

# A seasonal evergreen forest in Belize: unusually high tree species richness for northern Central America

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Most of the undisturbed forests of northern Central America remain undescribed. Some studies predict that tree species richness in lowland forests of northern Central America should be much lower than in similar forest types in southern Central America. This paper describes the physical and biological structure of two permanent, one-hectare plots on a valley floor in the Bladen Nature Reserve, Belize and compares these plots with other forests in the Neotropics. The plots have 91 and 89 species of trees  $\geq 10$  cm diameter (327 and 358 individuals, respectively) and comparable or higher measures of alpha-diversity than other such forests in Central America. The recorded tree species richness from other forests in northern Central America may be lower than those in southern Belize. The plots are dominated by *Mortoniella pittieri* Woodson (Apocynaceae), a disjunct from Costa Rica and Nicaragua. More than 50% of the tree species have distributions ranging into Bolivia or Peru, and >75% are wide-ranging species. The plots have a lower tree density and a higher proportion of large trees (>70 cm dbh) than other wet Neotropical forests. Like other Neotropical forests, tree species in the plots are generally aggregated and have a high proportion of vertebrate-dispersed fruits. © 2002 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2002, 138, 275–296.

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## INTRODUCTION

Within the tropics, tree species richness increases with rainfall and decreases with increasing latitude and seasonality (Gentry, 1988; Clinebell *et al.*, 1995; Wright, 1999). Also, the latitudinal gradient in tree species may be asymmetric about the equator for wet or moist lowland forests, with a stronger decline in richness in northern Central America than in southern South America (Sarukhán, 1968; Gentry, 1982, 1988). This decline should be expected, given the ecologically recent establishment of rainforest in northern Central America (Colinvaux, 1997; Burnham & Graham, 1999), and Central America's short history and recent (geological) connection to South America's immense pool of tree species. Moreover, northern Central America experiences lower rainfall and stronger seasonality than the latitudes closer to the equator (Lauer, 1983).

The plot data that exist for Central America show a strong decline in species richness toward the Tropic of Cancer (Gentry, 1988; see review by Leigh, 1999). Tree species richness per hectare (for trees  $\geq 10$  cm dbh) range from 200–300+ in the aseasonal areas of South America, to 90–100 tree species in the seasonal forests of southern Central America, and to 50–75 tree species in southern Mexico. As in most of the Neotropics, however, reliable, published plot data are scarce for lowland, moist-to-wet forests in northern Central America. Perhaps the best-documented closest, lowland tropical forest is Los Tuxtlas, Mexico, with comparable rainfall (4.7 myr<sup>-1</sup>) to parts of Central America. At 18°35'N however, Los Tuxtlas is essentially subtropical in other aspects of its climate, and with 75 tree species ha<sup>-1</sup> ( $\geq 10$  cm dbh) (Bongers *et al.*, 1988; see Table 1), it is unlikely to be the most speciose rainforest in Mexico (Wendt, 1993). Most of the field studies in the region give estimates of 60–78 tree species ha<sup>-1</sup> in lowland forests, but these studies are often immersed in the 'grey literature' and/or have limited results. Studies by Stevenson (1942) and

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**Table 1.** Tree species richness in lowland forest plots (1 ha, individuals  $\geq 10$  cm diameter, except where noted) in Central America and Mexico

Site	Latitude	Basal Area (m <sup>2</sup> )	Rain (m yr <sup>-1</sup> )	<i>N</i>	<i>S</i>	$\alpha$	Ref.
<b>BELIZE</b>							
Bladen Nat. Res. (BNR)	16°34'N		2.5				(This study)
Plot 1, $\geq 10$ cm		30.3		327	91	41.8	
Plot 1, $\geq 5$ cm†		31.5		705 (176)†	114	38.5	
Plot 2, $\geq 10$ cm		31.5		358	89	38.0	
Plot 2, $\geq 5$ cm†		32.5		680 (150)†	104	34.2	
Quebrada de Oro, BNR	16°31'N	32.8	2.5	359	73+	27.7	(1)
Columbia	c. 16°28'N	24.9–38.0	c. 2.5	318–614	58–77+	17.2–24.1	(2)
Chiquibul	c. 16°35'N	19–25	1.5–2.0	610–684	64–68	18.0–18.8	(2)
Rio Bravo	17°30'+N	17.6–36.6	1.5	374–701	46–59	13.8–15.3	(3)
Mtn. Pine Ridge	17°+N	17–20	1.6	371‡	50–59	NA	(4)
<b>MEXICO</b>	18°35'N	34.9	4.7	335(–345)	75*	30.0	(5)
Los Tuxtlas							
<b>GUATEMALA</b>	17°N	20.7–36.6	1.5	420–645**	53–82**	12.7–21.9**	(6)
Tikal							
<b>COSTA RICA‡</b>	10°26'N	24.7	4.0	447	93	37.1	(7)
La Selva							
<b>PANAMA</b>	9–09'N	28.5	2.6	425	91	36.0	(8)
Barro Colorado Island							

*N* = number of individuals; *S* = number of species;  $\alpha$  = Fisher's index of diversity (see text for explanation).

† in parentheses are numbers of stems of *Astrocaryum mexicanum*  $\geq 5$  cm diameter.

\* reported in the appendix in (5); 78 is the maximum possible number if indet., unreported species are trees.

\*\* Values inferred from figures in (6), for trees  $\geq 7.5$  cm diameter.

‡ average value(s) for plots given.

(1) Brokaw *et al.* (1997); (2) Smith (1995); (3) Brokaw & Mallory (1993); (4) Kellman *et al.* (1994); (5) Bongers *et al.* (1988); (6) Schulze & Whitacre (1999); (7) Lieberman *et al.* (1985); (8) Leigh (1999).

Smith, 1945a,b), for example, were comprehensive even by today's standards, but they used small plots (0.04–0.06 ha per study) and were conducted in an era of uncertain tropical plant taxonomy. Smith (1995) and Bird (1998) recorded up to 77 species in the Maya Mountains of southern Belize, but many individuals went uncollected and/or their identities were undetermined. Brokaw *et al.* (1997) conducted a forest inventory near the site examined in this study, finding at least 73 tree species (including 8 indet.) in one hectare, but Brokaw *et al.*'s study used non-contiguous belt transects and did not collect voucher specimens.

Undisturbed lowland forests in northern Central America are rare, and usually confined to inaccessible places, but they may yield information with important implications. For example, floristic studies of such areas across the Neotropics can give clues to what extent tree taxa may have migrated from neighbouring regions, and comparisons of undisturbed and disturbed forests may reveal specific requirements for protection or trends in the recovery of diversity. It

remains possible that sites of relatively high tree diversity exist in northern Central America, but vouchered plot surveys in the region are greatly needed. This study examines the richness and physical, spatial and biological structure of two permanent, one-hectare plots in lowland rainforest (*s. l.*) in southern Belize, a poorly known area of northern Central America. The results of these analyses are compared with studies of other forests of similar climate and topography in the Neotropics, in order to elucidate potential causes of the similarities and differences that may be observed among the forests.

## MATERIAL AND METHODS

### STUDY SITE

The Bladen Nature Reserve (BNR) lies between 16°24'34"N and 16°36'18"N latitude in the Maya Mountains of southern Belize (Fig. 1). The BNR is approximately 350 km<sup>2</sup> in area, with a rugged topography covering elevations from approximately 40 m to



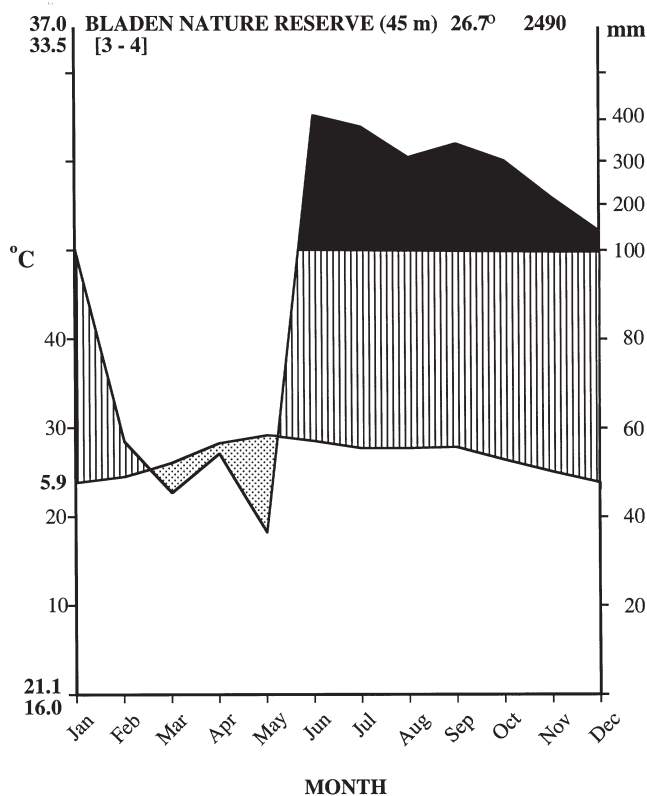
**Figure 1.** Position of Belize and the plots in the lowlands of the north-eastern Bladen Nature Reserve, Maya Mountains, at 16°34'N.

1000 m. The BNR encompasses a watershed bisected by the Bladen Branch of the Monkey River. The watershed is composed mostly of the Coban (Late Cretaceous) limestone and the Bladen (Palaeozoic) volcanics formations, with some pockets of alluvium and Santa Rosa metasediments (limestone and granite) (Bateson & Hall, 1977).

The climate of the area can be classified as tropical wet seasonal (Walsh, 1996), with an annual rainfall of about 2500–3000 mm and a strong dry season from February to May (Fig. 2). The forests of the BNR range from evergreen forests on the floors of valleys to semi-deciduous with pockets of deciduous forest on exposed

limestone outcrops. Wright *et al.* (1959) describes the area including what is now the BNR as Tropical Moist Forest Zone. Wright *et al.*'s survey of Belize emphasizes potential land-use and soils, and therefore the vegetation is only generally described.

