathysa bathysoides (Steyerm.) P.G. Delprete	1.32	2.54	1.72	5.57
	Eschweilera subglandulosa (Steud. ex Berg) Miers	1.24	1.97	2.06	5.27
	Socratea exorrhiza (Mart.) Wendl.	0.56	2.25	2.41	5.22
	Guazuma ulmifolia Lam.	1.89	1.69	1.37	4.96
	Inga burgonii (Aubl.) DC.	1.46	1.41	1.72	4.58
	Sloanea robusta Uittien	1.23	1.41	1.37	4.02
	Erisma sp. 1	2.75	0.56	0.69	4.00
	Inga edulis Mart.	1.18	1.41	1.37	3.97
	Ecclinusa guianensis Eyma	1.09	1.13	1.37	3.59
	Protium crenatum Sandw.	1.05	1.13	1.37	3.55
	Sterculia sp. 1	2.18	0.56	0.69	3.43
	Protium opacum Swart.	1.54	0.85	1.03	3.41
	P. aff. *spruceanum* (Benth.) Engl.	0.57	1.41	1.37	3.36
	Brownea coccinea Jacq.	0.14	1.41	1.72	3.27
	Apeiba intermedia Uittien	1.99	0.56	0.69	3.24
	Licania aff. *densiflora* Kleinh.	0.68	1.13	1.37	3.19
KA	*Caraipa densifolia* Mart.	10.78	4.09	1.74	16.61
	Coccoloba fallax Lindau	6.43	3.16	2.49	12.08
	Protium heptaphyllum (Aubl.) Marchand	2.80	3.90	2.49	9.19
	Lecythis corrugata Poiteau	2.82	2.97	2.99	8.77
	Eschweilera subglandulosa (Steud. ex Berg) Miers	3.10	2.79	1.99	7.87
	Tetragastris altissima (Aubl.) Swart.	3.87	1.49	1.24	6.60
	Attalea maripa (Aubl.) Mart.	3.96	1.49	0.75	6.20
	Protium sagotianum March.	2.93	1.49	1.24	5.66
	P. tenuifolium (Engl.) Engler	1.86	2.04	1.74	5.65
	Euterpe precatoria Mart.	0.81	2.23	1.99	5.04
	Piptocoma schomburgkii (Sch. Bip.) J.F. Pruski	1.53	2.42	1.00	4.94
	Ecclinusa guianensis Eyma	1.85	1.30	1.49	4.65
	Trichilia pleeana (Juss.) C.DC.	1.61	1.49	1.49	4.58
	Eschweilera aff. *parvifolia* Mart. ex A.P.D.C.	0.91	1.86	1.49	4.26
	Ocotea schomburgkiana Benth. and Hook. f.	0.78	1.49	1.74	4.01
	Sterculia sp. 1	3.11	0.37	0.50	3.97
	Schefflera morototoni (Aubl.) Maguire, Steyerm. and Frodin	1.16	1.30	1.49	3.96
	Raputia aromatica Aubl.	1.15	1.49	1.00	3.63
	Parinari excelsa Sabine	1.84	0.93	0.75	3.52
	Brownea coccinea Jacq.	0.31	1.30	1.74	3.35
	Cedrela odorata L.	1.79	0.56	0.75	3.10
	Tapirira guianensis Aubl.	0.76	1.30	1.00	3.05

Table 2. (continued).

Site	Latin name	RDe	RDo	RF	IVI
	Chrysophyllum argenteum subsp. *auratum* Jacq. (Miq.) Penn.	0.89	1.12	1.00	3.00
	Himatanthus articulatus (Vahl) Woodson	0.77	0.93	1.24	2.95
	Licania densiflora Kleinh.	1.00	0.93	1.00	2.92
MA	*Oenocarpus bacaba* Mart.	6.46	10.48	4.70	21.63
	Pseudolmedia laevis (R. and P.) Macbr.	3.65	6.75	4.42	14.82
	Qualea paraensis Ducke	5.78	4.80	2.76	13.33
	Pourouma melinonii Benoist subsp. *melinonii*	3.05	4.97	3.31	11.34
	Helicostylis tomentosa (Poepp. and Endl.) Rusby	2.59	4.44	3.59	10.62
	Attalea maripa (Aubl.) Mart.	7.37	1.07	1.38	9.82
	Erisma uncinatum Warm.	6.06	1.42	1.93	9.41
	Socratea exorrhiza (Mart.) Wendl.	0.99	5.15	3.04	9.18
	Attalea sp. 1	5.69	1.07	0.28	7.03
	Brosimum lactescens (Moore) Berg	2.37	1.95	1.66	5.98
	Aspidosperma marcgravianum Woodson	2.37	1.60	1.66	5.62
	Trichilia inaequilatera T.D. Pennington	1.44	2.31	1.10	4.86
	Protium heptaphyllum (Aubl.) Marchand	0.60	1.78	2.21	4.59
	Licania apetala (E. Mey.) Fritsch	1.34	1.42	1.10	3.86
	Ceiba sp. 1	2.74	0.36	0.55	3.65
	Vochysia vismiifolia Spruce ex Warm.	0.88	1.07	1.66	3.61
	Ceiba pentandra (L.) Gaertn.	2.92	0.18	0.28	3.38
	Euterpe precatoria Mart. var. precatoria Mart.	0.44	1.78	1.10	3.32
	Micropholis egensis (A.DC.) Pierre	1.90	0.53	0.83	3.26
	Spondias mombin L.	2.43	0.53	0.28	3.24
	Caryocar microcarpum Ducke	2.28	0.36	0.55	3.18
	Protium tenuifolium (Engl.) Engler	0.32	1.07	1.66	3.04
	Trattinnickia lawrancei Standl. var. *boliviana* Sw.	1.65	0.53	0.83	3.01
	Brosimum guianense (Aubl.) Huber ex Ducke	1.08	1.07	0.83	2.98
	Aspidosperma aff. *excelsum* Benth.	1.70	0.36	0.55	2.61
MO	*Bathysa bathysoides* (Steyerm.) P.G. Delprete	10.10	11.87	3.77	25.74
	Micrandra aff. *siphonioides* Bentham	8.82	8.99	2.51	20.33
	Micropholis egensis (A.DC.) Pierre	11.65	0.72	0.75	13.13
	Erisma uncinatum Warm.	5.98	1.44	2.01	9.43
	Sloanea laxiflora Spruce ex Bentham	2.01	3.42	3.27	8.69
	Pseudolmedia laevis (R. and P.) Macbr.	2.23	3.42	3.02	8.66
	Pourouma minor Benoist	1.68	3.06	2.51	7.25
	Parkia pendula (Willd.) Benth. ex Walp.	5.76	0.18	0.25	6.19
	Erisma sp. 1	3.78	0.90	1.01	5.69
	Sloanea laurifolia (Benth.) Benth.	1.37	2.52	1.76	5.64
	Brosimum utile (H.B.K.) Pittier	0.66	2.16	2.76	5.58
	Protium sagotianum March.	0.62	2.52	2.01	5.15
	Socratea exorrhiza (Mart.) Wendl.	0.43	2.16	2.51	5.10
	Trichilia pleeana (Juss.) C.DC.	1.81	1.80	1.26	4.87
	Pseudolmedia laevigata (R. and P.) Trecul	0.88	1.80	1.76	4.44
	Piptadenia psilostachya (DC.) Benth.	3.90	0.18	0.25	4.33
	Attalea maripa (Aubl.) Mart.	1.63	1.26	1.26	4.15
	Sloanea sp. 2	0.72	1.62	1.76	4.10
	Virola elongata (Benth.) Warb.	0.26	1.44	1.76	3.46
	Pterocarpus rohrii Vahl	1.93	0.36	0.50	2.79

