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Different floristic patterns of woody understorey and canopy plants in Colombian Amazonia

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ABSTRACT. Distribution patterns of vascular plants with diameter at breast height (dbh) ≥ 2.5 cm were studied on the basis of compositional data from 30 small plots located in a rain-forest area in Colombian Amazonia. The research questions were: How are distribution patterns of species in relation to local abundance in plots? Do understorey species (defined as species with individuals that never attained dbh ≥ 10 cm anywhere) show better correlations with soils and environment than canopy species (defined as species with individuals that attained dbh ≥ 10 cm)? Are patterns found in the entire range of landscape units comparable to those found in well-drained uplands alone? Species that occurred in more than one plot showed higher local abundances. This pattern was consistent among environmental generalists and specialists. Locally rare species (with only one individual in a plot) occurred mostly in well-drained uplands. Considering all landscape units, Mantel tests showed substantial correlations between environmental data (soil chemical data, drainage and flooding) and species composition. Canopy species were only slightly less correlated with environmental data than understorey species. Elimination of the spatial component in the data did not reduce these correlations. In well-drained uplands, understorey species were better correlated with soils than canopy species. Here, however, the spatial configuration of the plots became more important in explaining species patterns.

KEY WORDS: beta diversity, Gower's coefficient, Mantel correlation, rain forest, rarity, soil, spatial effect, Steinhaus similarity coefficient

INTRODUCTION

The identification and explanation of plant distributions at local and regional scales in Amazonia, and the humid tropics in general, are gaining increasing

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attention (Caley & Schluter 1997, Hubbell 1997, Pitman *et al.* 1999, Terborgh & Andresen 1998). In humid tropical forests, spatial patterns of species are aggregated (Condit *et al.* 2000, Denslow 1987, Hubbell 1979), and tend to show high numbers of scattered and rare species (Hubbell 1995, 1997). Recent comparisons at regional scales in Peruvian Amazonia show that many locally rare tree species have wide regional distributions (Pitman *et al.* 1999, see also Murray *et al.* 1999).

In upper Amazonia, Gentry (1988, see also Tuomisto *et al.* 1995) suggested that forests are a fine-grained mosaic of many different forest types, each characterized by local assemblages of edaphic specialists. Spatial studies of canopy trees (in this study defined as plants with diameter at breast height (dbh) ≥ 10 cm) in Colombian (Duivenvoorden 1995, Duivenvoorden & Lips 1998) and Peruvian Amazonia (Pitman *et al.* 1999), however, showed that beta diversity at mesoscales (i.e. over geographical distances of 1–10^3 km) is low, especially in the well-drained upland forests which are the most widespread forest type in this region.

Better understanding of plant distribution patterns is highly relevant as forests with high levels of local endemic species occurring in fine-grained patches require completely different strategies of conservation than forests built up by populations of locally scarce but widely distributed generalist species. Insights into the degree of environmental preference of forest taxa are also highly necessary for calibration of the growing body of palynological data from the lowland tropics (van der Hammen & Hooghiemstra 2000).

Most studies on plant-edaphic relationships in tropical forests (e.g. Baillie *et al.* 1987, Clark *et al.* 1998, 1999; Duivenvoorden 1995) focused on canopy trees. However, tropical forests contain many more plant species among the individuals in the understorey (Duivenvoorden 1994, Gentry & Dodson 1987). It may well be that understorey species show greater edaphic specificity than large, well-established trees (Zagt & Werger 1998). Chance elements related to unpredictable events of gap formation influence the successful establishment of large trees. Also, it might be argued that for understorey plants which live predominantly in shaded conditions, edaphic heterogeneity might be an important source of variation for genetic selection. On the other hand, several authors have reported on evidence for spatially heterogeneous light conditions at forest floors and their effects on plant performance (Nicotra *et al.* 1999, Terborgh & Mathews 1999, Svenning 2000).

The current study was set up to compare patterns of these species groups in a series of 0.1-ha plots, well distributed in the principal landscape units of a part of Colombian Amazonia. The research questions were: How are the principal distribution patterns of species in relation to local abundance in plots? Do understorey species show better correlations with soils and environment than canopy species? Are patterns found in the entire range of landscape units comparable to those found in well-drained uplands alone?

STUDY AREA

The study area comprises about 1000 km^2 and is situated along the middle stretch of the Caquetá River in Colombian Amazonia, roughly between 1°–2°S and 70°–73°W. The principal landscape units found here are well-drained floodplains, swampy areas (including permanently inundated backswamps and basins in floodplains or fluvial terraces), areas covered with white-sand soils (found on high terraces of the Caquetá River and in less dissected parts of the Tertiary sedimentary plain), and well-drained uplands (which are never flooded by river water and include low and high fluvial terraces of the Caquetá River and a Tertiary sedimentary plain) (Duivenvoorden & Lips 1993, Lips & Duivenvoorden 1996). Soils and landscape units are called well-drained when soil drainage (according to FAO 1977) is imperfectly to well-drained (FAO drainage class ≥ 2), and poorly drained when soils are poorly to very poorly drained (FAO drainage class < 2). A previous ordination analysis of forest compositional patterns of the current data set (Duque *et al.* 2001), allowed the recognition of four forest types which correspond closely to the main landscape units: well-drained floodplain forests, well-drained upland forests (tierra firme), swamp forests (excluding any white-sand forests) and white-sand forests. The area receives a mean annual precipitation of about 3060 mm (1979–1990) and monthly rainfall is never below 100 mm (Duivenvoorden & Lips 1993). Mean annual temperature is 25.7 °C (1980–1989) (Duivenvoorden & Lips 1993).

METHODS

Vegetation sampling and identification of botanical vouchers

In each of the above-mentioned landscape units, 30 plots were located (Figure 1). In order to establish the plots, starting locations along the Caquetá River and the direction of the tracks along which the forests were entered, were planned on the basis of the interpretation of aerial photographs (Duivenvoorden 2001). During the walk through the forests, soils and terrain forms were rapidly described, and the forest was visually examined. In this way sites with homogeneous soils and physiognomically homogeneous forest stands were identified. In these stands, rectangular plots were delimited by compass, tape and stakes, working from a random starting point, with the restriction that the long side of the plot was parallel to the contour line. Plots were located without bias with respect to floristic composition or forest structure (including aspects of tree density, tree size and presence of lianas). All plots were established in mature forests that did not show signs of recent human intervention, at a minimum distance of 500 m between plots (Figure 1). Plots were mapped with GPS. Plot size was 0.1 ha and most plots were rectangular in shape (20 × 50 m). Plots were subdivided into subplots of 10 × 10 m, in which all vascular plant individuals with dbh ≥ 2.5 cm (dbh = diameter at 1.30 m height) were numbered. The dbh of all individuals was measured with tape. Their height

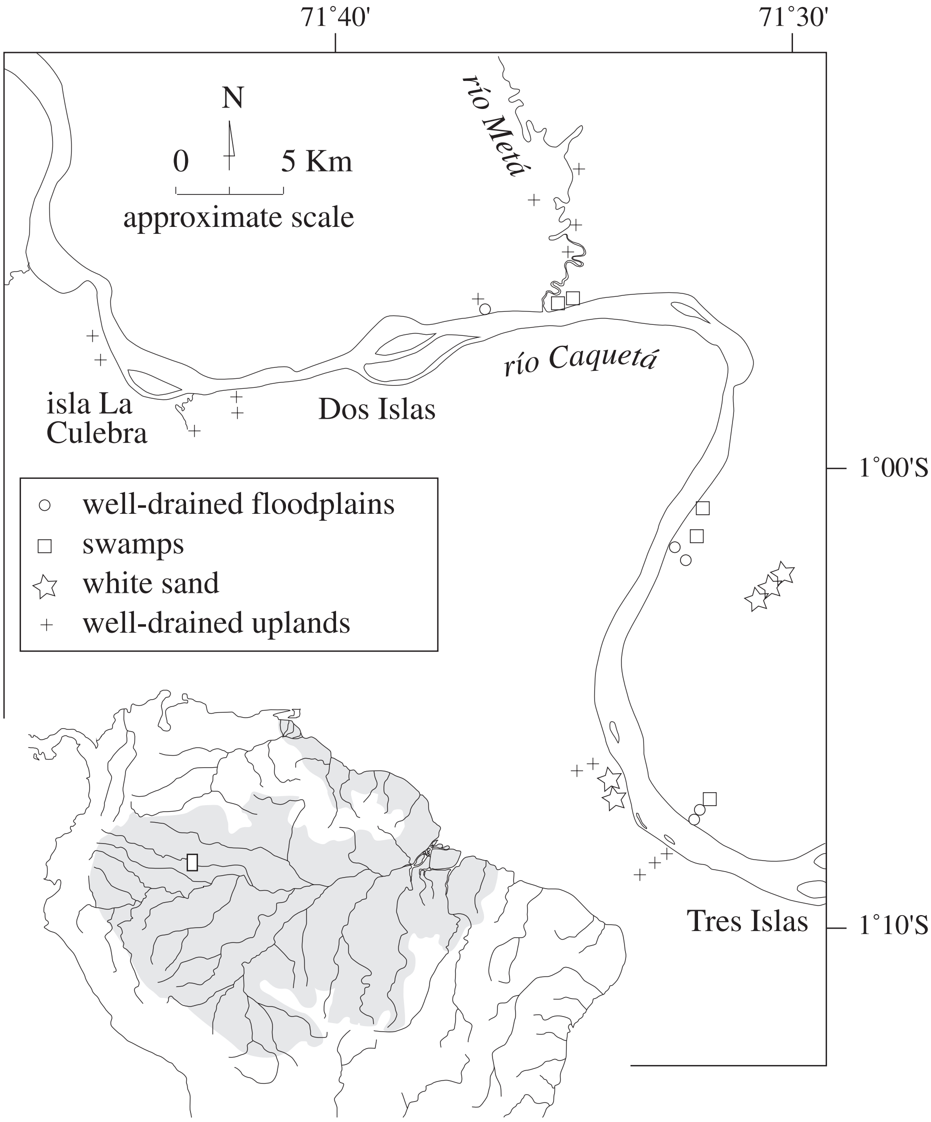

Figure 1. Location of 0.1-ha sample plots in the Metá area (Colombian Amazonia).

was estimated using long poles as a reference measure. Fieldwork took place in 1997 and 1998.