The plots used in this study are located in the floor (c. 45 m elevation) of a valley of the far north-eastern BNR, where the Bladen Branch emerges from a shallow gorge. The topography of the plots is flat, with an inclination of less than 5%. The area is immediately encompassed to the north and south by karst hills. This evergreen forest grows on the relatively fertile, fairly well-drained Monkey River clay loam soil



**Figure 2.** Climate diagram for the north-eastern Bladen Nature Reserve (following Walter & Lieth, 1960). Numbers in bold type from the top down on the left Y-axis (left ordinate) are, respectively, maximum temperature recorded, mean daily temperature of the warmest month, mean daily temperature fluctuation, mean daily minimum temperature of the coldest month, and coldest temperature recorded. The station from which the data were taken, elevation, mean annual temperature, and mean annual rainfall (3–4 year data) are located at the top of the figure. Rainfall (mm) is on the right Y-axis. The vertical shading represents the humid season, and black areas correspond to rainfall > 100 mm (compressed into 1/10th of the scale below 100 mm).

(Wright *et al.*, 1959), on alluvium over a limestone substrate. No flooding has been observed in the plots prior to the study, but one major flood lasting 12 h did occur within the last ten years (R. Klinger, pers. comm.).

The last significant human occupation of the area was by the Maya on a relatively small scale some 1000 years before present (P. Dunham, pers. comm.). No physical evidence, local knowledge, or record of significant logging operations could be found for the study site. As in most of the Neotropics, however, some mahogany and cedar trees (*Swietenia macrophylla* King and *Cedrela odourata* L., respectively) were removed from the area. For example, in the late 1800s a relatively small mahogany logging operation was

conducted 5–6 km upstream from the study area (Fowler, 1879). Most of the logging was probably done by a few individuals removing less than 40 trees from a very large area (seven licence applications, three showing royalties paid, to remove a total of 160 mahogany or cedar trees were approved for the entire Bladen Branch in 1916–17; Belize National Library, Minute Papers for regulations of 1897, section 36).

#### PLOT ESTABLISHMENT AND MEASUREMENTS

Two permanent one-hectare plots (each 100 m × 100 m) were established in 1996, based on the physical structure of the forest and proximity to the Bladen Branch of the Monkey River, before the authors collected and became familiar with the local flora. Forest resembling ‘mature-phase’ forest (*sensu* Whitmore, 1978) in physical structure was selected to represent the areas of forest on younger alluvium (50 m away from the Bladen Branch) and older alluvium (250 m away from the Bladen Branch, and 50 m from the base of a limestone slope). The nearest edges of the two plots were separated by 200 m.

The plots were surveyed into a grid of 20 m × 20 m quadrats, and 10 m × 10 m subquadrats, in which all trees ≥ 5 cm diameter at 130 cm height (hereafter ‘diameter’ or  $D_{130}$ , Brokaw & Thompson, 2000) were tagged, measured for diameter, identified and mapped. Trees at the boundary of the plot were included only if the centres of their boles were within the plot boundary. Tree measurements were conducted using the protocol of Dallmeier *et al.* (1992). Individual trees were mapped, to the nearest centimetre, as distances from two adjacent 10 m markers, using metre tapes held at 130 cm above the soil surface. Cartesian coordinates for each individual were generated using triangulation, after correcting distances for tree diameter. Heights of trees representing the range of height variation throughout each plot were estimated using a clinometer (Korning & Karsten, 1994). Voucher specimens were collected for most trees, with the exceptions of individuals that were common and distinctive, and for which there was no confusion about their identity (e.g. *Schizolobium parahyba*, *Attalea cohune*). Herbarium specimens were deposited at Belmopan (BRH), Davis (DAV), Chicago (F), St. Louis (MO), and/or San Francisco (CAS) (a list of specimens and their distribution is available from the first author). Authorities for species names can be found in Appendix 2.

#### DATA ANALYSES

Unless noted otherwise, the data analyses presented here are for trees ≥ 10 cm  $D_{130}$ . The 10 cm minimum diameter tends to be the standard for sam-



pling and analyses (e.g. studies compared within Richards, 1996; Condit *et al.*, 1998; Leigh, 1999) and is used here to facilitate comparison with other plots in the Neotropics.

The spatial structure of the forest was examined via K-function analyses (Ripley, 1977, 1981) using a BASIC program developed by R. P. Duncan (Uni. Canterbury, NZ). Species having at least four stems were included in the spatial analyses. The univariate K-function algorithm was used to determine if the spatial pattern of 'adults' ( $\geq 15$  cm  $D_{130}$ ) or 'juveniles' ( $< 15$  cm  $D_{130}$ ) deviated from random patterns. A comparable bivariate algorithm was used to determine whether spatial associations of adult and juvenile trees deviated from random associations (e.g. Lotwick & Silverman, 1982; Duncan, 1991). The bivariate function was applied only to those species with four or more stems in each size class, and only to those species in which reproduction was observed to occur exclusively in larger size-classes (e.g. *Manilkara chicle*). For small-tree species that were observed in reproductive condition in large and small size classes (e.g. *Mouriri myrtilloides* ssp. *parvifolia*), only the univariate function was applied. Values of K(t) were square-root transformed (Ripley, 1977) and compared with a 95% confidence envelope generated from Monte Carlo simulations.

Jaccard's similarity coefficient was calculated to determine the similarity of the two plots with respect to species composition ( $c/(a + b - c)$ , where  $a$  = species in sample unit 1,  $b$  = species in sample unit 2, and  $c$  = no. of species shared between the two plots; Jaccard, 1902). Given the comparable numbers of stems in the two plots (327 vs 358), the index should not be significantly biased by a difference in sample size between the two plots. Although 'importance value' (*sensu* Curtis & Cottam, 1962) has become entrenched in the literature of tropical forest plot descriptions, the utility of such an arbitrary measure is questionable (Greig-Smith, 1964; Goodall, 1970; Mueller-Dombois & Ellenberg, 1974; Campbell, 1994); for example, equal values of the measure may be produced by two plots of very different structure. Instead, chord distance (Pielou, 1984) was calculated in order to compare the two plots with respect to the proportional abundance (measured in basal area) of the tree species. This is a standardized measure of resemblance that ranges from 0 to  $\sqrt{2}$  (approximately 1.41).

Both species–area and species–individual curves for each plot were generated by using species and individual counts from nested, non-overlapping quadrats within each plot. These types of curves were also generated for both plots combined. The two plots are not contiguous, although they are only separated by 200 m, therefore species richness for the combined two hectares should be an inflated representation of any

two contiguous hectares. Species richness strongly depends on the number of stems for samples of  $< 3000$  stems (Condit *et al.*, 1998). Since the same plot size may have different numbers of stems among sites, variation among species–area curves for trees may reflect tree density as well as numbers of species for increasing areas. Therefore, species richness alone is an inadequate comparative measure of diversity among sites that differ in stem density. Fisher's diversity index  $\alpha$  (Fisher *et al.*, 1943) varies much less than species richness with sample size (Condit *et al.*, 1996; Leigh, 1999). This index accounts for the number of individuals sampled, based on a log-series distribution of the species abundances, and has become commonly used as an index of diversity in tropical forests (see Condit *et al.*, 1998 and Leigh, 1999 for discussions of this index). Fisher's  $\alpha$  was calculated for each plot and compared with values for other forest sites in Central America.

## RESULTS AND DISCUSSION

### PHYSICAL STRUCTURE

The canopies of both plots were closed but uneven, with distinct layers not evident above 15 m from the forest floor. Most of the canopy trees ranged between 20 and 30 m tall, with larger trees (e.g. *Manilkara chicle*, 1.3 m  $D_{180}$ ) reaching 40 m tall. The understorey trees were 5–10 m tall (e.g. *Protium schippii*) and the herb layer ranged from 0.2 m (e.g. *Selaginella* spp.) to 1+ m tall (e.g. *Calathea* spp.).

Plots 1 and 2 had 327 and 358 trees  $\geq 10$  cm diameter, respectively. When this minimum diameter was lowered to 5 cm; the number of stems increased to 705 and 680 trees (116% and 90% increases in numbers of stems for Plots 1 and 2, respectively) (Table 1). The low density of trees in these plots appeared to be consistent with mature-phase, wet forests in the lowlands of the Maya Mountains (Brewer, unpubl. data; Smith, 1995; Brokaw *et al.*, 1997). Generally in this region, stem densities have been found to be lower, and basal area higher, in lowland wet forests than other Central American wet forests (Table 1). Tree density and basal area in the plots were similar to those values for lowland forests of Los Tuxtlas, Mexico (Bongers *et al.*, 1988).

In the BNR, tree density increased – and average diameter decreased – with increasing elevation on soils over a limestone substrate (Brewer, unpubl. data; Iremonger & Sayre, 1994). This trend probably reflects the increasing edaphic drought associated with increasing elevation on limestone (Furley & Newey, 1979). Variation in tree densities at larger scales in the tropics, except at the extremes in soil fertility and moisture, is not easily explained but is probably correlated with multiple factors (Richards, 1996). The

high proportion of large trees in the lowlands of the BNR and nearby forests (e.g. >70 cm diameter; Smith, 1995; Brokaw *et al.*, 1997; this study) probably precludes the development of dense stands of trees. Such a high proportion of large trees may reflect high soil fertility, adequate rainfall, and a lack of frequent, catastrophic disturbances such as hurricanes (Brokaw *et al.*, 1997).