Table 2. (continued).

Site	Latin name	RDe	RDo	RF	IVI
	Dacryodes peruviana (Loes.) Lam	0.96	0.72	1.01	2.69
	Trichilia inaequilatera T.D. Pennington	0.29	0.90	1.26	2.45
	Inga burgonii (Aubl.) DC.	0.56	0.72	1.01	2.29
	Caraipa densifolia Mart.	0.48	0.72	1.01	2.21
	Pourouma sp. 2	0.24	0.90	1.01	2.15

indicate that these are high-diversity forests with only one or two or even no dominant species (i.e., ≥10% of relative density, dominance, or frequency).

A total of 133 species were represented at IG, of which there are two species that stand out from the rest: *B. alicastrum* and *M. egensis*. However, their importance values (IVI) account for only 8.3 and 7.3% of the total importance value, respectively, and the greater part of these values derive from the large size (relative dominance = 16.92 and 16.49, respectively) rather than the density or the frequency of the stems. Other relatively important species found in this plot include *T. pleeana*, *C. fallax*, *Sloanea laxiflora*, *Pseudolmedia laevis*, *Urera caracasana*, and *M. melinoniana*. All of the rest account individually for less than 2% of the total IVI. The general lack of dominant species is reflected in the fact that the five most important species account for only 26% and the top 25 species account for 57% of the total IVI. The number (38) of families represented in the plot is close to the amount (40) expected for a 1-ha sample of mixed forest (Galeano et al. 1998). The most important families were Sapotaceae, which ranked first in species richness and basal area and second in density, and Moraceae, which displayed the highest density, second highest basal area, and fourth highest number of species. The 10 most important families account for 66% of the total FIV (Tables 3 and 4).

The plot at KA displays the highest values of taxonomic diversity (191 species, 51 families) and perhaps noncoincidently also the highest degree of evenness or lack of dominance by any particular species or family (cf. Valencia et al. 1994). The putatively dominant species is *Caraipa densifolia*, although its importance value amounts to only 5.5% of the total. Other conspicuous species (IVI > 2% of the total) include *C. fallax*, *Protium heptaphyllum*, *Lecythis corrugata*, *Eschweilera subglandulosa*, *Tetragastris altissima*, and *Attalea maripa*. The five most important species make up 18% while the 25 most important species comprise 46.5% of the total IVI (Table 2). The relatively low importance of any particular species and the general dispersion of importance among many species in this plot are compositional characteristics more resemblant of the extremely high diversity, aseasonal pluvial forest plots of upper Amazonian Peru (Gentry 1988a) and Ecuador (Valencia et al. 1994) and represent a challenge to the proposition that at the local level (1 ha scale) all neotropical forests are dominated by a small group of common species (Boom 1986; Campbell 1994; but see Pitman et al. (2001) for an assessment of this issue

Table 3. The 25 families with the highest importance value in each forest plot.