Botanical collections (numbers MS2900-7049 and AD3900-4092) were made of all species found in each plot. Identification took place at the Herbario Amazónico (COAH), the herbarium of the Missouri Botanical Garden (MO), the herbarium of the Universidad de los Andes in Santafé de Bogotá, and the Herbarium of the University of Aarhus (AAU). The nomenclature of families and genera follows Mabberley (1989). Within families or groups of closely allied families, specimens that could not be identified as species because of a lack of sufficient diagnostic characteristics, were clustered into morphospecies on the basis of simultaneous morphological comparisons with all other specimens.

Soil data

Roughly in the central part of each plot, a soil core was taken to 1.20 m depth in order to describe the mineral soil horizons (in terms of colour, mottling, horizon boundaries, presence of concretions and texture) and to define soil drainage (in classes of FAO 1977). At each augering position a soil sample was taken at a depth of 65–75 cm. Due to an unplanned delay in soil sampling in one floodplain plot and two plots in white-sand forests, samples from only 27 plots were analysed. For analyses, soil samples were dried at temperatures below 40 °C, crumbled and passed through a 2-mm sieve. At the soil laboratory of the Institute for Biodiversity and Ecosystem Dynamics at the Universiteit van Amsterdam, total content of Ca, Mg, K, Na and P was determined by means of atomic emission spectrometry of a subsample of 100–200 mg from the sieved fraction, that had been digested in a solution of 48% HF and 2M H_2SO_4 (after Lim & Jackson 1982). Total content of C and N was determined for the sieved fraction by means of a Carlo Erba 1106 elemental analyser.

Categories of floristic composition

Three categories of floristic data are considered in the analysis: all species (dbh ≥ 2.5 cm); canopy species (species with individuals that were found with dbh ≥ 10 cm); and understorey species (species with individuals recorded with a maximal dbh of less than 10 cm, anywhere in the plots). Understorey species are thus represented by plants that will never attain dbh ≥ 10 cm, or by juvenile individuals of plants that may develop into big canopy trees. For the species-environment analysis in well-drained uplands (see Table 6), only understorey species among individuals with heights below 10 m are considered (Welden *et al.* 1991).

Distribution patterns and forest preference

Species found with a maximum density of 1 stem per plot, are defined as locally rare (after Pitman *et al.* 1999). Otherwise species are referred to as locally abundant. Species are called environmental specialists when found in only one of the main landscape units defined in this study. When recorded in more than one of these landscape units, species are considered environmental generalists.

Correlation of species with soils, landscape units and geographical space

The correlations between species, environmental variables, and geographical space, were calculated by Mantel and partial Mantel tests (Leduc *et al.* 1992, Legendre & Legendre 1998), as made available in R-Package (Casgrain & Legendre 2000). In these tests, geographical space is used in much the same way as environmental variables, to define and test correlation between matrices (Legendre 1993).

In all Mantel tests, matrices of similarity coefficients were used. Species matrices were calculated with the Steinhaus index. This asymmetrical quantitative coefficient permits usage of species abundance data (Legendre & Legendre 1998). Environmental matrices were calculated with Gower's symmetrical similarity coefficient. This coefficient permits simultaneous incorporation of both nominal and quantitative variables (Legendre & Legendre 1998). Spatial information was quantified by means of Euclidean distances between plots. Probabilities of r-values were defined on the basis of 999 permutations.

RESULTS

Floristic data

A total of 13,989 individual vascular plants (dbh ≥ 2.5 cm) was recorded in the 30 plots of 0.1 ha each. A total number of 4343 botanical collections were made, representing 89 families, 378 genera and 1502 species, including 478 morphospecies (31% of all species). The most common species found in the area are listed in Appendix 1 (a complete species listing is annexed to Sánchez *et al.* 2001); 303 morphospecies (20% of all species) were identified only to genus, and 159 only to family (10% of all species). In the 15 plots of 0.1 ha established in the well-drained uplands, 81 families, 310 genera and 1124 species were found.

Altogether 650 canopy species were recorded (43% of all species found), 16 of which were liana species, and 852 understorey species (57% of all species) were found. Of these, 161 species were lianas.

Distribution patterns

Average plot densities of individuals (dbh ≥ 2.5 cm) in the main landscape units ranged between 273–669 per 0.1 ha (Table 1). A proportion of 15–32% of these individuals had dbh ≥ 10 cm. Average species densities (dbh ≥ 2.5 cm) fluctuated between 36–183 per 0.1 ha. Average canopy species densities were between 16–54 per 0.1 ha.

Table 1. Densities of species and plant individuals in two dbh classes, recorded in 0.1-ha plots in the main landscape units of the Metá area (Colombian Amazonia). Shown are averages ± SD of n plots.

	Species	Individuals	Species	Individuals	n
	dbh ≥ 2.5 cm		dbh ≥ 10 cm		
Well-drained floodplains	93 ± 16	273 ± 53	35 ± 9	57 ± 9	5
Swamps	72 ± 18	669 ± 302	27 ± 8	160 ± 115	5
White sands	36 ± 18	521 ± 212	16 ± 7	111 ± 40	5
Well-drained uplands	183 ± 21	436 ± 68	54 ± 7	79 ± 14	15

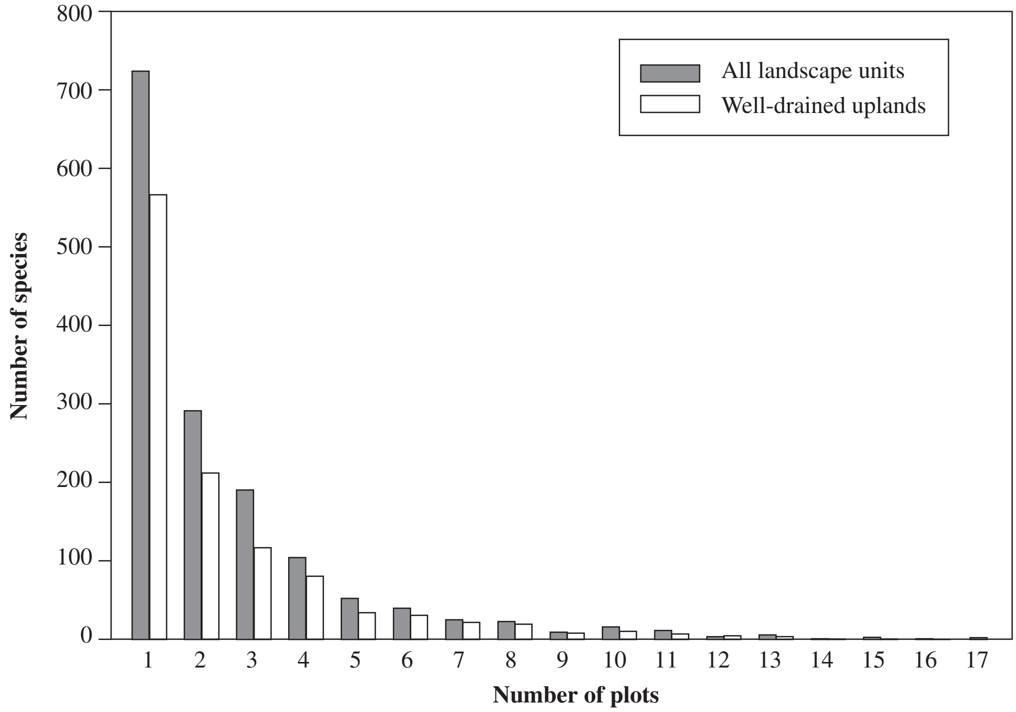

Figure 2. Number of species (dbh ≥ 2.5 cm) recorded in an increasing number of plots of 0.1 ha, in the Metá area (Colombian Amazonia).

Many species were restricted to only a few plots (Figure 2). For example, almost half of all the species (dbh ≥ 2.5 cm) were found in only one plot, and 80% of the species were found in three plots or less. Most species were also represented by only a few individuals (Figure 3). About 43% of all species were only found as one individual, and 80% of the species as three individuals or less (Figure 3). In both cases, patterns in well-drained uplands were quite similar to patterns in all landscape units together.

There were slightly more locally abundant species (57% of all species dbh ≥ 2.5 cm) than locally rare species (43% of all species dbh ≥ 2.5 cm) (Table 2). Most species occurred in only one landscape unit. Those species that were found in more than one plot tended to achieve higher local abundance than species restricted to a single plot. Among the entire set of species recorded, including the species that were found in only one plot, the number of locally rare species in relation to that of the locally abundant species was higher.

In the well-drained uplands the locally rare species contributed almost 50% of the total species richness (Table 3). In all other landscape units, locally abundant species prevailed. When the species that were found in only one plot were excluded, local abundance became proportionately more important, especially in the well-drained uplands.