#### SPATIAL PATTERNS OF TREES

Published analyses of spatial patterns of trees in lowland Neotropical forests have been confined to plots in southern Central America and South America. In the BNR plots, 39 species had the minimum number of stems (four) for K-function spatial analysis. Only significant ( $P < 0.05$ ) patterns over relatively broad scales ( $t > 3$  m), or consistently significant patterns (repeated smaller-scale patterns within and between the two plots), are described here (see also Appendix 1). For example, only adults of *Brosimum alicastrum* (Moraceae) (at a scale of 41–50 m from any individual tree in Plot 2) and adults and juveniles combined of *Manilkara chicle* (Sapotaceae) were significantly hyperdispersed ('segregated') over broad scales. Juveniles of *Ampelocera hottlei* (Ulmaceae; Plot 1 only), *Aspidosperma spruceanum* (Apocynaceae; Plot 2 only), *Celtis schippii* (Celtidaceae), *Drypetes brownii* (Euphorbiaceae), and *Guarea glabra* (Meliaceae; Plot 1 only), or 10% of the species analysed, were also significantly hyperdispersed at intermediate and broad scales. From the bivariate analysis of spatial pattern between adults and juveniles of the 15 species with three or more individuals per size class, seven species were aggregated, three species were hyperdispersed, four species showed no pattern, and one species (*Pouteria durlandii* Sapotaceae) was aggregated in Plot 1 and hyperdispersed in Plot 2. Hyperdispersion is congruent with the Janzen–Connell hypothesis (Janzen, 1970; Connell, 1971) of recruitment being favoured away from parent trees and/or density-dependent predation or pathogen attack for some species under some conditions.

Sixty-nine percent of the species were significantly aggregated in their spatial distributions in at least one plot (Appendix 1). The trend towards aggregation is consistent with data from large plots further south in the tropics that show most species are aggregated in their distributions, even though the intensity of this pattern may be mitigated by herbivores and pathogens (Condit *et al.*, 2000). Species aggregation may reflect topographic features. However, one-hectare plots did not cover enough topographic relief per plot for topographic pattern analysis, and the plots in this study were topographically homogeneous. Species aggrega-

tion may reflect dispersal limitation such as that found in similar forests in Panama (Hubbell *et al.*, 1999; Condit *et al.*, 2000).

#### SPECIES RICHNESS AND FLORISTICS

There were 116 and 140 species found between the two plots for trees  $\geq 10$  cm and  $\geq 5$  cm diameter, respectively (Appendix 2). Plots 1 and 2 had 91 and 89 species  $\geq 10$  cm, respectively (Table 1). Lowering the minimum diameter to 5 cm increased species richness to 114 species (25% increase) and 104 species (17% increase) in Plots 1 and 2, respectively. Fisher's  $\alpha$  values for the plots were lower at the minimum diameter of 5 cm than the 10 cm minimum (Table 1), due to the dominance of *Astrocaryum mexicanum*, which represented 47% of the stems 5–10 cm diameter in each plot.

In the combined plots, 37 families and 87 genera were represented by trees  $\geq 10$  cm  $D_{130}$  (Appendix 2). Each plot has four families not represented in the other plot. The families in the BNR plots show a similar pattern, in rank of species richness, to Mexican rainforest families (Wendt, 1993) and to the Neotropics as a whole. Like many other lowland Neotropical sites (Gentry, 1988), the BNR plots are dominated in species and basal area by the Fabaceae. A notable exception is the relatively high richness and dominance of the Apocynaceae in the plots (Table 2). Like Mexican rainforests, the BNR plots also have higher relative richness of the Tiliaceae and Flacourtiaceae than do the Neotropics in general.

Of the 140 species in both plots (> 5 cm diameter), 81 species had individuals < 10 cm diameter (Table 3). Of these, 33 species (24%) had individuals found only between 5 and 10 cm diameter. Of these 'small' species, 45% (11% of all species > 5 cm) are rarely or never found to reach 10 cm diameter (e.g. *Astrocaryum mexicanum*) and are most abundant on valley floor forests; they are less common in other forest types at other topographic positions and/or on other soil types (Brewer, unpubl. data). A census of species with a 10 cm minimum diameter would miss about 24% of the tree species present in the two hectares (Table 3), including a substantial portion (10%) that are more common in other forest types in the area (Brewer, unpubl. data). In these plots, significant increases in richness occur below 10 cm diameter, as is true for plots in Malaysia and Panama (Condit *et al.*, 1996), but few new species were observed below 5 cm diameter (Brewer, pers. obs.).

How do the BNR plots compare to the rest of the Neotropics? Published plot inventories of rainforest trees north of Costa Rica are scarce, but enough plots have been established such that some preliminary trends may be recognized (Table 1 and see Gentry

**Table 2.** Families of trees with individuals  $\geq 5$  cm diameter in two one-hectare plots in the Bladen Nature Reserve, Belize. Ordered by number of species (S) and basal area (BA, m<sup>2</sup>). *N* = number of individuals

Sorted by species				Sorted by basal area			
Family	S	<i>N</i>	BA	Family	BA	<i>N</i>	S
Fabaceae	20	98	9.958	Apocynaceae	11.872	77	6
Rubiaceae	11	76	2.191	Fabaceae	9.958	98	20
Moraceae	9	46	7.712	Moraceae	7.712	46	9
Sapotaceae	8	106	7.463	Sapotaceae	7.463	106	8
Meliaceae	7	86	2.502	Arecaceae	5.630	377	3
Lauraceae	7	18	0.765	Anacardiaceae	3.238	54	2
Apocynaceae	6	77	11.872	Meliaceae	2.502	86	7
Flacourtiaceae	6	19	0.410	Bombacaceae	2.195	38	2
Annonaceae	5	14	0.474	Rubiaceae	2.191	76	11
Tiliaceae	4	12	1.383	Tiliaceae	1.383	12	4
Euphorbiaceae	4	40	1.168	Euphorbiaceae	1.168	40	4
Melastomataceae	4	33	0.267	Burseraceae	0.967	85	3
Arecaceae	3	377	5.630	Combretaceae	0.917	6	2
Burseraceae	3	85	0.967	Rhizophoraceae	0.790	35	1
Chrysobalanaceae	3	10	0.242	Lauraceae	0.765	18	7
Sapindaceae	3	4	0.086	Rutaceae	0.747	11	2
Anacardiaceae	2	54	3.238	Boraginaceae	0.547	12	2
Bombacaceae	2	38	2.195	Ulmaceae	0.539	30	1
Combretaceae	2	6	0.917	Annonaceae	0.474	14	5
Rutaceae	2	11	0.747	Flacourtiaceae	0.410	19	6
Boraginaceae	2	12	0.547	Celtidaceae	0.276	12	1
Myristicaceae	2	9	0.246	Melastomataceae	0.267	33	4
Clusiaceae	2	6	0.073	Sterculiaceae	0.261	3	1
Verbenaceae	2	2	0.028	Myristicaceae	0.246	9	2
Rhizophoraceae	1	35	0.790	Chrysobalanaceae	0.242	10	3
Ulmaceae	1	30	0.539	Elaeocarpaceae	0.227	11	1
Celtidaceae	1	12	0.276	Ebenaceae	0.159	3	1
Sterculiaceae	1	3	0.261	Indet.	0.155	2	1
Elaeocarpaceae	1	11	0.227	Olacaceae	0.104	8	1
Ebenaceae	1	3	0.159	Caricaceae	0.102	8	1
Indet.	1	2	0.155	Bignoniaceae	0.102	3	1
Olacaceae	1	8	0.104	Sapindaceae	0.086	4	3
Caricaceae	1	8	0.102	Clusiaceae	0.073	6	2
Bignoniaceae	1	3	0.102	Polygonaceae	0.054	2	1
Polygonaceae	1	2	0.054	Malpighiaceae	0.053	1	1
Malpighiaceae	1	1	0.053	Oleaceae	0.033	6	1
Oleaceae	1	6	0.033	Verbenaceae	0.028	2	2
Piperaceae	1	7	0.027	Piperaceae	0.027	7	1
Violaceae	1	6	0.021	Violaceae	0.021	6	1
Simaroubaceae	1	3	0.014	Simaroubaceae	0.014	3	1
Myrtaceae	1	1	0.009	Myrtaceae	0.009	1	1
Malvaceae	1	2	0.008	Malvaceae	0.008	2	1
Araliaceae	1	1	0.003	Araliaceae	0.003	1	1
Capparidaceae	1	1	0.003	Capparidaceae	0.003	1	1
Urticaceae	1	1	0.002	Urticaceae	0.002	1	1

**Table 3.** A breakdown of the trees < 10 cm  $D_{130}$  in two one-hectare plots in southern Belize by local distribution. Numbers of species of 'small' (always < 10 cm diameter) and 'large' trees, and trees more commonly found in forests on the floors of valleys and trees more common to other forest types are included

Category	Species	Percent of small species	Percent of all species
Total Species < 10 cm*	81	100	57.9
Species only 5–10 cm	33	40.7†	23.6
Small trees in valley floor forest	15	45.5	10.7
Large trees in valley floor forest	5	15.2	3.6
Small trees common in other forest types	8	24.2	5.7
Large trees common in other forest types	5	15.2	3.6

\*The number of species in the plots that were represented by at least 1 stem < 10 cm diameter.

†Percent of the total number of species represented by stems < 10 cm diameter.

1988). Most Neotropical forests comprise mainly species that occur at low population densities. On Barro Colorado Island, a forest in Panama with richness and diversity similar to the BNR plots, 33% of the species have less than one individual  $ha^{-1}$ , the threshold density for the definition of rare by Hubbell & Foster (1986). Similarly, 27% of the species were represented by only one individual in the two BNR plots combined. In contrast, more than 88% of the tree species in the Manu River Basin are represented by less than one individual  $ha^{-1}$ . In each of the BNR plots, 42% of the species were represented by only one individual, and 36% of the species had a maximum of one individual  $ha^{-1}$ , the threshold density for being 'locally scarce' according to Pitman *et al.* (1999). The latter figure should be lower if more plots were to be sampled, as tropical trees tend to be clumped in their distribution (Hubbell, 1979; Condit, *et al.*, 2000; this study), and a larger sample size of plots would be more likely to capture a higher maximum local population density for some of the species. Nevertheless, per-species tree densities in the plots were low; more than half of the species (64% and 59% in Plots 1 and 2, respectively) were represented by two or fewer individuals. These low densities belie an oligarchy of dominance, a condition that may be more common than previously known for tropical forests (Pitman *et al.*, 2001). The top five or six (Plots 2 and 1, respectively) species in the BNR plots represented 49% of the basal area in each plot and the top 11 species in each plot represented over 50% of the number of stems  $\geq 10$  cm diameter per plot (Table 4, Fig. 3).