IG		KA		MA		MO	
Family	FIV	Family	FIV	Family	FIV	Family	FIV
Sapotaceae	43.43	Burseraceae	30.80	Arecaceae	47.24	Euphorbiaceae	29.79
Moraceae	37.79	Clusiaceae	23.72	Moraceae	34.40	Rubiaceae	26.57
Burseraceae	20.48	Lecythidaceae	18.07	Vochysiaceae	29.91	Moraceae	22.20
Mimosaceae	19.98	Chrysobalanaceae	17.24	Fabaceae	18.78	Sapotaceae	20.65
Meliaceae	17.54	Fabaceae	14.79	Burseraceae	16.26	Burseraceae	20.50
Elaeocarpaceae	16.33	Sapindaceae	14.12	Cecropiaceae	12.30	Mimosaceae	18.63
Sterculiaceae	12.16	Meliaceae	13.67	Chrysobalanaceae	12.20	Vochysiaceae	18.63
Cecropiaceae	10.56	Arecaceae	12.19	Apocynaceae	11.98	Elaeocarpaceae	17.39
Lecythidaceae	9.96	Sapotaceae	10.43	Meliaceae	8.94	Cecropiaceae	12.36
Polygonaceae	9.40	Polygonaceae	10.11	Myrtaceae	8.16	Fabaceae	11.57
Rubiaceae	9.04	Euphorbiaceae	9.19	Melastomataceae	7.92	Meliaceae	10.63
Tiliaceae	8.30	Rubiaceae	8.93	Bombacaceae	7.29	Arecaceae	8.48
Arecaceae	7.16	Moraceae	7.54	Mimosaceae	6.86	Myristicaceae	8.11
Vochysiaceae	6.71	Caesalpiniaceae	6.80	Lecythidaceae	6.60	Caesalpiniaceae	7.38
Myristicaceae	6.49	Myristicaceae	6.61	Sapotaceae	6.57	Flacourtiaceae	6.57
Urticaceae	5.89	Sterculiaceae	6.25	Caesalpiniaceae	6.54	Sapindaceae	5.80
Lauraceae	5.57	Rutaceae	6.03	Caryocaraceae	4.62	Melastomataceae	4.63
Annonaceae	4.41	Mimosaceae	5.75	Myristicaceae	4.29	Clusiaceae	4.22
Fabaceae	4.38	Nyctaginaceae	5.59	Anacardiaceae	4.27	Chrysobalanaceae	4.06
Clusiaceae	3.79	Annonaceae	5.41	Sapindaceae	4.15	Leguminosaceae	3.63
Chrysobalanaceae	3.72	Lauraceae	4.71	Flacourtiaceae	4.08	Sterculiaceae	3.43
Flacourtiaceae	3.68	Myrtaceae	4.59	Clusiaceae	3.80	Violaceae	3.42
Caesalpiniaceae	3.45	Asteraceae	4.47	Euphorbiaceae	3.41	Lauraceae	3.32
Boraginaceae	3.36	Malpighiaceae	4.32	Rubiaceae	3.38	Bignoniaceae	3.00
Apocynaceae	3.33	Ochnaceae	4.06	Olacaceae	2.53	Lecythidaceae	2.38

Table 4. The five families with the highest number of species, individuals and basal areas.

Site	No. species		No. individuals		Basal area (cm^2)	
IG	Sapotaceae	11	Moraceae	42	Sapotaceae	858.68
	Mimosaceae	10	Sapotaceae	34	Moraceae	646.63
	Burseraceae	9	Elaeocarpaceae	28	Burseraceae	214.31
	Moraceae	9	Mimosaceae	26	Meliaceae	184.42
	Meliaceae	7	Burseraceae	26	Mimosaceae	169.31
KA	Burseraceae	13	Burseraceae	58	Burseraceae	273.69
	Fabaceae	13	Lecythidaceae	44	Clusiaceae	237.38
	Sapindaceae	12	Clusiaceae	38	Lecythidaceae	147.46
	Chrysobalanaceae	11	Chrysobalanaceae	31	Polygonaceae	128.74
	Meliaceae	9	Sapindaceae	26	Arecaceae	114.82
MA	Fabaceae	19	Arecaceae	119	Arecaceae	679.27
	Moraceae	13	Moraceae	90	Vochysiaceae	479.79
	Burseraceae	11	Vochysiaceae	56	Moraceae	354.99
	Chrysobalanaceae	11	Cecropiaceae	36	Bombacaceae	179.96
	Vochysiaceae	10	Burseraceae	35	Apocynaceae	168.54
MO	Burseraceae	14	Rubiaceae	72	Sapotaceae	508.45
	Moraceae	12	Euphorbiaceae	69	Euphorbiaceae	466.96
	Euphorbiaceae	11	Moraceae	61	Vochysiaceae	459.14
	Fabaceae	10	Elaeocarpaceae	48	Mimosaceae	452.01
	Sapotaceae	10	Burseraceae	46	Rubiaceae	423.54

at large scales). The Burseraceae was the dominant family, tied with Fabaceae for the highest number of species (13) and unrivaled with regard to density and basal area. The second most important family was Clusiaceae, which is nowhere near as prominent in any of the other plots (however, it does appear to be similarly important in other neotropical lowland areas, cf. Faber-Langendoen and Gentry 1991). This result may be influenced by the transitional savanna-forest vegetational conditions. The top 10 families comprise 55% of the total FIV, which is somewhat below the proportions (66–67%) observed in the other plots and may be associated with the higher family diversity (Tables 3 and 4).

One hundred-and-eighty-two species and 42 families were represented in the MA plot inventory. Different from the plots at IG and KA, this plot did have one species, *Oenocarpus bacaba*, that was particularly dominant in terms of density, with 59 individuals censused. Although this species also occurs in locally abundant stands elsewhere in Amazonia (Rankin-de-Mérona et al. 1992; Ferreira and Prance 1998; Milliken 1998), it is relatively rare (1 or 2 individuals) or absent in the other plots included in this study, thus indicating a patchy distribution throughout the Maigualida region. Other prominent species found in this plot were *Pseudolmedia laevis*, *Qualea paraensis*, *Pourouma melinonii*, *Helicostylis tomentosa*, *Attalea maripa*, *E. uncinatum*, *Socratea exorrhiza*, and *Attalea* sp. 1. Collectively these nine species constitute 36% and the top 25 species make up 56% of the total IVI (Table 2). At the family level,

the conspicuous presence of palms (47.24 FVI) is the most salient feature distinguishing this community. They are by far the most abundant (119) and dominant in terms of overall size. The abundance and dominance of palms is a feature more characteristic of terra firme forests of western Amazonia rather than of Guayana, although they are common in inundated forests of the latter region (Terborgh and Andresen 1998; ter Steege et al. 2000). The fact that a portion of this plot is periodically exposed to flooding may therefore help to explain this result. The second and third families in terms of importance values were Moraceae and Vochysidaceae. Moraceae figures as one of the three most important families in two other plots as well (IG and MO) but the importance level of Vochysidaceae registered here appears to be unique to this plot. The most species rich family was Fabaceae (19 species), followed by Moraceae (13 species), Burseraceae (11 species), and Chrysobalanaceae (11 species). The 10 most important families make up 67% of the total FIV (Tables 3 and 4).