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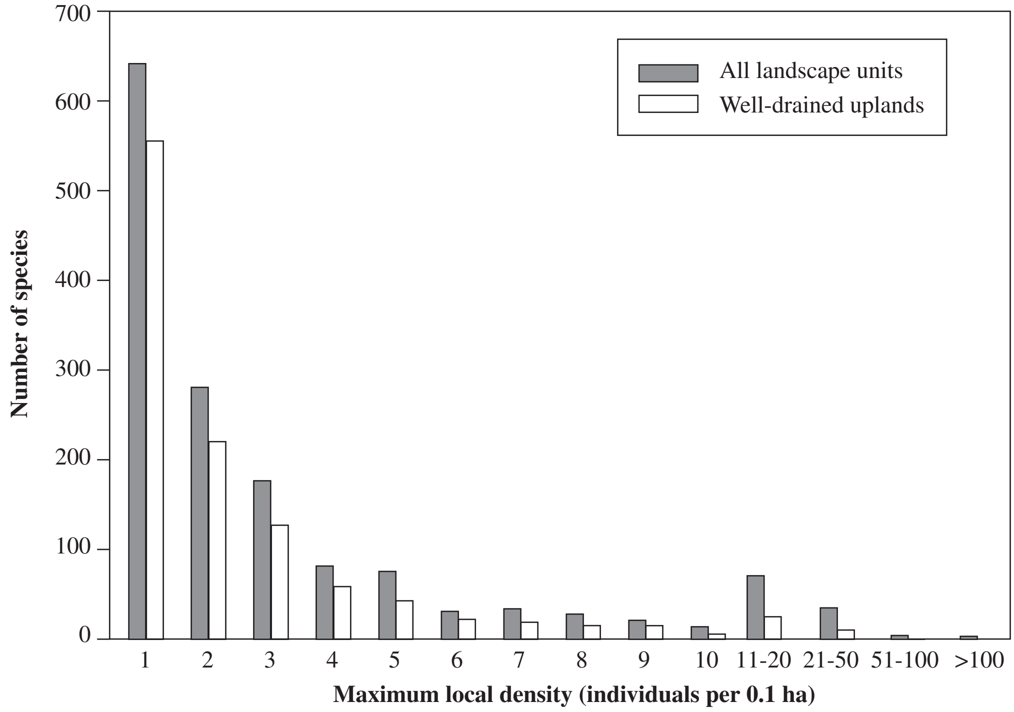

Figure 3. Number of species (dbh ≥ 2.5 cm) recorded with an increasing number of individuals in plots of 0.1 ha, in the Metá area (Colombian Amazonia).

Table 2. Number of locally rare and locally abundant vascular plant species (dbh ≥ 2.5 cm) in view of species presence in one or more landscape units in the Metá area (Colombian Amazonia). Landscape units considered are well-drained floodplains, swamps, well-drained uplands and white-sand areas.

	Species in two or more plots				All species
	Number of landscape units where species are found				
	4	3	2	1	
Locally abundant species	3	42	170	404	861
Locally rare species	0	2	29	127	641

Table 3. Number of locally rare and locally abundant vascular plant species (dbh ≥ 2.5 cm) in different landscape units, in the Metá area (Colombian Amazonia).

	Landscape units				
	Well-drained flood plains	Swamps	Well-drained uplands	White sands	All
All species					
Locally abundant	200 (61%)	141 (62%)	563 (50%)	85 (69%)	861 (57%)
Locally rare	127 (39%)	88 (38%)	555 (50%)	38 (31%)	641 (43%)
Species found in two or more plots					
Locally abundant	137 (71%)	108 (68%)	436 (68%)	62 (75%)	614 (79%)
Locally rare	57 (29%)	52 (32%)	201 (32%)	21 (25%)	163 (21%)

Species–environment correlations

The abiotic variables used to correlate species data with environmental information included flooding, drainage and physico-chemical soil variables (Table 4). When the entire data set derived from plots in all landscape units was analysed, the species composition of both canopy and understorey was strongly correlated with soils and flooding (Mantel r = 0.55 and Mantel r = 0.64, respectively; see Table 5). The spatial configuration of the plots correlated rather poorly with species patterns, even though this correlation was just significant (P = 0.05) for understorey species. When the effect of soils and flooding was removed, the correlation between species patterns and spatial positioning of the plots improved. The environmental information and location of the plots were just significantly correlated (Mantel r = 0.11, P = 0.04).

Restricting the analyses to the well-drained uplands, the species–environment relationships were less pronounced (Table 6). It became particularly poor among canopy species (Mantel r = 0.15, P = 0.12). Understorey species composition continued to show a significant correlation with soils and flooding (Mantel r = 0.30; P = 0.004), even when the spatial effect of the positioning of the plots was taken away (partial Mantel r = 0.33; P = 0.0002). Conversely, the location of the plots became an important factor in explaining species patterns, particularly among understorey species (Mantel r = 0.52), after correction for the environmental effect on species patterns (partial Mantel r = 0.53 for understorey species). The environmental information and location of the plots were not significantly correlated (Mantel r = 0.04, P = 0.27).

DISCUSSION

Floristic patterns

The proportion of identified species (69% of all species) in the current study is quite comparable to identification results found in other studies applying similar diameter limits in the same region (e.g. 65% reported by Grandez *et al.* (2001) in Peruvian Amazonia, and 74% claimed by Romero-Saltos *et al.* (2001) in Ecuadorian Amazonia). The unidentified specimens in this study (31% of all species) were mostly sterile and largely taken from juvenile individuals, which tend to show high morphological variability (Romoleroux *et al.* 1997). Some of the morphospecies might turn out to represent species new to science (R. Liesner and H. van der Werff, *pers. comm.*). However, other morphospecies may well correspond to one of the identified species, despite the efforts simultaneously to compare all specimens from the same genus or family.

Species distribution

Species that occurred in more than one plot showed higher local abundances. Positive abundance–distribution relationships are often found in many organisms and at a variety of spatial scales (see an overview in Gaston & Kunin

Table 4. Environmental variables used in the Mantel analyses, and their variation (average ± SD in case of quantitative variables and frequencies in case of nominal variables) recorded in 27 plots distributed over all landscape units, in the Metá area (Colombian Amazonia) (see also Figure 1).

	Well-drained flood plains	Swamps	Well-drained uplands	White sands	All
Number of plots	4	5	15	3	27
Quantitative variables					
Drainage	3 ± 0.6	0 ± 0.0	4 ± 0.0	0 ± 0.0	2 ± 1.9
Soil elemental concentration					
Ca (mmol kg^{-1})	130 ± 92	5 ± 1.8	2 ± 0.6	2 ± 1.2	20 ± 56
Mg (mmol kg^{-1})	320 ± 119	83 ± 34.8	30 ± 20.1	2 ± 0.3	80 ± 114
K (mmol kg^{-1})	370 ± 41	173 ± 77.9	53 ± 37.5	1 ± 0.7	120 ± 129
Na (mmol kg^{-1})	290 ± 174	29 ± 12.7	9 ± 6.8	0 ± 0.0	50 ± 117
P (mmol kg^{-1})	10 ± 4	17 ± 8.2	5 ± 1.4	1 ± 0.3	10 ± 6
C (%)	0 ± 0.1	15 ± 15.3	0 ± 0.1	3 ± 1.0	3 ± 8.2
N (%)	0 ± 0.0	1 ± 0.7	0 ± 0.0	0 ± 0.0	0 ± 0.5
Nominal variables (frequencies in %)					
Flooding by river water	100	100	0	0	40
Texture					
Sand	0	0	0	100	11
Clay-loam	0	0	20	0	11
Sandy clay	0	0	7	0	4
Silty clay	0	0	7	0	4
Organic clay	0	60	0	0	11
Clay	100	40	67	0	59

Table 5. Mantel and partial Mantel correlation of species composition with space and environment in all landscape units (27 plots). Matrix A is composed of Steinhaus similarity coefficients between species data. Environment is the matrix composed of Gower's similarity coefficients between environmental data. Space is the matrix composed of Euclidean distances between plots. Mantel r is the Mantel correlation coefficient between matrix A and matrix B. Partial Mantel r is the Mantel correlation between matrix A and matrix B when the effect of matrix C is removed.

All landscape units		Mantel r	Partial Mantel r	Probability
Matrix A = All species (dbh ≥ 2.5 cm)				
Matrix B				
Environment		0.63		0.001
Space		0.08		0.105
Matrix B	Matrix C			
Environment	Space		0.65	0.001
Space	Environment		0.19	0.004
Matrix A = Canopy species				
Matrix B				
Environment		0.55		0.001
Space		0.09		0.09
Matrix B	Matrix C			
Environment	Space		0.57	0.001
Space	Environment		0.17	0.005
Matrix A = Understorey species				
Matrix B				
Environment		0.64		0.001
Space		0.11		0.05
Matrix B	Matrix C			
Environment	Space		0.66	0.001
Space	Environment		0.24	0.002

1997, see also Brown 1984, Hanski *et al.* 1993). The most important explanations mentioned are sampling artifacts (locally rare species are less likely to be included in small sample plots and hence may appear with a more limited regional distribution), metapopulation dynamics (details in Hanski 1982, Hanski *et al.* 1993) and different degrees of ecological specialization (generalists would be able to exploit a wider range of resources and show less habitat specialization). In the current study generalist species (found in more than one main landscape unit) and specialist species (found in only one main landscape unit), showed a more-or-less similar abundance–distribution pattern. However, the estimates of local population size or environmental preference of many species were crude as the plot samples contained only a few individuals of these species. Also, the applied definition of local rareness and local abundance is arbitrary. It should be stressed that the great majority of the so-called locally abundant species are found with a low number of individuals per plot (see Figure 3). The term 'locally abundant' may be considered as somewhat misleading in this context (Pitman *et al.* 1999).

When poorly distributed species (found in only one plot) are removed, the contribution of locally rare species to the entire species pool decreases most in well-drained upland forests. Species that occur with one individual in only one plot are therefore relatively common in well-drained uplands, and contribute to the high alpha diversity in these uplands.

Table 6. Mantel and partial Mantel correlation of species composition with space and environment in the well-drained uplands (15 plots). Matrix A is composed of Steinhaus similarity coefficients between species data. Environment is the matrix composed of Gower's similarity coefficients between environmental data. Space is the matrix composed of Euclidean distances between plots. Mantel r is the Mantel correlation coefficient between matrix A and matrix B. Partial Mantel r is the Mantel correlation between matrix A and matrix B when the effect of matrix C is removed.