The species richness of trees in the plots is the highest recorded for Belize and is at least 18% higher than the richness published for lowland plots in the region (Table 1). The plots also have higher or equally

high values of Fisher's  $\alpha$  compared to other Central American lowland forest plots farther south (Table 1), in large part because of relatively low stem densities. Like the rest of Central America, however, the BNR tree richness is much less than that published for equatorial South America (e.g. >200 spp.  $\geq 10$  cm dbh  $ha^{-1}$  in Peru, Gentry, 1988 or Ecuador, Valencia *et al.*, 1994).

The richness of tree species declines with latitude but the decline is especially strong in the Neotropics north of 12°N (Gentry, 1988). This sudden decline beyond northern Nicaragua should be expected. Southern Central America is geologically young and much of northern Central America was submerged for millions of years (Donnelly *et al.*, 1986; Coates, 1997), limiting speciation time and even the time that tree taxa could migrate from North and South America. Many tree taxa that are adapted to wet and warm climates, such as those taxa found in the lowlands of the Amazon basin, would have been slowed or prevented from immigrating to northern Central America by periodic and prolonged droughts that occurred in the region (Gentry, 1982; Colinvaux, 1997). Perhaps equally important, however, is that the region that includes Belize and northern Central America must have been heavily deforested, or lacked well-developed forests on a large scale at the height of the Maya civilization, as evidenced by the extent of marginal lands that were converted for agriculture (e.g. Wright *et al.*, 1959; Turner, 1974; Adams *et al.*, 1981; Turner & Harrison, 1981) to support a population that may have reached 600 people  $km^{-2}$  (Puleston, 1974). Thus 'old growth' forest in southern Belize may only be about 1000 years old, or approximately the equivalent of only one to four generations for some emergent tree species (Chambers *et al.*, 1998).

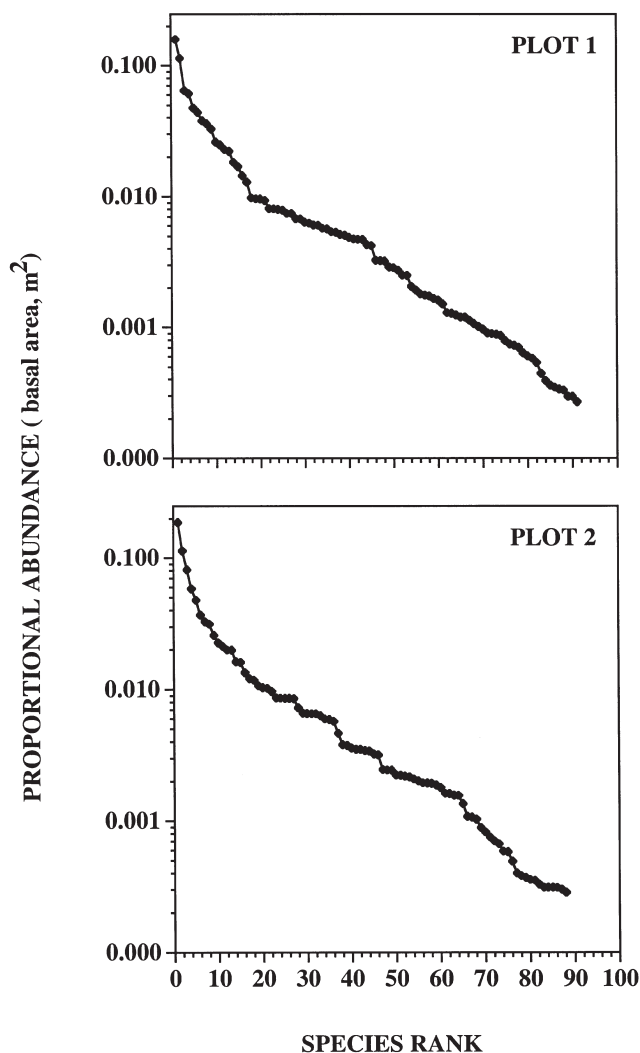


**Table 4.** The top 30 tree species ( $\geq 5$  cm  $D_{130}$ ) in total basal area (BA), in two hectares of lowland evergreen seasonal forest in southern Belize. Numbers of individuals ( $N$ ) are shown. Species in bold were found in one or both plots only as trees < 10 cm  $D_{130}$ . See Appendix I for authors' names

Species	Family	Plots 1 & 2		Plot 1		Plot 2	
		$N$	BA(m <sup>2</sup> )	$N$	BA(m <sup>2</sup> )	$N$	BA(m <sup>2</sup> )
<i>Mortoniella pittieri</i>	Apocyn.	42	10.762	18	4.834	24	5.927
<i>Attalea cohune</i>	Arec.	47	4.727	13	1.151	34	3.576
<i>Brosimum alicastrum</i>	Mor.	19	4.536	8	1.965	11	2.571
<i>Schizolobium parahyba</i>	Fab.	9	3.666	8	3.459	1	0.207
<i>Manilkara chicle</i>	Sapot.	34	3.083	18	1.880	16	1.203
<i>Spondias mombin</i>	Anacardi.	50	2.889	25	1.354	25	1.534
<i>Dialium guianense</i>	Fab.	33	2.557	8	0.683	25	1.874
<i>Chrysophyllum venezuelanense</i>	Sapot.	16	1.779	8	1.449	8	0.330
<i>Pouteria sapota</i>	Sapot.	7	1.468	4	0.752	3	0.716
<b><i>Quararibea funebris</i></b>	Bombac.	<b>37</b>	<b>1.156</b>	<b>35</b>	<b>1.134</b>	<b>2</b>	<b>0.022</b>
<i>Guarea glabra</i>	Meli.	64	1.111	28	0.744	36	0.367
<i>Lonchocarpus pentaphyllus</i>	Fab.	5	1.064	4	1.001	1	0.064
<i>Ceiba pentandra</i>	Bombac.	1	1.039	–	–	1	1.039
<i>Ficus popenoei</i>	Mor.	1	0.994	–	–	1	0.994
<i>Terminalia amazonia</i>	Combret.	4	0.910	3	0.792	1	0.119
<i>Pterocarpus rohrii</i>	Fab.	10	0.872	2	0.039	8	0.833
<i>Alseis yucatanensis</i>	Rubi.	14	0.849	5	0.211	9	0.637
<i>Guarea grandifolia</i>	Meli.	10	0.810	6	0.302	4	0.508
<i>Cassipourea guianensis</i>	Rhizophor.	20	0.790	10	0.056	10	0.094
<i>Drypetes brownii</i>	Euphorbi.	30	0.762	23	0.546	7	0.215
<b><i>Astrocaryum mexicanum</i></b>	Arec.	<b>326</b>	<b>0.755</b>	<b>176</b>	<b>0.407</b>	<b>150</b>	<b>0.348</b>
<i>Protium schippii</i>	Burser.	78	0.705	40	0.389	38	0.316
<i>Ficus</i> sp. 3	Mor.	1	0.671	–	–	1	0.671
<i>Pouteria durlandii</i>	Sapot.	30	0.623	8	0.220	22	0.403
<i>Simira salvadorensis</i>	Rubi.	13	0.580	3	0.296	10	0.284
<i>Zanthoxylum riedelianum</i>	Rut.	9	0.565	5	0.194	4	0.372
<i>Mortoniendron vestitum</i>	Tili.	4	0.564	4	0.564	–	–
<i>Luehea speciosa</i>	Tili.	5	0.556	1	0.439	4	0.116
<i>Ampelocera hottlei</i>	Ulm.	30	0.539	16	0.218	14	0.321
<i>Ficus insipida</i>	Mor.	4	0.514	–	–	4	0.514

The current composition of Central America's flora has a much greater affinity for South than North America (Gentry, 1982, 1988), and it has been generally assumed that most modern tropical taxa in Central America are derived from South America (e.g. Raven & Axelrod, 1974; Cronquist, 1988). Thus it may not be surprising that the documented composition of lowland forests in the region seems to uphold the contention of Gentry (1988) that Central American wet forests, even relatively diverse ones such as those in the BNR plots, are composed primarily of highly vagile species that might otherwise be considered 'weedy' in South America. For example, a total of 60% of the tree species in the BNR plots are found from Mexico or Guatemala to South America; 56% can be found as far south as Bolivia or Peru. Species in the plots that are

widely distributed throughout Central America, primarily or exclusively, comprise an additional 21% of the plot trees. Therefore the majority of the taxa currently found in the wetter, valley-floor forests of Belize are likely vagile and effective colonizers from South America. However, Burnham & Graham (1999) emphasize the complexity of multiple origins of northern Central America's forests. Recent palaeobotanical evidence (Graham, 1995, 1998, 1999) and an analysis of the affinities of extant tree taxa of Mexican rainforests (Wendt, 1993) reveal a significant proportion of tree taxa in the region having come from northern sources. Finally, Brewer (2000) found that the proportion of species with widespread distributions decreased with elevation above the forests on the valley floor of the study area.



**Figure 3.** Proportional abundance (measured as basal area,  $m^2$ ) of species by their rank for each of the two plots. The top 6 and 5 species each have 49% of the total basal area for Plots 1 and 2, respectively. The top 11 species in each plot contain 50% of the stems in their respective plots.

Most of the remaining species are found exclusively (or primarily) north of  $12^\circ N$  latitude (11%), or grow only in the southern Mexico/Petén/southern Belize area (4%). Wendt (1993) points out that forests on karst outcrops in Mexico have a high proportion of taxa endemic to northern Central America, whereas a much lower proportion of endemic or local tree species are found on lower-elevation forests on deep soils. Whether this assertion will hold true for the Maya Mountains awaits further study.

A few species (4%) are unique because of the large disjunction(s) or gap(s) in their known distributions.