MO was represented by 187 species and 45 families, which can be considered as falling within the normal range of species and families for high-diversity moist and wet neotropical lowland forests (Faber-Langendoen and Gentry 1991: 8). Two species may be singled out here as being significantly more important than the rest. They were *Bathysa bathysoides* and *Micrandra* aff. *siphonioides*, with 66 and 50 individuals, respectively. Other species with a notable presence were *M. egensis*, *E. uncinatum*, *Attalea maripa*, *Pseudolmedia laevis*, *Parkia pendula*, *Sloanea laxiflora*, and *Pourouma minor*. These eight species made up 33% while 25 species comprised 55.5% of the total IVI (Table 2). The two most important families were Euphorbiaceae and Rubiaceae, the only plot in which these families appear within the top 10 FIV. However, the other families within the first five, Moraceae, Sapotaceae, and Burseraceae, are among the highest FIV in at least one other plot. The most diverse families are the Burseraceae (14 species), Moraceae (12 species), and Euphorbiaceae (11 species). The top 10 families constitute 66% of the total FIV (Tables 3 and 4).

Collectively considered, a total of 2012 stems ≥ 10 cm dbh were recorded in the four forest plots, of which there were 533 species in 232 genera and 65 families that have been determined so far and there are another four individuals that remain unidentified even at the family level (see the Amazonian Plot Network database webpage at http://www.bio.uu.nl/~herba/research. html or Zent et al. (in preparation) for detailed taxonomic identification of the entire inventory). Comparison of our results with those obtained elsewhere in Amazonia and the Guayana shield reveals some interesting consistencies as well as inconsistencies with the family compositional traits previously observed in these respective regions. The 25 most diverse families in our 4 ha inventory are presented in rank order in Table 5. All but four of the top 20 contributors to species richness in lowland neotropical moist and wet sites (Gentry 1988b) are included within our list of 25. Furthermore, Leguminosae (Fabaceae *sensu lato*, including Mimosaceae and Caesalpiniaceae) is virtually always the most diverse family throughout the subcontinent (Gentry 1988b; cf. Valencia et al.

Table 5. Rank order of families by species, individuals, and basal area.

Family	No. genera	No. species	Species rank	No. individuals	Individuals rank	Basal area (cm^2)	B.A. rank
Fabaceae	18	38	1	68	12	459.84	9
Burseraceae	6	31	2	165	3	801.89	5
Moraceae	8	25	3	207	1	1227.76	2
Sapotaceae	10	24	4	81	9	1542.19	1
Meliaceae	8	22	5	90	6	433.36	10
Mimosaceae	9	22	5	60	13	703.54	6
Sapindaceae	6	22	5	48	17	105.33	26
Euphorbiaceae	8	20	8	93	5	530.72	7
Rubiaceae	14	20	8	105	4	527.2	8
Chrysobalanaceae	5	19	10	53	14	262.97	16
Vochysiaceae	5	18	11	87	7	1066.52	3
Caesalpinaceae	11	17	12	39	18	233.57	18
Myrtaceae	7	15	13	24	22	58.18	31
Cecropiaceae	3	13	14	83	8	314.19	14
Flacourtiaceae	3	13	14	19	25	124.85	22
Annonaceae	6	12	16	16	26	31.58	37
Clusiaceae	6	12	16	53	14	386.13	11
Lecythidaceae	3	12	16	73	11	250.69	17
Myristicaceae	4	12	16	50	16	110.41	25
Apocynaceae	4	11	20	25	21	228.52	19
Arecaceae	6	10	21	177	2	916.74	4
Elaeocarpaceae	1	10	21	78	10	358.67	12
Melastomataceae	3	10	21	23	23	66.85	29
Malpighiaceae	4	8	24	8	34	37.11	35
Lauraceae	5	7	25	21	24	94.16	28