Uplands well-drained		Mantel r	Partial Mantel r	Probability
Matrix A = All species (dbh ≥ 2.5 cm)				
Matrix B				
Environment		0.24		0.034
Space		0.56		0.001
Matrix B	Matrix C			
Environment	Space		0.26	0.034
Space	Environment		0.57	0.001
Matrix A = Canopy species				
Matrix B				
Environment		0.15		0.12
Space		0.29		0.002
Matrix B	Matrix C			
Environment	Space		0.15	0.14
Space	Environment		0.29	0.002
Matrix A = Understorey species (height < 10 m)				
Matrix B				
Environment		0.3		0.004
Space		0.52		0.001
Matrix B	Matrix C			
Environment	Space		0.33	0.002
Space	Environment		0.53	0.001

Species–environment patterns in all landscape units (whole area)

Most species occur in only one landscape unit (Table 2). Because the plots are well distributed in the area this result suggests that species have rather strong preferences for one of the principal landscape units in the area. However, processes of dispersal among species may have led to relatively high species overlap between neighbouring plots in one landscape unit. The Mantel tests serve to quantify these spatial effects.

The Mantel analysis of species found among all individuals (dbh ≥ 2.5 cm) recorded in all landscape units (Table 5) shows a substantial amount of correlation between the matrices of species and environmental data (Table 5). Despite their rather low plot densities, canopy species are only slightly less correlated with environmental variables than understorey species. Elimination of the spatial component in the data, does not reduce these correlations. It seems therefore that forest plots which share certain properties of flooding, drainage and soil fertility (including white-sand soils) contain more-or-less similar assemblages of vascular plant species. Conclusions about environmental preferences of species should always be corroborated by experiments to discover causative mechanisms and underlying eco-physiological processes.

Indications for recurrent patterns of vascular plant species composition in similar landscape units in north-west Amazonia are not new (e.g. Duivenvoorden 1995, Tuomisto *et al.* 1995). Pitman *et al.* (1999) concluded that beta

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diversity among tree species in south-west Amazonia (Manu area, Peru) is weak, and found that 26% of tree species (dbh ≥ 10 cm) were restricted to one forest type (with species from two or more plots). In the present study, this percentage is slightly higher (35%). Perhaps the variation in soils and flooding among the plots studied by Pitman *et al.* was lower than in the current study. This may be due to their larger plot size (0.825–2.5 ha) which increases within-plot environmental heterogeneity or to smaller gradients among soils in the footslope zone of the Andes (less white-sand soils, ubiquitous enrichment by volcanic ash) compared with wider soil gradients found further downstream. Pitman *et al.* found plot densities of individuals with dbh ≥ 10 cm ranging between 282–858 ha^{-1}. These densities are in the same range as those found with dbh ≥ 2.5 cm in the 0.1-ha plots (Table 1).

Species–environment patterns in well-drained uplands

In the well-drained uplands, where the factor of flooding and drainage is held more or less constant, the Mantel correlation between the overall set of species (found among all individuals of dbh ≥ 2.5 cm) and soils is low but significant (Table 6). This correlation is due to understorey elements, because patterns in canopy species are no longer associated with soils. The understorey species-to-soil correlation remains significant when effects of space are removed. In a comparable sampling design of well-distributed 0.1-ha plots, Duivenvoorden (1995) claimed low but significant species-to-soil relationships in well-drained uplands of the middle Caquetá area (Colombia) for trees (dbh ≥ 10 cm). When correcting for effects of space and forest structure a partial canonical correspondence analysis showed that about 6% of the tree species patterns were significantly correlated with soils (Duivenvoorden 1995). The lack of correlation with canopy species in the current study might be due to the comparatively low number of plots analysed (15 vs. 39 by Duivenvoorden 1995). Comparison of Mantel tests and correspondence analysis is outside the scope of this study (see Legendre & Legendre 1998).

In the well-drained uplands, the spatial configuration of the plots is more important than soils in explaining species patterns. Many soil-independent processes (Condit 1996), like herbivory, seed dispersal by animals, plagues and attacks by fungi, species migration, colonization and competition for space and light in dynamic forest ecosystems affect species composition at scales wide enough to influence species composition in neighbouring plots in the area of the current study. The spatial effect is more pronounced in well-drained uplands than in the whole of the study area, both in absolute terms and in comparison to the environmental effect. Apparently, the wider the gradient in soils and flooding, the less important the role of the above-mentioned spatial processes.

Canopy species vs. understorey species in relation to environment

In the well-drained uplands, just as in the whole data set, understorey species are better correlated with soils than canopy species. Also, the spatial configuration of plots has a greater effect on understorey species patterns than on canopy species patterns. It seems likely that the current presence of many canopy individuals in the plots is an unpredictable result of light-induced growth due to events of gap formation in the recent past. The presence of understorey individuals, on the other hand, might be more limited by seed dispersal, germination and survival in heterogeneous light environments (Hubbell 1997, Nicotra *et al.* 1999, Terborgh & Mathews 1999). Better adaptation to specific local soil properties might improve the competitive strength of these species. As indicated above, such processes might take place at scales sufficiently wide to facilitate some spatial dependence among the plots included in the current survey.

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APPENDIX

Appendix 1. Vascular plant species recorded with more than four individuals (dbh = 2.5 cm) in 30 plots of 0.1 ha, in the Metá area (Colombian Amazonia). n = total number of individuals; Min dbh = minimal dbh; max dbh = maximal dbh; F = number of individuals in well-drained floodplains; S = number of individuals in swamps; U = number of individuals in well-drained uplands; W = number of individuals in white-sand areas.

	n	Min dbh (cm)	Max dbh (cm)	F	S	U	W
Anacardiaceae							
Anacardium giganteum Hancock ex Engler	9	2.5	37.7			9	
Campnosperma gummiferum (Bentham) Marchand	10	6	21.6		10		
Tapirira guianensis Aublet	46	2.6	21.5		27	18	1
Thyrsodium herrerense Encarnacion	6	4.3	14.8			6	
Annonaceae							
Anaxagorea cf. *angustifolia* Timmerman	27	2.6	6.2	3	24		
Anaxagorea rufa Timmerman	8	2.5	4.7			8	
Annona dolichophylla R.E. Fries	15	2.6	24.5	9	1	5	
Annona hypoglauca Martius	7	4.5	29.7	7			
Annona MS3648	9	2.7	8			9	
Bocageopsis canescens (Spruce ex Bentham) R.E. Fr.	9	2.8	14.8			3	6
Bocageopsis multiflora (Martius) R.E. Fries	20	2.8	11.4		15	5	
Diclinanona calycina (Diels) R.E. Fries	6	2.5	29.8			6	
Diclinanona tessmannii Diels	16	2.5	17	5		7	4
Duguetia flagellaris Huber	7	2.5	3.8	2		5	
Duguetia macrophylla R.E. Fries	6	2.6	5.6	4		2	
Duguetia odorata (Diels) J.F. Macbride	10	2.6	14.8	6		4	
Duguetia stenantha R.E. Fries	5	2.5	5.3			5	
Duguetia cf. *ulei* (Diels) R.E. Fries	7	2.7	4.2			5	2
Ephedranthus amazonicus R.E. Fries	5	2.7	12			5	
Guatteria cf. *decurrens* R.E. Fries	40	2.7	16.6		6	10	24
Guatteria ferruginea St.Hilaire	7	2.7	8.3			7	
Guatteria insculpta R.E. Fries	23	2.5	33.3		6	16	1
Guatteria macrocarpa R.E. Fries	6	2.8	9.3			6	
Guatteria macrophylla Blume	46	2.6	11.6	5		39	2
Guatteria MS3131	5	2.7	5	1			4

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APPENDIX *cont.*

	n	Min dbh (cm)	Max dbh (cm)	F	S	U	W
Guatteriasa tabapensis Aristeg. ex D.M. Johnson & A. Murray	18	2.5	26.5		7		11
Guatteriella tomentosa R.E. Fries	6	4.2	13.5			6	
Oxandra euneura Diels	49	2.7	7.3			49	
Oxandra leucodermis (Spruce ex Bentham) Warming	91	2.5	17.5				91
Oxandra mediocris Diels	8	2.6	17.6	8			
Oxandra polyantha R.E. Fries	1710	2.5	23.2		1710		
Oxandra xylopioides Diels	11	2.8	3.6				11
Pseudoxandra leucophylla (Diels) R.E. Fries	43	2.6	13	1	31	11	
Pseudoxandra aff. *polyphleba* (Diels) R.E. Fries	7	2.7	6.6	1		6	
Unonopsis elegantissima R.E. Fries	8	2.6	3.7			8	
Unonopsis floribunda Diels	15	2.5	12.8	15			
Unonopsis guatterioides (A.DC.) R.E. Fries	21	2.5	15.2	4	11	6	
Unonopsis stipitata Diels	48	2.5	7.8			48	
Unonopsis veneficiorum (C. Martius) R.E. Fries	9	2.6	12.1	9			
Xylopia cf. *calophylla* R.E. Fries	34	2.5	19.3		33	1	
Xylopia cuspidata Diels	7	2.6	4.2			7	
Xylopia nervosa (R.E. Fries) Maas	7	4	24.3	2	5		
Apocynaceae							
Aspidosperma excelsum Bentham	45	2.5	27.3		41		4
Aspidosperma MS3230	21	2.6	16	4	17		
Aspidosperma MS6443	10	4	37.4	10			
Aspidosperma cf. *multiflorum* A.DC.	6	2.5	48.7	6			
Couma catingae Ducke	5	3.5	29.6				5
Forsteronia affinis Muell. Arg.	7	3.2	7.3			7	
Lacmellea foxii (Stapf) Markgraf	11	2.7	10.8			10	1
Macoubea guianensis Aublet	18	3.8	28.7			7	11
Malouetia tamaquarina (Aublet) A.DC.	26	2.6	12.7	4	22		
Odontadenia funigera Woodson	11	3	5		11		
Tabernaemontana disticha A. DC.	10	3.3	6.4			10	
Aquifoliaceae							
Ilex guayusa Loesener	7	4	20		2	1	4
Ilex MS6237	6	2.7	6.6		6		
Araliaceae							
Dendropanax palustris (Ducke) Harms	225	2.5	21				225
Bignoniaceae							
Arrabidaea fanshawei Sandwith	12	2.7	8.5			12	
Arrabidaea prancei A.Gentry	8	2.5	7			8	
Digomphia densicoma (Martius ex DC) Pilger	572	2.5	52.5				572
Distictis pulverulenta (Sandwith) A.Gentry	8	2.8	5.5			8	
Jacaranda macrocarpa Bureau & K. Schumann ex K. Schumann	28	2.5	17.5			28	
Memora bracteosa (DC.) Bureau ex K. Schumann	6	2.7	5.6	5		1	
Memora cladotricha Sandwith	13	2.5	4.3			13	
Paragonia pyramidata (L.C. Richard) Bureau	17	3	7.6	17			
Tabebuia insignis (Miquel) Sandwith var. *monophylla* Sandwith	84	2.7	9.3		1		83
Tabebuia ochracea (Chamisso) Standley	92	2.5	32				92
Bombacaceae							
Matisia lasiocalyx K. Schumann	14	3.7	17.8	14			
Matisia aff. *malacocalyx* (A. Robyns & Nilsson) W.S. Alverson	25	2.5	11			25	
Pachira brevipes (A. Robyns) W.S. Alverson	96	2.5	28.2				96
Pachira foscolepidota (Steyermark) W.S. Alverson	14	3.6	13				14
Scleronema micranthum (Ducke) Ducke	103	2.5	73.5			33	70
Boraginaceae							
Cordia nodosa Lamarck	14	2.7	7.5			14	