Of these species, *Mortoniella pittieri* (Apocynaceae) is the most unusual. Previous to the collections in the BNR, the monotypic genus *Mortoniella* had been found only in Nicaragua and Costa Rica (J. Zarucchi, pers. comm.). The apparent disjunction of this species is possibly an artefact of incomplete collections in Honduras and eastern Guatemala. Perhaps it is overlooked because its overall vegetative appearance is quite similar to the abundant familial relative *Aspidosperma megalocarpon*, another common canopy tree in the area. The distinctive fruits and leaves of *M. pittieri* are readily available on the forest floor throughout the year, however, and the distribution of *M. pittieri* in the area surrounding the BNR suggests true gaps in distribution. Where we have found it, *M. pittieri* is abundant and dominant, including the site of the two BNR plots. In the combined plots, *M. pittieri* had more than twice the basal area of (and a similar number of stems to) the second most dominant species, *Attalea cohune* (Arecaceae). So far, however, we have only been able to find this species in a limited number of sites of lower-elevation, limestone forests near where the Bladen and Trio branches of the Monkey River flow out of the surrounding hills (Brewer, unpubl. data). The distribution of the species in the plots suggests that *M. pittieri* arrived in the BNR relatively recently, since it is almost always found on younger alluvium, closer to Bladen Branch. Near the BNR some individuals have been observed on the lower parts of limestone slopes, and in Nicaragua this species is found at higher elevations.

If the distribution of *M. pittieri* is not an artefact of incomplete collecting, anemochory may be the reason for *M. pittieri*'s disjunct and spotty distribution. The small, wind-dispersed seeds of *M. pittieri* might be subject to rare, long-distance dispersal events generated by the large storms or hurricanes that periodically strike the region. Wilkinson (1997) has suggested that birds or other animals may be responsible for the large-scale movement of some tree species typically believed to be wind-dispersed.

*Chrysophyllum venezuelanense* (Sapotaceae) has a wider range in the Neotropics, but it also has gaps in its distribution between Petén/Belize, Nicaragua/Costa Rica, and Veracruz, Mexico (Pennington, 1990). Furthermore, this mammal-dispersed species has been collected only infrequently in northern Central America (Pennington, 1990). Like *M. pittieri*, *C. venezuelanense* is one of the few dominant tree species in the immediate area but has a limited local distribution (Brewer, unpubl. data). *Sapium laurifolium* (Euphorbiaceae) is another species that is common and widespread in southern Central America and South America, has limited collections from northern Central America, but is not uncommon in the study site. It is possible that the apparently unusual distri-

bution of this species is an artefact of the difficult and unclear taxonomy of the genus *Sapium* (Burger & Huft, 1995), which has other, closely related species in Belize that are widespread in the Neotropics. *Miconia virescens* (Melastomataceae) is a relatively rare, bird-dispersed species (Brewer, pers. obs.) that is found in eastern Guatemala and Belize, and further south in Panama and northern South America (Standley & Williams, 1963). Other tree taxa with unusual distributions have been collected nearby in the BNR, such as a new species from a previously exclusively South American genus *Elvasia* (*E. bispala* Sastre & Whiteford, Ochnaceae in Sastre *et al.*, 1999) and *Christiana africana* (Tiliaceae; SW Brewer 330, 375), a tree found in the southern Central American isthmus, northern South America, and Africa. The apparently limited distributions of a few tree species may simply reflect a lack of knowledge of the species' true distributions. Yet the patchy nature of the collections of these species, and other species that are more common in the southern extent of their respective ranges, may reflect real, isolated dispersal events and the continued migration of tree species from the much richer forests to the south. Despite having a strong floristic element from South America, the lower-elevation forests of the north-eastern BNR are clearly unique for northern Central America in their richness and some aspects of their composition. Such high species richness may extend throughout the Maya Mountains where rainfall is high and the soils are relatively rich, but few vouchered, quantitative forest data have been published from this area. The estimate of 43–76 tree species ( $\geq 10$  cm  $D_{130}$ ) per hectare for the nearby Columbia Forest Reserve is low, considering the high proportion (13%) of unidentified individuals and the incomplete voucher collections (Bird, 1998).

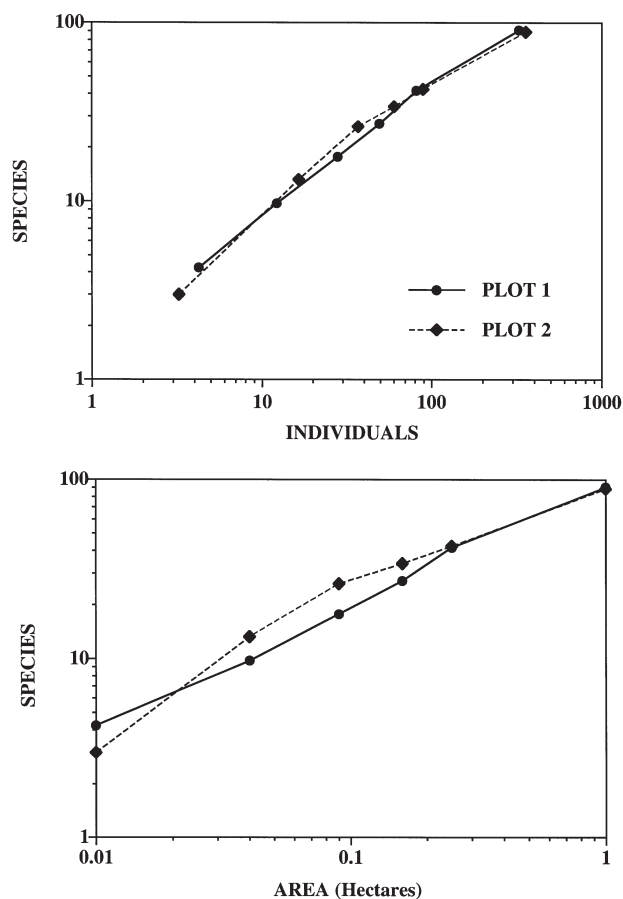
What explains the distinctive nature of the BNR plots? The Maya Mountains encompass an interface of forests on two different substrata of very different age: Cretaceous limestone and Palaeozoic volcanics (Bateson & Hall, 1977). Furthermore, the limestone forests experience edaphic drought and resultant large changes in flora with relatively small changes in elevation (Iremonger & Sayre, 1994; Brewer, unpubl. data). Consequently, the BNR plots harbour species that are rare on the floors of valleys but common and even abundant on nearby slopes (e.g. *Oxandra belizensis*, *Pouteria amygdalina*, etc.). The predominance of zoochory among these species (see below, and Brewer, unpubl. data) makes sources of propagules from species pools in the area readily available to the plots. Thus, a 'mass effect' (Shmida & Wilson, 1985) of nearby sources of species may be maintaining the populations of some species that might otherwise go locally extinct due to low and unstable population sizes. Furthermore, some of the forests of the south-western Maya

Mountains appear to be protected from catastrophic disturbance such as hurricanes. The remote and rugged terrain, and a low human population density, have discouraged the kinds of commercial agriculture and clear-cut logging that have denuded forests elsewhere in Central America. Therefore, the regional pool of potential occupants of the plots may be high because of local landscape diversity, and possibly because of a lack of severe disturbances. These same factors that maintain species richness in the study area may also facilitate the establishment and/or arrival of taxa from farther south in the Neotropics. Landscape diversity, for example, may increase the likelihood of establishment of arriving species with relatively narrow regeneration requirements. Once established, species with small populations may be less likely to go extinct via catastrophic disturbances.

Despite their richness for northern Central America, the BNR plots are depauperate compared with their counterparts at similar latitudes in southern South America, although data from lowland forests of comparable rainfall in non-Amazonian Bolivia are scarce. The distribution of lowland rainforest in Bolivia/Brazil is very restricted at its southern limits, around 16°S in the continental interior (Richards, 1996). The BNR plots do have higher richness (average 90 vs. 79) than one lowland plot in Bolivia that has similar rainfall and latitude (15°S and 2500 mm) (Smith & Killeen, 1998). The higher richness in the BNR may be explained by the relatively young age of the substrate and geologically recent development of lowland rainforest in southern Bolivia, as well as the low winter temperatures in the Bolivian plot (Smith & Killeen, 1998). Otherwise, Atlantic coastal forest (Table 34.2 in Ferreira & Rankin-de-Mérona, 1998) and higher-elevation Bolivian forests (up to 146 species  $ha^{-1}$ , Smith & Killeen, 1998) at similar latitudes are much richer than the BNR plots.

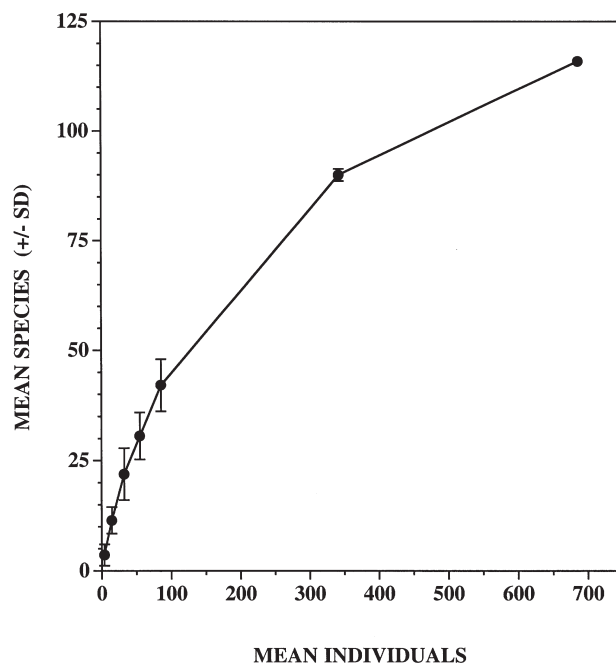
#### SPECIES-AREA AND SPECIES-INDIVIDUAL RELATIONSHIPS

Species–area curves from plot studies consistently demonstrate that one-hectare samples do not adequately characterize the tree *composition* present in a given lowland tropical forest (e.g. Condit *et al.*, 1996). Although the plots were only separated by 200 m, intermediate values of 0.55 and 0.68 were calculated for Jaccard's coefficient and chord distance, respectively, for trees  $\geq 10$  cm diameter. Thus, composition and proportional abundances of species between the two plots were of moderate similarity and demonstrate the need for larger plots in order to capture the variety of species composition at the site. The value for similarity (Jaccard's coefficient) between the BNR plots



**Figure 4.** Species–area and species–individuals curves for each plot, using trees  $\geq 10$  cm diameter. The curves were generated by graphing the mean number of species and individuals in nested, non-overlapping subplots.

is comparable with the values for similarity among low-diversity gallery forests of Venezuela (0.39–0.57, Stergios *et al.*, 1998). Compared with forests of comparable latitude and richness in Bolivia (0.23, Smith & Killeen, 1998) or to regenerating lowland Amazonian forests (0.10–0.21, Campbell *et al.*, 1992), the BNR plots have much higher values of similarity. Unfortunately, similarity values for plots in lowland forests of an area are rarely published. For comparisons of species richness among forests, however, small-plot samples may be useful as long as they sample enough individuals (Condit *et al.*, 1998). The slopes of the species–area and species–individual curves are comparable between the two plots (Fig. 4). Moreover, the species–individual curve generated from both plots combined at this site shows that change in richness begins to decrease noticeably between 100 and 350 cumulative individuals, or the equivalent of 0.25–1.0 hectares (Fig. 5).