1994; Ferreira and Prance 1998) and this general rule was upheld by our data, even though we separated the mimosoids and caesalpinioids from the Fabaceae. The most abundant families in all sampled plots were: Moraceae, Arecaceae, Burseraceae, Rubiaceae, and Euphorbiaceae, respectively (Table 5). Of these five families, only the Burseraceae are included in the top five whereas Arecaceae, Rubiaceae, and Euphorbiaceae are placed within the top 10 in a regionwide survey of the most abundant families in the Guayana shield forest plots (ter Steege et al. 2000). The most dominant families in all sampled plots were: Sapotaceae, Moraceae, Vochysiaceae, Arecaceae, and Burseraceae, respectively (Table 5). The relative abundance and/or dominance of Moraceae, Sapotaceae, Burseraceae, and Arecaceae have also been reported at numerous other lowland neotropical forest survey sites (Boom 1986, 1990; Faber-Langendoen and Gentry 1991; Rankin-de-Mérona et al. 1992; Valencia et al. 1994; Ferreira and Prance 1998, 1999; Milliken 1998; Terborgh and Andresen 1998; Knab-Vispo et al. 1999; see also Mori et al. 1983), but other families considered to be dominant within the Guayana shield region, namely Lecythidaceae and Chrysobalanaceae (ter Steege et al. 2000), do not place within the top 10 families in our sample. The most diverse genera are *Protium*
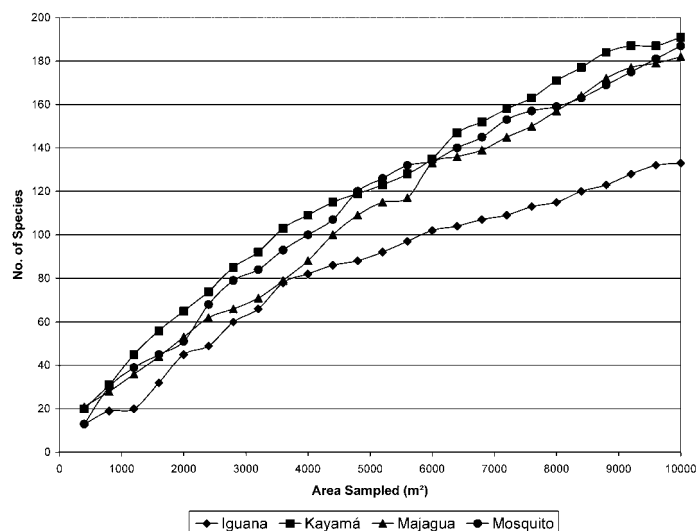
Figure 3. Cumulative species–area curve in the four forest plots.

with 18 species, followed by *Inga* with 14, *Brosimum* with 11, *Sloanea* with 10, and *Trichilia*, *Pouteria* and *Licania* each with 9 species.

Species diversity

Some idea of the species richness of the Sierra Maigualida forests can be gained by inspecting the cumulative species–area curves for the four forest plots shown in Figure 3. A random order selection of quadrats was employed in plotting the curves. Those corresponding to KA, MA, and MO show quite similar trajectories and end with rather small differences between them regarding the total number of species accumulated. At these sites, species are steadily accumulated at a rate of 8.9–9 species per quadrat ($400 \, m^2$) up through the first $6000 \, m^2$ of sampled area, after which the slope declines but still moves steadily upward at a rate of 4.9–6.6 species per quadrat. The IG curve is clearly divergent from the rest, increasing at a rate of 8.7 species per quadrat up through the first $3600 \, m^2$, after which the rate of increase dips to 3.4 species per additional quadrat over the remaining sample area. However, the lower species richness registered at IG may be less an intrinsic property of this forest than it is an artifact of the significantly lower individual density (355 vs. > 500) (cf. Valencia et al. 1998). In any case, none of the curves shows any sign of leveling off to an asymptote, thus indicating that the 1 ha inventory format does not provide for an adequate sample of the local species richness at any of the study locations. According to the first-order jackknife richness estimator (Heltshe and Forester 1983; Colwell 1997), the four samples represent less than two thirds (IG: 66%; KA: 65%;
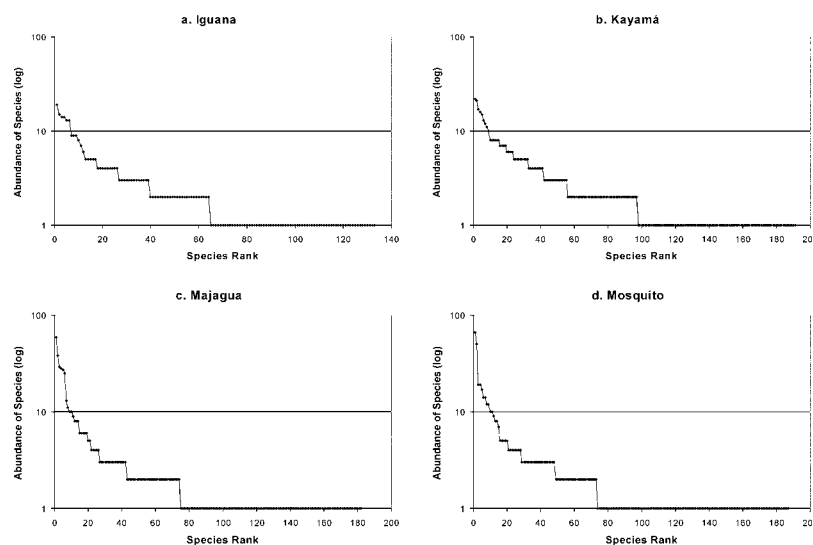
Figure 4. Species abundance plots for the four forest plots.

MA: 61%; MO: 63%) of the total number of species expected to be found in these forests if the sampling area were to be extended. However, given the considerable microhabitat diversity caused by abrupt or very small-scale variations of altitude, topography, rock outcrops, soil type, surface moisture, canopy height, and insolation, it remains to be seen whether the simple extension of the sampling area proportional to the calculated richness estimates would provide a comprehensive sample of the full extent of diversity of these forests.

The ranked species-abundance patterns of the different plots are depicted in Figure 4. All of the plots display the typical inverse distribution found in high-diversity primary forests, characterized by many species ($\geq 50\%$) represented by one to few individuals and few species represented by many ($\geq 10\,\mathrm{ha}^{-1}$) individuals (cf. Faber-Langendoen and Gentry 1991; Valencia et al. 1994). The number of species with a density of $\geq 10\,\mathrm{ha}^{-1}$ varies slightly below or above 5% of the total number of species recorded at all sites, as follows: 6 (4.6%) at IG, 9 (4.8%) at KA, 10 (5.5%) at MA, and 11 (5.9%) at MO. However, the most abundant species at IG and KA have considerably lower densities (19 and 22, respectively) than the most abundant species at MA and MO (66 and 59, respectively). Furthermore, the lower curves displayed by the IG and KA plots in comparison with those of MA and MO tell us that there is less dominance at the former and therefore they comprise more diverse assemblages as expressed by the more even distribution of individuals among species. The percentage of single occurrence species ranges from 49% (KA) to 61% (MO) and the number of species with 1–2 individuals ranges from 71% (IG) to 77%

Table 6. Proportion of single and double occurrence species in the four forest plots.