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APPENDIX *cont.*

	n	Min dbh (cm)	Max dbh (cm)	F	S	U	W
Burseraceae							
Crepidospermum prancei Daly	8	2.5	17			8	
Crepidospermum rhoifolium (Bentham) Swart	6	2.7	5.3			6	
Dacryodes MS2998	11	2.5	13.5			11	
Dacryodes MS3430	17	2.5	31.4			17	
Dacryodes nitens Cuatrecasas	8	2.8	19.5			8	
Dacryodes cf. *peruviana* (Loesener) J.F. Macbride	22	2.5	34.2	3		19	
Dacryodes cf. *roraimensis* Cuatrecasas	24	2.6	13.3			24	
Protium altsonii Sandwith	31	2.6	22.3			15	16
Protium apiculatum Swart	18	2.7	19			18	
Protium aracouchini (Aublet) Marchand	7	2.7	6.8			7	
Protium cf. *crassipetalum* Cuatrecasas	10	2.8	30			10	
Protium decandrum (Aublet) Marchand	11	3.3	24.8			11	
Protium cf. *divaricatum* Engler	7	3	11.6			7	
Protium hebetatum Daly	66	2.5	22.3			66	
Protium cf. *laxiflorum* Engler	7	2.7	8.3			7	
Protium MS2901	6	2.6	6.6	2	4		
Protium MS5830	5	2.7	3.7			5	
Protium nodulosum Swart	10	3.5	20.2	8		2	
Protium opacum Swart	12	3.3	27.8			12	
Protium paniculatum Engler var. *paniculatum*	51	2.5	17.3			51	
Protium unifoliolatum Engler	13	2.6	16.5	13			
Tetragastris cf. *altissima* (Aublet) Swart	6	2.7	16.6	1		5	
Trattinnickia cf. *lawrencei* Standley	5	2.7	8.2			5	
Capparidaceae							
Capparis schunkei Macbride	15	2.5	7.3			15	
Caryocaraceae							
Caryocar glabrum (Aublet) Persoon	6	4	25.8			6	
Caryocar cf. *nuciferum* Linnaeus	9	2.8	11.4		1	8	
Cecropiaceae							
Cecropia distachya Huber	8	4	22.7			8	
Coussapoa cf. *orthoneura* Standley	5	2.5	6.4		5		
Pourouma cucura Standley & Cuatrecasas	6	5.6	45.2	6			
Pourouma myrmecophila Ducke	14	2.7	15.2			14	
Pourouma tomentosa Martius ssp. *tomentosa*	15	2.7	15.8			15	
Celastraceae							
Goupia glabra Aublet	8	6.3	61.6			8	
Hippocratea MS3216	5	2.6	4.2	5			
Salacia bullata Mennega	6	2.7	4.3			6	
Salacia gigantea Loesener	23	2.5	16.5	22		1	
Salacia macrantha A.C. Smith	6	2.5	5.5		1	5	
Tontelea cf. *coriacea* A.C. Smith	6	2.7	8.3			6	
Tontelea aff. *corymbosa* (Huber) A.C. Smith	6	2.5	7.5			6	
Chrysobalanaceae							
Couepia canomensis (Martius) Bentham ex Hooker f.	5	2.8	28			5	
Couepia chrysocalyx (Poeppig & Endlicher)Benth ex Hooker	22	2.6	22.2	2		20	
Couepia guianensis Aublet	5	3	11.3			5	
Couepia MS4947	7	2.6	25.7			7	
Hirtella duckei Huber	8	2.7	5.2			8	
Hirtella guainiae Spruce ex Hooker f.	15	2.7	6.8	11	2	2	
Licania apetala (E.Meyer) Fritsch	18	2.7	24.3			18	
Licania granvillei Prance	18	2.7	23			18	
Licania guianensis (Aublet) Grisebach	8	2.8	7.7			8	
Licania harlingii Prance	5	3.8	16.4		1	4	
Licania heteromorpha (Martius ex Hooker f.) Bentham	41	2.5	22.6			41	
Licania heteromorpha (Martius ex Hooker f.) Bentham var. *glabra* (Martius ex Hooker f.) Prance	7	2.5	21.6	2	1	4	

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APPENDIX *cont.*

	n	Min dbh (cm)	Max dbh (cm)	F	S	U	W
Licania intrapetiolaris Spruce ex Hooker f.	8	2.8	41.4	2		4	2
Licania laevigata Prance	40	2.5	27.5			40	
Licania lata J.F.Macbride	6	2.5	62.3	6			
Licania longistyla (Hooker f.) Fritsch	21	2.8	12		21		
Licania micrantha Miquel	15	3.3	28.3	1	3	11	
Licania mollis Bentham	15	2.5	19.7			15	
Licania MS5402	6	3.4	21.7			6	
Licania octandra (Hoffsgg. ex Roemer & Schultes) Kuntze ssp. *grandifolia* Prance	11	2.6	13		10	1	
Licania triandra Martius ex Hooker f.	9	2.5	27.7	3		6	
Licania urceolaris Hooker f.	11	3	14.5			11	
MS3602	9	3.4	24.5			9	
Parinari klugii Prance	10	4	91.3		10		
Parinari cf. *rodolphii* Huber	36	2.5	19.7		35	1	
Combretaceae							
Buchenavia macrophylla Spruce ex Eichler	7	2.7	10.8	1	5	1	
Buchenavia MS6194	9	4.8	100		9		
Buchenavia cf. *viridiflora* Ducke	17	3.5	20.3		16	1	
Connaraceae							
Connarus ruber (Poeppig) Planchon	5	3.2	5.5	5			
Pseudoconnarus macrophyllus (Poeppig) Radlkofer	22	2.5	5			22	
Convolvulaceae							
Dicranostyles ampla Ducke	11	2.6	8.2			11	
Dicranostyles holostyla Ducke	10	2.5	5.8	1	3	6	
Maripa glabra Choisy	8	3.5	6.8			8	
Maripa janusiana D'Austin	18	2.5	9.5		16	2	
Turbina MS6375	8	2.5	5.8	8			
Costaceae							
Costus scaber Ruiz & Pavón	16	3	3	16			
Cucurbitaceae							
Cayaponia oppositifolia Harms	7	3.2	14	7			
Cyatheaceae							
Cyathea macrosora (Baker) Domin	6	2.7	5.5			6	
Dichapetalaceae							
Tapura peruviana K. Krause var. *petioliflora* Prance	7	2.7	5.3	1		6	
Dilleniaceae							
Doliocarpus cf. *macrocarpus* Martius ex Eichler	5	3.8	11.4			5	
Pinzona coriacea Martius & Zuccarini	11	3	10.6			11	
Dipterocarpaceae							
Pseudomonotes tropenbosii Londoño, Alvarez & Forero	20	2.5	77.5			20	
Ebenaceae							
Diospyros aff. *glomerata* Spruce	8	2.6	4.2			8	
Diospyros cf. *tetrandra* Hiern	6	2.8	3.7		1	5	
Elaeocarpaceae							
Sloanea AD4020	19	2.7	12				19
Sloanea durissima Spruce ex Bentham	12	2.6	21.6	1		11	
Sloanea gracilis Uittien	5	2.5	13.5	3		2	
Sloanea guianensis (Aublet) Bentham	6	3	10			6	
Sloanea laxiflora Spruce ex Bentham	5	3.8	35.8			5	
Sloanea longipes Ducke	5	3.2	9.9		4	1	
Sloanea parvifructa J.A. Steyermark	20	2.8	11.6				20
Ericaceae							
Satyria panurensis (Bentham ex Meisner) Bentham & Hooker f.	19	2.8	5			19	
Euphorbiaceae							
Alchornea aff. *schomburgkii* Klotzsch	10	2.5	22.4	1	6	3	
Amanoa guianensis Aublet	7	4.8	14.6			7	