**Figure 5.** Species–individuals curve for both plots combined, using trees  $\geq 10$  cm diameter. The right-most points correspond to 1 and 2 hectares, respectively. The curve was generated by graphing the mean number of species (+ standard error bars) and individuals in nested, non-overlapping subplots. The mean for the right-most point (685 individuals) was generated by combining the plot totals.

#### DISPERSAL MODES

Like other wet Neotropical forests (e.g. 87%–90%, van Roosmalen, 1985; 86%, Dirzo & Domínguez, 1986; up to 90%, Foster *et al.*, 1986; 68%, Roth, 1987), the BNR plots have a high proportion of zoochory. In the combined plots, 81% of the tree species are zoochorous (including auto-zoochory), 15% are anemochorous, and 4% are autochorous. These proportions of dispersal mode are virtually the same between the two plots; differences range from 1 to 3%. Of the top 20 species (comprising 72% of the total basal area), however, 30% are anemochorous and 70% are zoochorous.

#### CONCLUSIONS

The two hectares of lower-elevation forest in the Bladen Nature Reserve Belize are unique when compared to plots from the rest of northern Central America. The species richness of the plots is exceptionally high and the tree density exceptionally low for known tropical forests in northern Central America. Two hectares adequately represent species richness *per se* in the study area, but they comprise too small of a sample, however, for capturing the entire species



composition of the area. The BNR plots are similar to other Mexican and Belizean lowland forests in physical structure, and they are similar to other Neotropical forests in spatial patterns of trees and modes of dispersal. The plots are closer in species richness to forests further south, however, such as Barro Colorado Island, Panama, than other sites in Central America outside of Belize. The exceptional nature of the plots may be due to habitat heterogeneity and a mass effect of nearby sources of species, the geographical location, and possibly a relatively mild disturbance history of the area, and/or it may be an artefact of inadequate inventory of lowland evergreen forests in the region. The presence of such rich forest, in an area of Central America previously believed to be relatively species poor, is compelling evidence in support of the need for broader reconnaissance and protection of areas in northern Central America that harbour high biological diversity.

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## APPENDIX 1

Spatial structure of the more common species in the two one-hectare plots. Results show the pattern and distances (m) at which significant deviations from random pattern were detected using K-function analyses and 95% confidence envelopes. H = hyperdispersion (segregation), A = aggregation (clumping), significant at  $P < 0.05$ .  $N$  = number of individuals. NA: not available for analysis; ns: not significantly different ( $P > 0.05$ ) from random.

Species	Plot 1			Plot 2		
	H	$N$	A	H	$N$	A
<i>Alseis yucatanensis</i> (Ad. + Juv.)	–	5	14–15	23–25	9	–
Juveniles	NA	–	–	ns	2	–
Adults	NA	–	–	ns	7	–
Adults vs Juvs.	NA	–	–	ns	–	–
<i>Ampelocera hottlei</i>	45–50	16	–	–	14	24–50
Juveniles	44–50	13	–	–	10	7, 26, 32–33
Adults	–	3	34	ns	4	–
Adults vs. Juvs.	ns	–	–	–	–	26
<i>Aspidosperma spruceanum</i>	1–6	6	9–15	–	8	16, 20, 28–31, 43–44
Juveniles	–	4	7–9, 24	33–40	4	–
Adults	–	2	47–50	ns	4	–
Adults vs. Juvs.	–	–	9, 13–16	–	–	16–17, 40–43
<i>Astrocaryum mexicanum</i>	–	176	3–7, 10–31	–	150	4–50
<i>Attalea cohune</i>	ns	13	–	ns	34	–
<i>Brosimum alicastrum</i>	–	8	10, 12, 44–45	38–48	11	–
Juveniles	NA	–	–	ns	2	–
Adults	–	8	10, 12, 44–45	41–50	9	18–19, 42
Adults vs. Juvs.	NA	–	–	ns	–	–
<i>Castilla elastica</i>	–	7	46–50	ns	15	–
Juveniles	NA	–	–	ns	5	–
Adults	–	7	46–50	18	10	–
Adults vs. Juvs.	NA	–	–	46–50	–	–
<i>Cassipourea guianensis</i>	ns	10	–	ns	10	–
<i>Casearia sylvestris</i>	–	10	6–24, 33–50	NA	–	–
<i>Cecropia</i> spp.	–	–	–	21–33	9	–
<i>Celtis schippii</i>	24–40	8	–	NA	–	–
Juveniles	37–50	8	–	–	–	–
Adults	ns	8	–	–	–	–
Adults vs. Juvs.	ns	–	–	–	–	–
<i>Chionanthus ob lanceolatus</i>	5	–	2–6	NA	–	–
<i>Chrysophyllum venezuelanense</i>	ns	8	–	–	8	47–48
Juveniles	ns	2	–	ns	3	–
Adults	ns	6	–	ns	5	–
Adults vs. Juvs.	ns	–	–	–	–	34–44
<i>Cordia alliodora</i>	NA	–	–	–	6	8, 11–18
Juveniles	NA	–	–	–	3	8–15
Adults	NA	–	–	–	3	21–22
Adults vs. Juvs.	NA	–	–	–	–	11–19
<i>Dialium guianense</i>	–	8	21–31	–	25	9–10
Juveniles	ns	4	–	ns	7	–
Adults	ns	4	–	–	18	3, 7–10, 43–50
Adults vs. Juvs.	ns	–	–	–	–	47–48
<i>Drypetes brownei</i>	–	23	18–23, 26	ns	7	–
Juveniles	12–13, 18–19	12	–	ns	4	–
Adults	–	11	2, 17–23	ns	3	–
Adults vs. Juvs.	46	–	–	ns	–	–



Species	H	Plot 1		Plot 2		
		N	A	H	N	A
<i>Erythrina folkersii</i>	NA	–	–	–	5	7, 29–33, 43
<i>Faramea occidentalis</i>	–	10	8, 14–50	ns	6	
<i>Guarea glabra</i>	ns	28		–	36	39–50
Juveniles	19, 25, 28–30	19	–	9–11, 21–45	27	–
Adults	ns	9		–	9	22, 27–32
Adults vs. Juvs.	37–40		–	ns		
<i>Guarea grandifolia</i>	–	6	27	NA	–	–
Juveniles	ns	2		NA	–	–
Adults	ns	4		NA	–	–
Adults vs. Juvs.	ns			NA	–	–
<i>Heisteria media</i>	–	7	10, 13–15, 19–20	NA	–	–
<i>Jacaratia dolichaula</i>	NA	–	–	–	5	33–37
<i>Licania hypoleuca</i>	NA	–	–	–	6	15–18, 39–50
<i>Manilkara chicle</i>	36–50	18	–	7–9, 14–17	16	–
Juveniles	50	9	–	ns	6	
Adults	ns	9		16–17	10	–
Adults vs. Juvs.	36–49		–	ns		
<i>Mouriri myrtilloides</i>	–	13	10–23, 28–30, 33–50	–	15	11, 14, 16, 20
<i>Mortoniella pittieri</i>	–	18	6–10, 17–45	–	24	7, 19–37
<i>Pouteria durlandii</i>	–	8	10	ns	22	
Juveniles	–	4	10–12	–	13	47–50
Adults	–	4	19	–	9	14–50
Adults vs. Juvs.	–		10–19	29–42		
<i>Pouteria izabalensis</i>	–	8	28	NA	–	–
Juveniles	ns	3		NA	–	–
Adults	ns	5		NA	–	–
Adults vs. Juvs.	ns			NA	–	–
<i>Protium schippii</i>	–	40	10–25	46–50	38	12–13
<i>Psychotria chiapensis</i>	–	7	1, 13–15	NA	–	–
<i>Pterocarpus rohrii</i>	NA	–	–	ns	8	
Juveniles	NA	–	–	ns	8	
Adults	NA	–	–	–	3	30–34
Adults vs. Juvs.	NA	–	–	–		6
<i>Quararibea funebris</i>	–	35	23, 27–30, 35, 37	NA	–	–
Juveniles	–	15	35			
Adults	–	20	15–26, 36–50			
Adults vs. Juvs.	ns					
<i>Rinorea hummelii</i>	–	7	6–9, 14–29	NA	–	–
<i>Schizolobium parahyba</i>	–	8	7–25	NA		
<i>Simira salvadorensis</i>	NA	–	–	ns	10	
<i>Sloanea tuerckheimii</i>	NA	–	–	ns	9	
<i>Spondias mombin</i>	–	25	8–50	–	25	2–4, 15–46
Juveniles	–	12	20–25	–	10	20–21
Adults	–	13	11–50	–	15	14, 17–50
Adults vs. Juvs.	–	–	9–14, 19–20, 28–50	–		2–9, 18–41, 26–31, 37–42
<i>Stemmadenia donnell-smithii</i>	–	6	14–25	NA	–	–
Juveniles	–	4	19–26			
Adults	ns	2				
Adults vs. Juvs.	–	–	14–29			
<i>Zanthoxylum riedelianum</i>	–	5	16–18, 28–31	NA	–	–

## APPENDIX 2

Species of trees in two one-hectare plots in lowland evergreen forest in the Bladen Nature Reserve, Belize, Central America. *N* = number of individuals; BA = basal area (m<sup>2</sup>); D<sub>130</sub> = stem diameter at 130 cm above the ground.