Site	Absolute density (percent of total)		Absolute frequency (percent of total)	
	1 stem (%)	1–2 stems (%)	1 quadrat (%)	1–2 quadrats (%)
IG	69 (52)	94 (71)	71 (50)	98 (74)
KA	94 (49)	137 (72)	106 (55)	148 (77)
MA	108 (59)	140 (77)	124 (68)	150 (82)
MO	114 (61)	139 (74)	119 (64)	145 (78)

Table 7. Diversity measures for plants ≥ 10 cm dbh in the four 1-ha forest plots, Sierra Maigualida, Venezuela.

Site	N[a]	S[b]	S/N[c]	D[d]	α[e]	$1/\lambda$[f]	H'[g]	E[h]
IG	355	133	0.37	22.48	77.19	65.86	6.42	0.91
KA	538	191	0.36	30.22	105.74	91.08	6.92	0.91
MA	563	182	0.32	28.58	93.29	35.98	6.29	0.84
MO	556	187	0.34	29.43	98.94	33.92	6.36	0.84

[a]N is the number of individuals censused.
[b]S is the total number of species recorded.
[c]S/N refers to the rate of species increase per individual censused.
[d]D is Margalef's index of species richness, $D = (S-1)/\ln N$.
[e]α is Fischer's index of diversity, $S = \alpha \ln(1 + N/\alpha)$.
[f]$1/\lambda$ is the reciprocal of Simpson's concentration index, $\lambda = \sum (n_i(n_i - 1))/(N_i(N_i - 1))$.
[g]H' is the Shannon–Wiener information index, $H = -\sum p_i \log_2 p_i$.
[h]E is Pielou's measure of evenness, $E = H/\ln S$.

(MA) (Table 6). The flip side of these diversity measures is that 5% of the species account for between 26% (IG and KA) and 43% (MA) of all individuals. Meanwhile the proportions of singleton and doubleton species as calculated on the basis of frequency or occurrence within one of the 25 quadrats are nearly parallel with, although slightly above, the corresponding amounts calculated on the basis of density, with 50–68% of all species appearing in a single quadrat and 74–82% appearing in no more than two quadrats (Table 6). These statistics point to the generally low tendency of clumped distribution of most species, at least at the limited scale of 1 ha. Taken together, these data confirm the rare local occurrence and dispersed distribution of most of the species encountered in the present study, which also suggests that considerable expansion of the area sampled would be required to inventory the full suite of species richness of this region (cf. Pitman et al. 1999).

A variety of commonly used density-dependent indices of diversity were calculated (Table 7) in order to permit a more exact comparison of the alpha diversities displayed at the different forest sites. The measures selected for this part of the analysis vary essentially according to the relative weighting that they give to the properties of species richness, abundance, and evenness (Magurran 1988). Whereas the species density per ha (S) indicates that the IG forest is the poorest (133) and KA the richest (191) in terms of species richness per unit of

area, the measure of numerical species richness (S/N) shows in contrast that IG is the richest (0.37), with KA in second place (0.36), in terms of the number of species per specified number of individuals. According to Margalef's index of species richness (D), which represents a measure mathematically intermediate between the previous two measures, KA is once again considered to be the most diverse (30.22), followed closely by MO (29.43) and MA (28.58) and distantly by IG (22.48). The log series index of diversity (α), a widely re-commended measure but one which is insensitive to changes in evenness, also depicts KA as the most diverse (105.74) and IG as the least diverse (77.19). Thus the latter two measures, which put more emphasis on the total species richness and take less account of the abundance pattern, identify KA as the most diverse forest site. Meanwhile MO and MA are rated as slightly less diverse while IG is considered to be significantly less diverse. The reciprocal of Simpson's concentration index ($1/\lambda$), which specifies the inverse of the prob-ability that two species selected at random would be of the same species, gives more weight to the abundances of the most common species. Given this par-ticular focus, it is not surprising that MO and MA are considered to be less diverse (33.92 and 35.98, respectively), since the most common species at these sites are considerably more dominant than the most abundant species found at IG and KA. By this measure, KA is seen as the most diverse forest, reflecting the generalized absence of dominance and high degree of evenness. The Shannon–Wiener information index (H'), which combines species richness and evenness into a single figure, identifies KA (6.92) once again as the most diverse plot, followed by IG (6.42), MO (6.36), and MA (6.29). These figures qualify the Maigualida forests as falling within the middle-to-upper range ($6 < H' < 7$) of diversity observed for lowland neotropical forests (Gentry 1988b). A t-test comparison of the Shannon-Wiener values between plots revealed that KA is significantly more diverse than the rest ($p < 0.001$) but there are no significant differences between any of the others. Pielou's measure of evenness (E) de-monstrates that a more equitable distribution of abundance prevails at IG and KA, where the observed evenness is calculated as 91% of the theoretical maximum, versus MA and MO (84%). In sum, the relatively high diversity values calculated for all of the samples in the present study can be interpreted as supporting the viewpoint that the Maigualida forests exhibit fairly high alpha diversity by lowland neotropical standards. Although the different measures of diversity employed here produce variable rankings among the four forest sites, nevertheless KA is almost always identified as the most diverse community. We hypothesize that this distinction is partly the result of the ecotonal or mixed vegetation association that prevails within the plot as well as throughout the surrounding area.