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APPENDIX *cont.*

	n	Min dbh (cm)	Max dbh (cm)	F	S	U	W
Conceveiba guianensis Aublet	16	2.6	15.5		15	1	
Drypetes amazonica Steyermark	22	2.5	70	22			
Hevea nitida Martius ex Muell.Arg.	27	2.6	20.2				27
Hevea pauciflora (Spruce ex Bentham) Muell.Arg.	85	2.5	41	2	14	60	9
Hyeronima alchorneoides Allemão var. *alchorneoides*	5	7.6	65	3		2	
Hyeronima oblonga (Tulasne) Muell.Arg.	11	3.3	14.2			11	
Mabea aff. *angularis* G. Den Hollander	24	2.5	10.2			24	
Mabea maynensis Muell.Arg.	17	2.7	8.2			17	
Mabea cf. *occidentalis* Bentham	6	3	3.8				6
Mabea speciosa Muell.Arg.	6	3	4.3			6	
Micrandra siphonioides Bentham	24	5.3	63.5		24		
Micrandra spruceana (Baillon) R.E. Schultes	67	2.6	53.3			67	
Nealchornea yapurensis Huber	8	2.6	15.5			8	
Omphalea diandra Linnaeus	6	3.8	7.2	6			
Podocalyx loranthoides Klotzsch	24	2.7	39	6	9	9	
Richeria grandis Vahl	5	2.7	3.7			5	
Sandwithia heterocalyx Secco	97	2.5	13.8			97	
Sapium marmierii Huber	8	6.5	25.4	8			
Senefeldera macrophylla Ducke	40	2.5	10.6			40	
Senefeldera cf. *verticillata* (Vell.) Croizat	53	2.5	14.4			53	
Flacourtiaceae							
Casearia cf. *arborea* (L.C. Richard) Urban	9	2.6	28.7	7		2	
Lindackeria paludosa (Bentham) Gilg	6	2.7	11.3			6	
MS6960	10	3.2	7.1		10		
Neoptychocarpus killipii (Monachino) Buchheim	54	2.5	6			54	
Ryania speciosa Vahl var. *tomentosa* (Miquel) Monachino	7	2.7	5.8			7	
Guttiferae							
Calophyllum AD3923	12	2.5	12.5				12
Calophyllum AD3969	6	5.2	51.7				6
Calophyllum longifolium Kunth	6	4	7.3		6		
Caraipa grandifolia Martius	30	2.6	17.3		29	1	
Caraipa myrcioides Ducke	5	2.8	41.8			5	
Chrysochlamys membranacea Planchon & Triana	6	2.5	12	2		4	
Clusia amazonica Planchon & Triana	6	2.8	5		3	3	
Clusia columnaris Engler	5	3	5			4	1
Clusia decussata Ruíz & Pavón	11	2.7	7.6			11	
Clusia gaudichaudii Choisy ex Planchon & Triana	6	2.7	4.8			6	
Clusia magnifolia Cuatrecasas	179	3	13.5				179
Clusia MS6280	11	2.5	6		1		10
Clusia spathulifolia Engler	67	3.5	21.8				67
Dystovomita AD3976	5	2.5	6.4				5
Dystovomita MS4875	52	2.5	13.2			22	30
Garcinia macrophylla Martius	14	2.6	26.6	5		9	
Garcinia spruceana (Engler) Hammel	5	2.5	17	2		3	
Haploclathra cf. *paniculata* (Martius) Bentham	10	2.8	35.5			10	
Lorostemon bombaciflorus Ducke	23	2.6	42.3		23		
Lorostemon colombianum Maguire	13	2.5	18			13	
Symphonia globulifera Linnaeus f.	5	3.1	5.5			5	
Tovomita cf. *brevistaminea* Engler	13	2.7	11.3	1		12	
Tovomita cf. *eggersii* Vesque	6	2.7	6.5			6	
Tovomita laurina Planchon & Triana	13	2.7	13.4			13	
Tovomita MS4222	44	2.5	6.8			44	
Tovomita MS4610	7	2.7	5.2			7	
Tovomita cf. *pyrifolia* A.C. Smith	6	4.3	13.1			6	
Humiriaceae							
Sacoglottis amazonica Martius	10	2.5	16.6			10	
Vantanea MS3381	16	2.7	23.3			16	

APPENDIX *cont.*

	n	Min dbh (cm)	Max dbh (cm)	F	S	U	W
Vantanea spichigeri A. Gentry	5	2.7	38.5			5	
Vantanea? MS3304	16	3	19.5		16		
Icacinaceae							
Dendrobangia boliviana Rusby	5	3	9.8			5	
Discophora froesii Pires	16	2.5	10				16
Discophora guianensis Miers	10	2.7	9.5			10	
Lacistemaceae							
Lacistema aggregatum (Bergius) Rusby	20	2.7	17.5			20	
Lauraceae							
Anaueria brasiliensis Kostermans	11	2.7	14			11	
Aniba cf. *panurensis* (Meissner) Mez	5	2.5	6			2	3
Aniba cf. *williamsii* O.C. Schmidt	6	2.8	13.3			6	
Endlicheria bracteata Mez	11	2.8	4.3		9	2	
Endlicheria krukovii (A.C. Smith) Kostermans	7	2.5	9.6	6		1	
Licaria aurea (Huber) Kostermans	9	2.7	8.4	2	1	6	
Licaria cannella (Meissner) Kostermans	11	2.5	25.3		1	10	
Licaria macrophylla (A.C. Smith) Kostermans	8	2.5	8.2			8	
Licaria MS4941	5	2.6	5.5			5	
Mezilaurus itauba (Meissner) Taubert ex Mez	6	9.3	135.4			6	
Mezilaurus sprucei (Meissner) Taubert ex Mez	9	2.5	35.4	4		5	
MS2926	5	2.7	6		1	4	
MS3340	7	2.7	14.8			7	
MS3378	11	2.5	7.3			11	
MS3385	15	2.5	11.6			15	
MS3475	8	2.5	4.4			8	
Ocotea aciphylla (Nees) Mez	63	2.7	28.5	2		61	
Ocotea amazonica (Meissner) Mez	12	3.2	61.5			12	
Ocotea argyrophylla Ducke	20	2.8	21.3			20	
Ocotea bofo H.B.K.	17	2.5	14.7		2	15	
Ocotea cf. *javitensis* (H.B.K.) Pittier	44	2.6	15.3			5	39
Ocotea matogrossensis Vattimo	9	3	10.3			9	
Ocotea MS4959	8	2.9	13.4			8	
Ocotea neblinae C.K. Allen	20	2.7	23.7		1		19
Ocotea olivacea A.C. Smith	12	2.5	17.3			12	
Ocotea cf. *petalanthera* (Meissner) Mez	8	2.7	26.3	8			
Ocotea rubrinervis Mez	5	3	10.3			5	
Ocotea cf. *tomentella* Sandwith	5	3	5.6			5	
Pleurothyrium panurense (Meisn.) Mez	9	2.7	6.8	9			
Lecythidaceae							
Cariniana decandra Ducke	6	2.7	6.3			6	
Cariniana multiflora Ducke	5	3.4	63			5	
Couratari oligantha A.C. Smith	28	2.5	32.8		28		
Couratari stellata A.C. Smith	14	2.5	18.2			14	
Eschweilera alata A.C. Smith	41	2.6	51.5			41	
Eschweilera albiflora (A.DC.) Miers	11	4.5	26.3	1	3	7	
Eschweilera andina (Rusby) J.F. Macbride	5	3	8.8	5			
Eschweilera bracteosa (Poeppig ex O. Berg) Miers	5	4.1	18.2			5	
Eschweilera coriaceae (A.DC.) S.A. Mori	95	2.5	39.5	5		90	
Eschweilera itayensis R. Knuth	10	2.6	23.2	3		7	
Eschweilera MS3354	24	2.6	7.8			24	
Eschweilera MS3719	21	2.5	25.8			21	
Eschweilera MS3776	67	2.8	34.7			67	
Eschweilera parvifolia Martius ex A.DC.	78	2.5	30			78	
Eschweilera punctata S.A. Mori	52	2.7	63.5			52	
Eschweilera rufifolia S.A. Mori	22	2.7	34.5			22	
Eschweilera tessmannii R. Knuth	29	2.5	25.2			29	

APPENDIX *cont.*

	n	Min dbh (cm)	Max dbh (cm)	F	S	U	W
Gustavia poeppigiana O. Berg	9	3.3	26.8	9			
Lecythis chartacea O. Berg	10	2.7	37.5			10	
Leguminosae							
Abarema claviflora (Spruce ex Bentham) Keinhoonte	14	2.8	8.8		1	13	
Acacia MS6430	5	3.4	7.4	5			
Bauhinia guianensis Aublet	6	2.7	6.3	5		1	
Brownea cf. *macrophylla* Linden ex Masters	70	2.7	23.3	70			
Clathrotropis macrocarpa Ducke	177	2.5	19.6			177	
Clathrotropis nitida (Bentham) Harms	22	2.8	35			22	
Derris longifolia Bentham	13	2.5	58	13			
Diplotropis martiusii Bentham	21	2.8	27.7	2	17	2	
Dipteryx nudipes Tulasne	8	2.6	37.3		3	5	
Heterostemon conjugatus Spruce ex Bentham	48	2.6	12.6			48	
Heterostemon mimosoides Desfontaines	11	4.2	48			11	
Inga acrocephala Steudel	13	2.8	25.7	3	1	9	
Inga aggregata G. Don	5	2.8	18			5	
Inga archeri Britton & Killip	5	3.2	9.4			5	
Inga bourgoni (Aublet) DC.	6	2.7	5.3	5		1	
Inga cf. *brachyrhachis* Harms	43	2.5	25.6		33	10	
Inga capitata Desvaux	6	2.6	6.4			6	
Inga chartaceae Poeppig	8	3	6		7	1	
Inga edulis Martius	6	5	43.6	6			
Inga marginata Willdenow	9	3.5	17.2		3	5	1
Inga pruriens Poeppig	8	2.6	23.3			8	
Inga ruiziana G. Don	16	2.5	6.5	2	2	12	
Inga tenuistipula Ducke	14	2.7	13.8	14			
Inga umbellifera (Vahl) Steudel	5	3	17.8	5			
Lonchocarpus nicou (Aublet) DC.	7	2.7	5.1	2		5	
Machaerium acutifolium Vogel	13	2.8	18.5		12	1	
Machaerium cf. *cuspidatum* Kuhlmann & Hoehne	9	3.2	8	8		1	
Machaerium inundatum (Martius ex Bentham) Ducke	8	2.8	8.6	6		2	
Machaerium macrophyllum Martius ex Bentham	47	2.5	7.7			47	
Machaerium madeirense Pittier	9	2.6	5.3	8		1	
Machaerium quinata (Aublet) Sandwith	9	2.5	12		7	2	
Macrolobium cf. *angustifolium* (Bentham) R.S. Cowan	28	2.6	39			2	26
Macrolobium discolor Bentham	101	2.5	33.7				101
Macrolobium gracile Spruce ex Bentham	36	2.5	21				36
Macrolobium cf. *limbatum* Spruce ex Bentham	31	2.8	15.6		28		3
Macrolobium multijugum (DC.) Bentham	35	2.5	28.6		4	5	26
Macrolobium suaveolens Spruce ex Bentham	57	2.6	36.5			3	54
Macrosamanea amplissima (Ducke) Barneby & Grimes	18	2.6	6.3		18		
Monopteryx cf. *inpae* W. Rodrigues	6	2.8	12.6			6	
Monopteryx uaucu Spruce ex Bentham	13	4	67.5			13	
MS3170	10	3.8	52.2	3		7	
MS3208	5	3.1	8.5	5			
MS3300	12	2.5	9.2		6	6	
MS3451	7	2.7	14.3			7	
MS4865	7	2.8	15.4			7	
MS6749	5	2.8	3.7			5	
Parkia basijuga Benth.	10	2.8	18.5			10	
Parkia cf. *panurensis* Bentham & Hopkins	13	2.5	38		5	5	3
Pithecellobium cauliflorum (Willdenow) Martius	82	2.5	16.8	2	80		
Swartzia cardiosperma Spruce ex Bentham	9	2.5	17.7			7	2
Swartzia laurifolia Bentham	34	2.6	16.5		20	14	
Swartzia MS3534	41	2.5	12.6			41	
Swartzia parvifolia Schery	9	2.7	7.3			9	
Swartzia cf. *pendula* Spruce ex Bentham	6	2.6	6.6		5	1	