Taxa	Plot 1				Plot 2			
	≥5 cm D <sub>130</sub>		≥10 cm D <sub>130</sub>		≥5 cm D <sub>130</sub>		≥10 cm D <sub>130</sub>	
	<i>N</i>	BA (m <sup>2</sup> )	<i>N</i>	BA (m <sup>2</sup> )	<i>N</i>	BA (m <sup>2</sup> )	<i>N</i>	BA (m <sup>2</sup> )
Anacardiaceae								
<i>Astronium graveolens</i> Jacq.	1	0.012	1	0.01	3	0.338	3	0.34
<i>Spondias mombin</i> L.	25	1.354	21	1.34	25	1.534	19	1.51
Annonaceae								
<i>Annona scleroderma</i> Saff.	1	0.004	–	–	–	–	–	–
<i>Cymbopetalum mayanum</i> Lundell	5	0.10	4	0.1	2	0.111	2	0.11
<i>Oxandra belizensis</i> (Lundell) Lundell	–	–	–	–	1	0.024	1	0.02
<i>Rollinia mucosa</i> (Jacq.) Baill.	3	0.171	2	0.16	1	0.061	1	0.06
<i>Xylopia frutescens</i> Aubl.	–	–	–	–	1	0.003	–	–
Apocynaceae								
<i>Aspidosperma megalocarpon</i> Müll. Arg.	1	0.076	1	0.08	3	0.237	2	0.23
<i>Aspidosperma spruceanum</i> Benth. ex Müll. Arg.	6	0.087	3	0.08	8	0.282	6	0.27
<i>Mortoniella pittieri</i> Woodson	18	4.834	17	4.83	24	5.927	23	5.92
<i>Stemmadenia donnell-smithii</i> (Rose) Woodson	6	0.061	3	0.05	4	0.053	3	0.05
<i>Tabernaemontana alba</i> Mill.	–	–	–	–	2	0.032	2	0.03
<i>Tabernaemontana arborea</i> Rose ex Donn. Sm.	4	0.226	4	0.23	1	0.057	1	0.06
Araliaceae								
<i>Dendropanax arboreus</i> (L) Decne. & Planch.	1	0.003	–	–	–	–	–	–
Arecaceae								
<i>Astrocaryum mexicanum</i> Liebm. ex Mart.	176	0.407	–	–	150	0.348	–	–
<i>Attalea cohune</i> Mart.	13	1.151	13	1.15	34	3.576	34	3.58
<i>Sabal mauritiiiformis</i> (H. Karst.) Griseb. & H. Wendl.	1	0.038	1	0.04	3	0.111	3	0.11
Bignoniaceae								
<i>Tabebuia guayacan</i> (Seem.) Hemsl.	1	0.036	1	0.04	2	0.066	2	0.07
Bombacaceae								
<i>Ceiba pentandra</i> (L) Gaertn.	–	–	–	–	1	1.039	1	1.04
<i>Quararibea funebris</i> (La Llave) Vischer	35	1.134	25	1.09	2	0.022	–	–
Boraginaceae								
<i>Cordia alliodora</i> (Ruiz & Pav.) Oken	–	–	–	–	6	0.21	5	0.21
<i>Cordia bicolor</i> A. DC.	2	0.059	2	0.06	4	0.278	3	0.27
Burseraceae								
<i>Bursera simaruba</i> (L) Sarg.	4	0.149	3	0.14	1	0.102	1	0.1
<i>Protium copal</i> (Schltdl. & Cham.) Engl.	2	0.009	–	–	–	–	–	–
<i>Protium schippii</i> Lundell	40	0.389	17	0.29	38	0.316	13	0.21
Capparidaceae								
<i>Forchhammeria trifoliata</i> Radlk.	1	0.003	–	–	–	–	–	–
Caricaceae								
<i>Jacaratia dolichaula</i> (Donn. Sm.) Woodson	3	0.035	1	0.03	5	0.068	4	0.06
Celtidaceae								
<i>Celtis schippii</i> Standl.	8	0.165	5	0.16	4	0.111	3	0.11

Taxa	Plot 1				Plot 2			
	≥5 cm D <sub>130</sub>		≥10 cm D <sub>130</sub>		≥5 cm D <sub>130</sub>		≥10 cm D <sub>130</sub>	
	N	BA (m <sup>2</sup> )	N	BA (m <sup>2</sup> )	N	BA (m <sup>2</sup> )	N	BA (m <sup>2</sup> )
Chrysobalanaceae								
<i>Hirtella triandra</i> Sw.	1	0.022	1	0.02	–	–	–	–
<i>Licania hypoleuca</i> Benth.	2	0.128	2	0.13	6	0.086	2	0.07
<i>Licania sparsipilis</i> S. F. Blake	1	0.006	–	–	–	–	–	–
Clusiaceae								
<i>Calophyllum brasiliense</i> Cambess.	–	–	–	–	2	0.063	1	0.06
<i>Garcinia intermedia</i> (Pittier) Hammel	2	0.005	–	–	2	0.004	–	–
Combretaceae								
<i>Terminalia amazonia</i> (J. F. Gmel.) Exell	3	0.792	3	0.79	1	0.119	1	0.12
<i>Terminalia oblonga</i> (Ruiz & Pav.) Steud.	2	0.007	–	–	–	–	–	–
Ebenaceae								
<i>Diospyros digyna</i> Jacq.	3	0.159	2	0.15	–	–	–	–
Elaeocarpaceae								
<i>Sloanea tuerckheimii</i> Donn. Sm.	2	0.028	1	0.02	9	0.198	6	0.19
Euphorbiaceae								
<i>Croton billbergianus</i> ssp. <i>pyramidalis</i> (Donn. Sm.) G. L. Webster	2	0.063	2	0.06	1	0.002	–	–
<i>Croton schiedeana</i> Schltdl.	1	0.024	1	0.02	2	0.015	1	0.01
<i>Drypetes brownii</i> Standl.	23	0.546	14	0.52	7	0.215	4	0.21
<i>Sapium laurifolium</i> (A. Rich.) Griseb.	3	0.284	3	0.28	1	0.019	1	0.02
Fabaceae								
<i>Acacia cornigera</i> (L) Willd.	–	–	–	–	1	0.01	1	0.01
<i>Acacia glomerosa</i> Benth.	–	–	–	–	2	0.2	2	0.2
<i>Albizia adinocephala</i> (Donn. Sm.) Britton & Rose	1	0.011	1	0.01	–	–	–	–
<i>Albizia niopoides</i> (Spruce ex Benth) Burkhardt var. <i>niopoides</i>	1	0.036	1	0.04	–	–	–	–
<i>Andira inermis</i> (W. Wright) Kunth ex DC.	–	–	–	–	3	0.181	3	0.18
<i>Cajoba arborea</i> (L) Britton & Rose	3	0.098	3	0.1	–	–	–	–
<i>Dialium guianense</i> (Aubl.) Sandwith	8	0.683	6	0.67	25	1.874	18	1.84
<i>Erythrina folkersii</i> Krukoff & Moldenke	–	–	–	–	5	0.026	1	0.01
<i>Inga acrocephala</i> Steud.	2	0.143	2	0.14	–	–	–	–
<i>Inga nobilis</i> ssp. <i>quaternata</i> (Poepp. & Endl.) T. D. Penn.	1	0.01	1	0.01	–	–	–	–
<i>Inga punctata</i> Willd.	–	–	–	–	2	0.036	1	0.03
<i>Inga sapindoides</i> Willd.	1	0.088	1	0.09	4	0.186	4	0.19
<i>Lecointea amazonica</i> Ducke	3	0.244	1	0.24	–	–	–	–
<i>Lonchocarpus</i> aff. <i>atropurpureus</i> Benth.	–	–	–	–	1	0.043	1	0.04
<i>Lonchocarpus pentaphyllus</i> (Poir) Kunth ex DC.	4	1.001	3	0.99	1	0.064	1	0.06
<i>Platymiscium dimorphandrum</i> Donn. Smith	1	0.008	1	0.01	3	0.073	2	0.07
<i>Pterocarpus rohrii</i> Vahl	2	0.039	2	0.04	8	0.833	4	0.82
<i>Schizolobium parayhya</i> (Vell.) S. F. Blake	8	3.459	8	3.46	1	0.207	1	0.21
<i>Swartzia simplex</i> var. <i>ochracea</i> (DC.) R. S. Cowan	1	0.005	–	–	3	0.068	2	0.06
<i>Vatairea lundellii</i> (Standl.) Killip ex Record	–	–	–	–	3	0.332	2	0.33