The between-plot taxonomic similarity was assessed using Jaccard's coeffi-cient based on the occurrence of species at two sites and Sorenson's coefficient based on the density of individuals of the same species occurring at two sites (Table 8). According to the former measure, the degree of similarity in species composition for plot pairs ranges from 7.8% (IG, MA) to 15.7% (IG, MO),

Table 8. Similarity between species composition for trees ≥ 10 cm dbh at four forest plots of the Sierra Maigualida, Venezuela. Jaccard's coefficient based on the occurrence of species at the different sites; Sorenson's coefficient based on the density of individuals of the same species occurring at two sites.

Sorenson's coefficient[b]	Jaccard's coefficient[a]			
Site	IG	KA	MA	MO
IG	–	0.129	0.078	0.157
KA	0.204	–	0.113	0.109
MA	0.115	0.142	–	0.115
MO	0.263	0.15	0.193	–

[a]Jaccard's coefficient $C_J = j/(a + b-j)$, where j is the number of species common to both sites, a is the number of species in site A, and b is the number of species in site B.

[b]Sorenson's coefficient $C_N = 2jN/(aN + bN)$, where aN is the number of individuals in site A, bN is the number of individuals in site B, and jN is the sum of the lower of the two abundances of species which occur at the two sites.

while the mean similarity for any two plots is 11.7%. The general significance of this degree of floristic divergence is perhaps better appreciated by considering that this amount of species overlap is close to being equivalent to the similarities recorded between secondary and primary forests in eastern and central Brazil (Balée 1993; Ferreira and Prance 1999). In short, the species compositions of all of the forest sites inventoried in the present study are 80–90% different from one another. MA appears to be the most divergent of the four sites with a mean species overlap of 10.2%, while MO is the most alike any other with a mean species overlap of 12.7%. When the species proportions were taken into account, the similarities increased slightly, with a range of 11.5% (IG, MA) to 26.3% (IG, MO) and a mean similarity of 17.8%. MA was again the most outlier sample, with a mean similarity of 15%, and MO repeated as the sample having the highest shared composition, with a mean similarity of 20.2%. However, it should also be emphasized that these differences are not very great and in most cases the proportional composition of any one plot is at least 80% different from that of any other. One reason for this result is that there is little overlap in terms of the most important species across the four plots. Of the five most important species in each plot (Table 2), only three, *C. fallax*, *M. egensis*, and *S. laxiflora*, occur in more than one plot and none appear in more than two plots. Expanding the scope of the comparison to include the 25 most important species, five species (*A. maripa*, *T. pleeana*, *M. egensis*, *P. laevis*, and *S. exorrhiza*) are present in three plots, 14 species in two plots, and 52 species in one plot. Taking into account the entire inventory of species recorded in the present study, just seven species (*E. guianensis*, *M. egensis*, *P. laevis*, *P. tenuifolium*, *S. exorrhiza*, *S. pruriens*, and *Iryanthera juruensis*) could be found in all four plots and 39 species were represented in three plots. The number of species unique to a single plot was in all cases greater

than half the plot total, as follows: IG (75/133 = 56.4%), KA (125/191 = 65.4%), MA (106/187 = 66.5%), and MO (106/187 = 56.7%). This leaves 106 (20%) species of the grand total (533) as being represented in more than one plot. The general conclusion reached in reference to these results is that the lowland forests of the Sierra Maigualida may be expected to yield a high gamma diversity by virtue of the high degree of between-site dissimilarity as well as the high level of within-site alpha diversity.

Discussion

For the most part, the quantitative inventory carried out in lowland tierra firme forests of the Sierra Maigualida in terms of the number of stems, species, and basal areas falls within the ranges reported for other lowland neotropical humid forests (Knab-Vispo et al. 1999). However, from a regional perspective the most surprising result obtained here was that these forests display the highest levels of alpha diversity thus far discovered in the Venezuelan Guayana. Consistent with what we may expect for Guayana shield forests, the alpha diversity found here is significantly lower than the extremely high diversities (>275 species ha^{-1}) recorded in pluvial and moist forests of central and western Amazonia (Gentry 1988a; Valencia et al. 1994; De Oliveira and Mori 1999; see also Duivenvoorden and Lips 1998). But the levels of species richness (>180 species ha^{-1}) observed at KA, MO, and MA are well above the previous high of 137 species ha^{-1} recorded in terra firme forest in the lower Caura watershed (Knab-Vispo et al. 1999).

What might explain the exceptional richness of the Maigualida forests in comparison to other forest areas of the Venezuelan Guayana? Following Milliken's (1998) advice, the first possible explanation we can think of points to differences in research methods. The semi-random method we used to locate and lay out the plots probably had the effect of encompassing more vegetational variation associated with micro-habitat gradation (i.e., beta diversity) than is usually the case. Our choice of method was motivated by the goal of inventorying and characterizing a reasonably representative and unbiased sample of the primary forest component of the local environments inhabited by different Hotï communities. By contrast, the sampling technique favored in several other forest plot studies carried out in the region usually entails the delimitation of plot boundaries within homogeneous physiognomic, edaphic, or topographic areas, the latter being determined by the investigator(s) through a qualitative assessment of remote images, aerial reconnaissance, previous vegetation maps, and/or ground survey. The main research objective there, in addition to conducting floristic inventories and recording local ethnoecological knowledge, has been to map and classify different vegetation types in selected geographic areas (Aymard et al. 1997; Dezzeo and Briceño 1997; Rosales et al. 1997; Castellanos 1998; Knab-Vispo et al. 1999). So the method being used in their case has intentionally sought to factor out diversity caused by environmental gradients. While this may be valid from the