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APPENDIX *cont.*

	n	Min dbh (cm)	Max dbh (cm)	F	S	U	W
Swartzia racemosa Bentham	17	2.5	27.8	12		5	
Swartzia schomburgkii Bentham	45	2.6	73.5			45	
Tachigali cf. *colombiana* Dwyer	6	3.2	27.3		5	1	
Tachigali formicarum Harms	13	2.8	27.2	7	1	5	
Tachigali MS3476	24	2.6	40.8			24	
Tachigali MS3827	15	2.5	14			15	
Tachigali MS3846	7	2.7	49.5			7	
Tachigali paniculata Aublet	7	4.3	68			7	
Tachigali polyphylla Poeppig & Endlicher	6	2.5	13.4			6	
Tachigali ptychophysca Spruce ex Bentham	19	3	10.8				19
Tachigali tessmannii Harms	19	2.5	25.8			17	2
Tachigali ulei Harms	6	4.2	42.5			6	
Vatairea guianensis Aublet	35	3.3	27.5	1	33	1	
Zygia basijuga (Ducke) Barneby & Grimes	26	2.6	9			26	
Zygia latifolia (Linnaeus) Fawcett & Rendle	13	2.6	27.2	13			
Zygia macrophylla (Spruce ex Bentham) L. Rico	18	2.7	5.9	4	14		
Linaceae							
Hebepetalum humiriifolium (Planchon) Bentham	7	3.3	14			1	6
Roucheria calophylla Planchon	9	2.8	16.6		8	1	
Roucheria punctata (Ducke) Ducke	17	2.7	22.4			13	4
Loganiaceae							
MS3065	5	2.8	3.7	5			
Strychnos erichsonii Ri. Schomburgk ex Progel	5	2.5	6.5	5			
Strychnos cf. *peckii* B.L. Robinson	20	2.5	9.8		20		
Malpighiaceae							
Byrsonima coniophylla A. Juss.	12	3.5	6.6				12
MS3315	6	3.2	9		4	2	
Marcgraviaceae							
Marcgravia cf. *parviflora* L.C. Richard ex Wittmack	7	3	6		6	1	
MS2921	5	2.8	4.3		5		
Norantea guianensis Aublet	5	3.3	6.8			5	
Souroubea guianensis Aublet	9	2.7	5.4	8		1	
Melastomataceae							
Bellucia MS3064	5	4.7	20.8	5			
Bellucia MS6188	5	2.5	7.4		5		
Graffenrieda cf. *limbata* Triana	10	2.5	10.5				10
Macairea spruceana O. Berg ex Triana	11	3	5.2				11
Miconia cf. *elaeagnoides* Cogniaux	22	2.5	7.9	16	4	2	
Miconia spichigera Wurdack	8	2.7	4.5			8	
Miconia cf. *tomentosa* (L.C. Richard) D.Don	6	2.8	3.8			6	
Miconia cf. *trinervia* (Swartz) D. Don ex Loudon	24	2.7	8	2	22		
Mouriri cauliflora Martius ex DC.	17	2.5	7.4			17	
Mouriri huberi Cogniaux	5	2.7	22.5			5	
Mouriri nigra (DC.) Morley	19	2.5	14		1	18	
Mouriri vernicosa Naudin	6	3	15.6			6	
Meliaceae							
Guarea cinnamomea Harms	6	3.5	32.7			6	
Guarea MS4514	12	3	27.1	12			
Guarea grandifolia DC.	14	2.5	6.6			14	
Guarea kunthiana Adrien Jussieu	16	2.5	6.7	15		1	
Guarea macrophylla Vahl	5	2.6	5			5	
Guarea purusana C.DC.	41	2.6	49.5	41			
Trichilia martiana C.DC.	7	3	9.4	2	1	4	
Trichilia micrantha Bentham	11	2.7	13.4			11	
Trichilia cf. *obovata* W. Palacios	12	4.5	18.7		12		
Trichilia pallida Swartz	7	2.6	7	1		6	

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APPENDIX *cont.*

	n	Min dbh (cm)	Max dbh (cm)	F	S	U	W
Trichilia septentrionalis C.DC.	6	2.7	9.6			6	
Trichilia stipitata T.D. Pennington	11	2.5	6		8	3	
Menispermaceae							
Abuta grandifolia (Martius) Sandwith	8	2.7	12.7			8	
Abuta imene (Martius) Eichler	25	2.5	7			25	
Abuta obovata Diels	8	3	12.1			8	
Sciadotenia cf. *toxifera* Krukoff & A.C. Smith	5	3	11.5			5	
Telitoxicum minutiflora (Diels) Moldenke	6	3	5.4		3	3	
Telitoxicum MS3816	15	2.6	7.8			15	
Monimiaceae							
Siparuna decipiens (Tulasne) A.DC.	5	2.6	10.5			5	
Siparuna guianensis Aublet	18	2.6	8			18	
Siparuna MS3160	7	2.7	5.3	7			
Siparuna MS6928	5	3.6	43		5		
Siparuna pachyantha A.C. Smith	5	3.4	9.5			5	
Moraceae							
Brosimum lactescens (S. Moore) C. Berg	17	2.5	105	11	1	5	
Brosimum rubescens Taubert	11	2.7	29			11	
Brosimum utile (H.B.K.) Pittier ssp. *longifolium* (Ducke) C. Berg	13	2.5	23.1			13	
Brosimum utile (H.B.K.) Pittier ssp. *ovatifolium* (Ducke) C. Berg	14	2.7	48.5		3	9	2
Clarisia racemosa Ruíz & Pavón	6	4.2	37.4	2		4	
Ficus cf. *juruensis* Warburg ex Dugand	5	6.4	10	5			
Helicostylis elegans (J.F. Macbride) C. Berg	12	2.8	24.2			12	
Helicostylis scabra (J.F. Macbride)	11	2.8	29			11	
Helicostylis tomentosa (Poeppig & Endlicher) J.F. Macbride	6	2.6	9			6	
Maquira MS3114	5	3	69.3	5			
Naucleopsis glabra Spruce ex Pittier	6	3.2	26.8	3		3	
Perebea guianensis Aublet	12	2.7	6			12	
Perebea mennegae C. Berg	10	2.7	5.5			10	
Pseudolmedia laevigata Trécul	32	2.6	16.5		3	29	
Pseudolmedia laevis (Ruíz & Pavón) J.F. Macbride	15	2.8	25.7			15	
Sorocea hirtella Mildbraed ssp. *hirtella*	23	2.7	10.6			23	
Sorocea hirtella Mildbraed ssp. *oligotricha* Akkermans & C. Berg	24	2.5	22	10		14	
Sorocea muriculata Miquel	20	2.5	6.6	1	1	18	
Trymatococcus amazonicus Poeppig & Endlicher	16	2.7	9.4			16	
Myristicaceae							
Compsoneura cf. *capitellata* (A.DC.) Warburg	19	2.5	12.7			19	
Iryanthera elliptica Ducke	28	2.6	29			28	
Iryanthera juruensis Warburg	7	2.5	6.6			4	3
Iryanthera cf. *laevis* Markgraf	5	2.7	23			5	
Iryanthera lancifolia Ducke	13	2.6	17.8			13	
Iryanthera MS5064	9	3.3	13.5			9	
Iryanthera polyneura Ducke	113	2.5	22.8		1	78	34
Iryanthera tricornis Ducke	34	2.6	44			34	
Iryanthera ulei Warburg	56	2.5	16.5	12		44	
Osteophloeum platyspermum (A.DC.) Warburg	6	2.5	43.6			6	
Virola calophylla Warburg	37	2.7	31.8	13		24	
Virola duckei A.C. Smith	5	6.6	21			5	
Virola elongata (Bentham) Warburg	45	2.7	18		19	26	
Virola marlenei W.A. Rodrigues	15	2.5	6.7			15	
Virola MS3102	6	6.3	30	6			
Virola MS3311	5	2.7	5.2		5		
Virola MS3344	30	2.5	25.4			30	
Virola MS3580	18	2.5	21.7			18	

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APPENDIX *cont*.