Taxa	Plot 1				Plot 2			
	≥5 cm D <sub>130</sub>		≥10 cm D <sub>130</sub>		≥5 cm D <sub>130</sub>		≥10 cm D <sub>130</sub>	
	N	BA (m <sup>2</sup> )	N	BA (m <sup>2</sup> )	N	BA (m <sup>2</sup> )	N	BA (m <sup>2</sup> )
<b>Flacourtiaceae</b>								
<i>Casearia aculeata</i> Jacq.	–	–	–	–	1	0.003	–	–
<i>Casearia commersoniana</i> Cambess.	1	0.021	1	0.02	2	0.022	2	0.02
<i>Casearia sylvestris</i> Sw.	7	0.053	2	0.03	2	0.016	1	0.01
<i>Casearia tacanensis</i> Lundell	2	0.03	2	0.03	–	–	–	–
<i>Pleuranthodendron lindenii</i> (Turcz.) Sleumer	2	0.247	2	0.25	1	0.016	1	0.02
<i>Zuelania guidonia</i> (Sw.) Britton & Millsp.	1	0.002	–	–	–	–	–	–
<b>Lauraceae</b>								
Lauraceae	1	0.02	1	0.02	1	0.011	1	0.01
<i>Licaria cf. capitata</i> (Cham. & Schltld.) Kosterm.	1	0.011	1	0.01	1	0.27	1	0.27
<i>Licaria peckii</i> (I. M. Johnst.) Kosterm.	2	0.099	2	0.1	2	0.034	2	0.03
<i>Nectandra cf. cuspidata</i> Nees & Mart.	1	0.013	1	0.01	–	–	–	–
<i>Nectandra lundellii</i> C. K. Allen	3	0.174	3	0.17	–	–	–	–
<i>Nectandra aff. salicifolia</i> (Kunth) Nees	–	–	–	–	1	0.078	1	0.08
<i>Ocotea cernua</i> (Nees) Mez	3	0.03	2	0.03	2	0.026	1	0.02
<b>Malpighiaceae</b>								
<i>Malpighia</i> sp.	1	0.053	1	0.05	–	–	–	–
<b>Malvaceae</b>								
<i>Hampea stipitata</i> S. Watson	–	–	–	–	2	0.008	–	–
<b>Melastomataceae</b>								
<i>Miconia hyperprasina</i> Naudin	1	0.007	–	–	–	–	–	–
<i>Miconia virescens</i> (Vahl) Triana	2	0.012	1	0.01	–	–	–	–
<i>Mouriri exilis</i> Gleason	2	0.02	1	0.02	–	–	–	–
<i>Mouriri myrtilloides</i> ssp. <i>parvifolia</i> (Benth.) Morley	13	0.123	6	0.09	15	0.105	6	0.07
<b>Meliaceae</b>								
<i>Guarea glabra</i> Vahl	28	0.744	18	0.7	36	0.367	14	0.27
<i>Guarea grandifolia</i> DC.	6	0.302	5	0.3	4	0.508	4	0.51
<i>Swietenia macrophylla</i> King	1	0.243	1	0.24	1	0.049	1	0.05
<i>Trichilia hirta</i> L.	1	0.054	1	0.05	1	0.008	–	–
<i>Trichilia martiana</i> C. DC.	1	0.19	1	0.19	–	–	–	–
<i>Trichilia moschata</i> Sw. ssp. <i>moschata</i>	1	0.01	1	0.01	1	0.01	1	0.01
<i>Trichilia pallida</i> Sw.	3	0.01	–	–	2	0.008	–	–
<b>Moraceae</b>								
<i>Brosimum alicastrum</i> Sw.	8	1.965	7	1.96	11	2.571	11	2.57
<i>Castilla elastica</i> SessÉ	7	0.226	7	0.23	15	0.640	13	0.63
<i>Cecropia obtusifolia</i> Bertol.	–	–	–	–	2	0.147	2	0.15
<i>Cecropia peltata</i> L.	1	0.054	2	0.14	7	0.425	7	0.42
<i>Ficus insipida</i> Willd.	–	–	–	–	4	0.514	4	0.51
<i>Ficus popenoei</i> Standl.	–	–	–	–	1	0.994	1	0.99
<i>Ficus</i> sp. 3	–	–	–	–	1	0.671	1	0.67
<i>Pseudolmedia spuria</i> (Sw.) Griseb.	2	0.026	2	0.03	–	–	–	–
<i>Trophis racemosa</i> (L) Urb.	–	–	–	–	2	0.12	2	0.12
<b>Myristicaceae</b>								
<i>Compsonaura sprucei</i> (A. DC.) Warb.	4	0.024	1	0.01	4	0.039	1	0.03
<i>Virola koschnyi</i> Warb.	1	0.183	1	0.18	–	–	–	–
<b>Myrtaceae</b>								
<i>Plinia peroblata</i> (Lundell) Lundell	–	–	–	–	1	0.009	1	0.01



Taxa	Plot 1				Plot 2			
	≥5 cm D <sub>130</sub>		≥10 cm D <sub>130</sub>		≥5 cm D <sub>130</sub>		≥10 cm D <sub>130</sub>	
	N	BA (m <sup>2</sup> )	N	BA (m <sup>2</sup> )	N	BA (m <sup>2</sup> )	N	BA (m <sup>2</sup> )
Olacaceae								
<i>Heisteria media</i> S. F. Blake	7	0.098	4	0.08	1	0.005	–	–
Oleaceae								
<i>Chionanthus oblancoelatus</i> (B. L. Rob.) P.S. Green	5	0.023	–	–	1	0.01	1	0.01
Piperaceae								
<i>Piper schippianum</i> Trel. & Standl.	5	0.017	–	–	2	0.009	–	–
Polygonaceae								
<i>Coccoloba tuerckheimii</i> Donn. Sm.	1	0.05	1	0.05	1	0.004	–	–
Rhizophoraceae								
<i>Cassipourea guianensis</i> Aubl.	10	0.056	2	0.03	10	0.094	5	0.08
Rubiaceae								
<i>Alibertia edulis</i> (L. Rich.) A. Rich. ex DC.	1	0.004	–	–	–	–	–	–
<i>Alseis yucatanensis</i> Standl.	5	0.211	4	0.21	9	0.637	7	0.63
<i>Faramea occidentalis</i> (L) A. Rich.	10	0.038	–	–	6	0.032	1	0.01
<i>Guettarda macrosperma</i> (Sw.) DC.	2	0.01	–	–	1	0.004	–	–
<i>Morinda panamensis</i> Seem.	2	0.172	2	0.17	–	–	–	–
<i>Posoqueria latifolia</i> (Rudge) Roem. & Schult.	3	0.025	1	0.02	7	0.066	3	0.05
<i>Psychotria chiapensis</i> Standl.	7	0.038	2	0.02	2	0.008	–	–
<i>Randia armata</i> (Sw.) DC.	–	–	–	–	2	0.005	–	–
<i>Randia genipifolia</i> (Standl. & Steyerem.) Lorence	2	0.007	–	–	–	–	–	–
<i>Simira salvadorensis</i> (Standl.) Steyerem.	3	0.296	2	0.29	10	0.284	7	0.27
<i>Stenostomum lucidum</i> (Sw.) C. F. Gaertn.	1	0.245	1	0.25	3	0.108	3	0.11
Rutaceae								
<i>Zanthoxylum ekmanii</i> (Urb.) Alain	1	0.131	1	0.13	1	0.051	1	0.05
<i>Zanthoxylum riedelianum</i> Engl. incl. <i>Z. riedelianum</i> ssp. <i>mayanum</i> (Standl.) Reynel & <i>Z. riedelianum</i> ssp. <i>kellermanii</i> (P. Wilson) Reynel	5	0.194	5	0.19	4	0.372	4	0.37
Sapindaceae								
<i>Allophylus camptostachys</i> Radlk.	1	0.002	–	–	–	–	–	–
<i>Allophylus</i> aff. <i>psilospermus</i> Radlk.	1	0.039	1	0.04	–	–	–	–
<i>Exothea paniculata</i> (Juss.) Radlk.	1	0.034	1	0.03	1	0.011	1	0.01
Sapotaceae								
<i>Chrysophyllum venezuelanense</i> (Pierre) T. D. Penn.	8	1.449	6	1.44	8	0.33	6	0.32
<i>Manilkara chicle</i> (Pittier) Gilly	18	1.88	13	1.86	16	1.203	10	1.17
<i>Pouteria amygdalina</i> (Standl.) Baehni	1	0.008	–	–	–	–	–	–
<i>Pouteria campechiana</i> (Kunth) Baehni	–	–	–	–	2	0.016	1	0.01
<i>Pouteria durlandii</i> Standl. (Baehni)	8	0.22	4	0.21	22	0.403	16	0.38
<i>Pouteria izabalensis</i> (Standl.) Baehni	8	0.404	5	0.39	2	0.03	1	0.03
<i>Pouteria reticulata</i> (Engl.) Eyma	4	0.038	2	0.03	2	0.015	1	0.01
<i>Pouteria sapota</i> (Jacq.) H.E. Moore & Stearn	4	0.752	4	0.75	3	0.716	3	0.72
Simaroubaceae								
<i>Picramnia antidesma</i> ssp. <i>fessionia</i> (DC.) W. W. Thomas	3	0.014	–	–	–	–	–	–
Sterculiaceae								
<i>Guazuma ulmifolia</i> Lam.	2	0.184	2	0.18	1	0.077	1	0.08

Taxa	Plot 1				Plot 2			
	≥5 cm D <sub>130</sub>		≥10 cm D <sub>130</sub>		≥5 cm D <sub>130</sub>		≥10 cm D <sub>130</sub>	
	N	BA (m <sup>2</sup> )	N	BA (m <sup>2</sup> )	N	BA (m <sup>2</sup> )	N	BA (m <sup>2</sup> )
Tiliaceae								
<i>Heliocarpus americanus</i> L.	1	0.148	1	0.15	–	–	–	–
<i>Luehea speciosa</i> Willd.	1	0.439	1	0.44	4	0.116	3	0.11
<i>Mortoniendron vestitum</i> Lundell	4	0.564	1	0.56	–	–	–	–
<i>Trichospermum grewii</i> (A. Rich.) Kosterm.	1	0.046	1	0.05	1	0.069	1	0.07
Ulmaceae								
<i>Ampelocera hottlei</i> (Standl.) Standl.	16	0.218	3	0.16	14	0.321	9	0.31
Urticaceae								
<i>Myriocarpa longipes</i> Liebm.	1	0.002	–	–	–	–	–	–
Verbenaceae								
<i>Aegiphila monstrosa</i> Moldenke	–	–	–	–	1	0.01	1	0.01
<i>Vitex kuylenii</i> Standl.	–	–	–	–	1	0.018	1	0.02
Violaceae								
<i>Rinorea hummelii</i> Sprague	6	0.021	–	–	–	–	–	–
Indet.	1	0.055	1	0.05	1	0.101	1	0.1