standpoint of attempting to discriminate vegetation types and areas, it may also lead to underestimates of small-scale or within-site diversity, thus posing attendant problems for comparability across geographic regions, because considerable variations in terrain slope, soil quality, water drainage, light gaps, and canopy height among other environmental features may exist well below the standard measurement scale of 1 ha (Campbell et al. 1986; Gentry 1988a; Valencia et al. 1994). Another possible reason for species diversity underestimation in some of the other studies may be the heavy reliance on botanical determinations based on field identification by a solitary folk botanist who resides in the study area rather than herbarium specimen identifications (Catalán Castillo et al. 1980; Briceño et al. 1997; Dezzeo and Briceño 1997; Rosales et al. 1997; Salas et al. 1997; Castellanos 1998; Knab-Vispo et al. 1999). Our research on Hotï ethnobotanical knowledge indicates that approximately 23% of scientific species are under-differentiated (i.e., merged into larger groupings) in the folk classification system and even the most knowledgeable individuals in the four communities we studied, as determined through a consensus analysis of individual responses during tree identification tests, were able to identify no more than 85% of tree species at the folk specific taxonomic level (i.e. lowest level of category discrimination) (Zent 1999; Zent and Zent 2004). Thus reliance on folk botanists may lead to systematic underrepresentation of true species diversity (cf. Gentry 1988a; Rankin-de-Mérona et al. 1992). Lastly, we should also point out that our use of rectangular (20 m × 500 m) rather than square plots may have biased our results in favor of higher diversity, because the former are more likely to intercept more microhabitats. Square plots have been more commonly employed in the Venezuelan Guayana. However, plot shape difference may not be enough to explain all of the higher richness found in the Maigualida. A study comparing the effects of plot shape on tree diversity in Central Amazonia found that rectangular plots produce only modest advantages (2.2–6.2% more species) over square plots of equal area for capturing tree diversity, unless the plots are very elongated (e.g., 10 m × 1000 m) (Laurance et al. 1998).

The second possible reason for the higher recorded diversity of Maigualida forests has to do with the generally poor and spotty coverage of quantitative forest inventories considering the vastness of the region (Aymard et al. 1998). The most intensively studied areas to date are the tepui summits, Gran Sabana, Orinoco River gallery forests (Aymard et al. 1997), lowland forests around San Carlos de Río Negro (Uhl and Murphy 1981; Dezzeo et al. 2000), and the lower-middle Caura River (Huber and Rosales 1997). Outside the Maigualida, inventories of upriver and/or interfluvial forest zones are very rare. It may be significant that the two most diverse sites, KA and MO, correspond to lowland forests in the upper altitudinal range (300–500 m). In a study of the impact of altitudinal gradient on tropical forest composition in Costa Rica, Lieberman et al. (1996) found peak diversity at 300 m with decreasing amounts both above and below this elevation. However, more inventories need to be carried out in similar hydrogeographic and altitudinal zones to assess whether these environmental characteristics do in fact influence local species richness.

Another surprising result of the present study was the rather low level of similarity in terms of species composition and abundance (<20%) between plots. The low intersite similarity is partly explained by the relatively high proportion of singleton species per plot (average of 55% of all species in the plot) as well as the high proportion of the entire inventory of species that are unique to a single plot (80%). The relatively low overlap of the 25 most important species in the respective plots provides further evidence of between-plot dissimilarity. The main conclusion to be drawn from these data is that the majority of species inventoried here have rare, irregular, or clumped spatial distributions at the intersite scale and therefore the Maigualida region is probably characterized by high beta diversity. This result may be expected given the huge area and geomorphological variability of this mountain range, but in any case we are advised that an adequate appreciation of the overall species richness of the Sierra Maigualida, as well as other mountainous portions of the Guayana shield, will depend on the investigation of both alpha and beta diversities.

The surprising levels of diversity recorded within the plots as well as the low levels of similarity between the plots suggest that the northern sector of the Guayana shield may harbor forests richer in species than previously imagined. More extensive explorations and inventories throughout the Sierra Maigualida as well as other little known upland or interfluvial regions are needed to get a better idea of just how diverse these forests may be. The results also have implications for the reorientation of conservation policy in the region. Although the forests of the Venezuela Guayana are still largely intact, thanks in large part to an extensive network of protected areas (Huber 1995c), nevertheless there are growing signs that mining, logging and agricultural colonization are starting to have a degrading impact on the extent of the natural forest cover (Bevilacqua et al. 2002). Under previous policy, the designation of protected areas has been largely based on the selective representation of broadly defined biogeographic regions which are considered to be ecologically unique, interesting, or valuable. Meanwhile there have been no systematic attempts to inventory forests or to incorporate micro-scale information about biodiversity or ecological variability into conservation policy. One of the consequences of this macro-scale, generalized approach to defining protected areas has been to achieve extensive coverage of some areas while also leaving other important areas underrepresented. Thus for example lowland forests (<500 m) are the least well-protected, yet also the most extensive (Bevilacqua et al. 2002) and, according to our data, probably also the most diverse. It almost seems paradoxical that the most diverse communities are the least protected. Accordingly, we suggest that the high diversity lowland forests such as those found in the Sierra Maigualida should be given higher priority in conservation planning than is presently the case. Finally, it is worthwhile to point out that all of the forest plots studied here are rather close to indigenous communities, which therefore means that these areas are inhabited, exploited, and intervened by humans although such impacts are thought to be very low

level. Thus human occupation and use are not necessarily incompatible with the maintenance of high diversity forests, at least given the present parameters of population size, settlement pattern, exploitative technology, and consumption habits exhibited by the Hotï (cf. López-Zent 1998). Therefore it is not unreasonable to ask that the people who have traditionally inhabited this region should also be considered when drawing up protected areas or developing management plans.

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