	n	Min dbh (cm)	Max dbh (cm)	F	S	U	W
Virola MS4508	8	2.5	6.8	5		3	
Virola MS5088	5	2.5	21.5			5	
Virola MS6222	18	2.7	11.6		18		
Virola aff. *multinervia* Ducke	9	3.5	30.6			9	
Virola pavonis (A.DC.) A.C. Smith	44	2.5	36		5	38	1
Virola surinamensis (Rolander) Warburg	78	2.5	22.2	1	31		46
Myrsinaceae							
Stylogine cf. *longifolia* (Martius ex Miquel) Mez	12	2.6	6.4	12			
Myrtaceae							
Eugenia cf. *beaurepairiana* (Kiaersk.) Legrand	5	2.7	15.6	5			
Eugenia coffeifolia DC.	16	2.5	12.5			16	
Eugenia florida DC.	28	2.5	15	21	7		
Eugenia patens Poiret	8	3	8			8	
Marlierea caudata McVaugh	39	2.6	6.6		28	3	8
Marlierea cf. *schomburgkiana* Berg	17	3.3	10.2				17
Marlierea aff. *spruceana* O. Berg	30	2.5	7.7	1	29		
Marlierea cf. *umbraticola* (H.B.K.) O. Berg	18	2.6	7.7		15		
MS3412	6	3.3	21.7			6	
Myrcia fallax (L.C. Richard) DC.	9	2.6	15.3			9	
Myrcia splendens (Swartz) DC.	5	3	11.9			5	
Myrciaria cf. *floribunda* (West ex Willdenow) O. Berg	5	3.3	6	5			
Plinia cf. *duplipilosa* McVaugh	11	2.6	4.5			11	
Nyctaginaceae							
Neea cf. *macrophylla* Poeppig & Endlicher	8	2.5	5.5			8	
Neea parviflora Poeppig & Endlicher	7	2.8	17.6			7	
Neea spruceana Heimerl	12	2.7	10.5			11	1
Neea verticillata Ruíz & Pavón	9	2.7	5.4			4	5
Ochnaceae							
Ouratea chiribiquetensis Sastre	13	2.8	16.8		13		
Ouratea MS3608	6	2.6	9.8			6	
Olacaceae							
Aptandra caudata A. Gentry & Ortiz	9	2.7	4.8			9	
Aptandra cf. *tubicina* (Poeppig) Bentham ex Miers	31	2.6	38			1	30
Heisteria acuminata (Humboldt & Bonpland) Engler	5	3	4.8	4		1	
Heisteria barbata Cuatrecasas	11	2.7	10			11	
Heisteria duckei Sleumer	5	3	19			5	
Minquartia guianensis Aublet	11	3.6	29.8	2		9	
Tetrastylidium cf. *peruvianum* Sleumer	6	2.6	26			6	
Palmae							
Astrocaryum sciophillum (Miquel) Pulle	9	2.8	19	9			
Bactris maraja Martius var. *maraja*	19	2.5	5.5	19			
Euterpe precatoria Martius	70	2.5	18	24	44	2	
Iriartea deltoidea Ruíz & Pavón	18	4.4	25.5	16		2	
Iriartella setigera (Martius) H. Wendland	33	2.5	5.5			33	
Lepidocaryum tenue Martius	22	2.6	4			22	
Mauritia carana Wallace	12	10.6	48.5				12
Mauritia flexuosa L.f.	72	3.2	44.7		72		
Mauritiella aculeata (Kunth) Burret	11	10	14.8				11
Oenocarpus bacaba Martius	5	3.4	11.6	1		4	
Oenocarpus bataua Martius	28	2.8	25.7		1	26	1
Socratea exhorriza (Martius) H. Wendland	28	2.7	14.5			28	
Wettinia augusta Poeppig & Endlicher	21	2.6	9.2			21	
Polygalaceae							
Moutabea cf. *guianensis* Aublet	24	2.6	14.7	9		15	
Quiinaceae							
Quiina peruviana Engler	13	2.9	11.6			13	

APPENDIX *cont.*

	n	Min dbh (cm)	Max dbh (cm)	F	S	U	W
Rhamnaceae							
Ampelozizyphus amazonicus Ducke	21	2.5	7.4			21	
Rhizophoraceae							
Sterigmapetalum obovatum Kuhlman	5	2.5	16.4			5	
Rubiaceae							
Alibertia cf. *hispida* Ducke	24	2.5	9.6			23	1
Alseis MS3154	8	3.2	11	8			
Botryarrhena pendula Ducke	9	2.7	7.4		7	2	
Calycophyllum MS4415	5	3	20.8			5	
Calycophyllum obovatum (Ducke) Ducke	83	2.5	21.8				83
Chimarrhis gentryana Delprete	5	4.2	23.4			5	
Coussarea brevicaulis Krause	12	2.5	17.5	12			
Coussarea cf. *cephaeloides* C.M. Taylor	5	2.8	9	5			
Coussarea aff. *macrophylla* Muell.Arg.	7	2.7	6.8	7			
Duroia bolivarensis Steyermark	21	2.6	21.6		20	1	
Duroia saccifera (Martius ex Roemer & Schultes) Hooker f. ex K. Schumann	17	2.7	8.8			17	
Faramea capillipes Muell.Arg.	6	2.5	3.8			6	
Faramea sessilifolia (H.B.K.) DC.	5	2.6	9	4	1		
Ferdinandusa chlorantha (Wedd.) Standley	16	2.7	9.3		7	3	6
Ferdinandusa cf. *loretensis* Standley	14	2.7	45.4	4		10	
Pagamea macrophylla Spruce ex Bentham	34	2.5	19.4			10	24
Palicourea nigricans Krause	7	2.5	14			7	
Platycarpum rugosum Steyermark	14	4.2	51.8		4	1	9
Posoqueria panamensis (Walp. & Duchass.) Walp.	8	2.8	7.2	3		5	
Psychotria cf. *sororiella* Muell.Arg.	6	2.5	4.2			6	
Remijia pedunculata (H. Karsten) Flueck.	8	2.6	16.6			8	
Rudgea cf. *duidae* (Standley) Steyermark	7	2.5	4.1			7	
Rudgea loretensis Standley	7	2.7	6.8	5		2	
Warszewiczia coccinea (Vahl) Klotzsch	6	2.8	58.2	5		1	
Warszewiczia schwackei K. Schumann	17	2.7	17.6			17	
Sabiaceae							
Ophiocaryon heterophyllum (Bentham) Urban	23	2.6	12.3		1	22	
Ophiocaryon cf. *klugii* Barneby	8	2.8	11.4			8	
Ophiocaryon manausense (W. Rodrigues) Barneby	25	2.6	8.8			25	
Sapindaceae							
Matayba inelegans Radlkofer	6	2.7	5.8			6	
Talisia eximia K.U. Kramer	13	2.7	7.4		2	11	
Talisia nervosa Radlkofer	17	2.7	7.3	1	7	8	1
Sapotaceae							
Chrysophyllum prieurii A.DC.	5	2.5	26.8			5	
Chrysophyllum sanguinolentum (Pierre) Baehni	52	2.5	45.8			25	27
Chrysophyllum sanguinolentum (Pierre) Baehni ssp. *balata* (Ducke) Pennington	8	7.6	34.8			4	4
Chrysophyllum superbum Pennington	6	2.8	5.2			6	
Ecclinusa lanceolata (Martius & Eichler) Pierre	16	2.5	6.6		2	14	
Micropholis casiquiarensis Aubréville	13	2.7	16.5			13	
Micropholis egensis (A. De Candolle) Pierre	5	2.6	7.6	2	3		
Micropholis guyanensis (A. De Candolle) Pierre	58	2.5	31	3		33	22
Micropholis maguirei Aubréville	35	2.6	39.8			4	31
Micropholis melinoniana Pierre	8	2.8	23			8	
Micropholis venulosa (Martius & Eichler) Pierre	6	3.7	31.8		1	4	1
MS3653	5	5.8	25.4			5	
Pouteria bangii (Rusby) Pennington	8	2.7	33.6	8			
Pouteria cuspidata (A. de Candolle) Baehni	49	2.5	20.4	5	7	36	1
Pouteria cf. *gongrijpii* Eyma	11	2.8	10.6			11	
Pouteria guianensis Aublet	34	2.5	23.8	5		29	

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APPENDIX *cont.*

	n	Min dbh (cm)	Max dbh (cm)	F	S	U	W
Pouteria MS3953	7	3.2	34.5			7	
Pouteria MS4770	5	3.8	5.2			5	
Pouteria MS5774	5	4	35.3			5	
Pouteria oblanceolata Pires	5	3.8	15.5			2	3
Pouteria reticulata (Engler) Eyma ssp. *reticulata*	9	2.8	19		2	3	4
Pouteria rostrata (Huber) Baehni	14	2.7	26.8			10	4
Pouteria torta (Martius) Radlkofer	31	2.6	30.5	23		8	
Pouteria cf. *williamii* (Aubréville & Pellegrin) Pennington	19	2.6	20.4			19	
Simaroubaceae							
Picramnia latifolia Tulasne	10	2.7	10	6		4	
Picramnia MS3384	7	2.7	8.8			6	1
Sterculiaceae							
Theobroma cacao Linnaeus	66	2.7	25.5	66			
Theobroma microcarpum Martius	9	3	35.8	9			
Theobroma subincanum Martius	13	2.8	12.3			13	
Violaceae							
Leonia cymosa Martius	27	2.5	6			27	
Leonia glycycarpa Ruíz & Pavón	8	2.5	30.5	6		2	
Leonia MS6512	18	2.6	31.3			18	
Rinorea MS3183	15	2.7	8.8	15			
Rinorea neglecta Sandwith	17	2.5	6.5	17			
Rinorea racemosa (Martius) Kuntze	64	2.5	13	24		40	
Vochysiaceae							
Erisma bicolor Ducke	11	2.6	16.2			11	
Erisma splendens Stafleu	5	3.3	10.8			5	
Qualea acuminata Spruce ex Warming	26	2.7	15		26		
Qualea ingens Warming	11	3.6	75.5	6	5		
Qualea paraensis Ducke	11	2.7	41.3			11	
Vochysia lomatophylla Standley	16	2.5	5.3	1		15	
Vochysia MS6230	19	2.6	39.5		19		

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