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Relationships of phytogeography and diversity of tropical tree species with limestone topography in southern Belize

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Abstract

Aim The flora of northern Mesoamerica conventionally has been thought to be derived from taxa that emigrated from South America, but this view has recently been challenged as too simple. The dominance of limestone substrata in much of northern Mesoamerica, and its rarity in the rest of the continental Neotropics, may be one cause of the complexity of northern Mesoamerican floristics. Furthermore, northern Mesoamerica experiences longer and more intense seasonal drought than the rest of the continental Neotropics. As edaphic drought is accentuated with elevation on limestone soils, it may be expected that different topographic features have different phytogeographical affinities for seasonally drought-prone areas of the Neotropics. The objective of this study was to test for effects of different topographic positions on the composition, phytogeography and diversity of tree species in a limestone area of Belize.

Location Maya Mountains, Belize, Mesoamerica.

Methods The diversity and local, regional, and hemispheric distributions of tree species on limestone valley floors, lower and upper slopes, and ridges were compared in southern Belize using 2×500 m transects as sample plots.

Results Stem density increased, and percentage of large trees decreased, significantly with elevation above the valley floors. The proportions of species that had widespread distributions decreased significantly with increasing elevation above the valley floors. The proportions of species having northern Mesoamerican distributions increased significantly with elevation above the valley floors. All of the forests generally had the strongest phytogeographical affinities for the Petén (Guatemala) and Mexico, but greater affinities for the Yucatán were observed with increasing elevation above the valley floors. Species with distributions including the Greater Antilles made up an increasingly significant element, in terms of species and numbers of stems, with increasing elevation above the floors of valleys. Valley floors and ridges had the highest percentages of species unique to their topographic positions, 61% and 39% of their species, respectively, and were very similar in diversity. Slope forests had the highest diversity of trees ≥ 5 cm d.b.h. and were transitional in composition among the topographic positions.

Main conclusions Despite relatively small changes in elevation, the composition, diversity and physical structure of the limestone forests changed significantly with topography. Such changes were presumably due to the greater edaphic drought experienced by these forests, and possibly due to lower levels of disturbance and differences in forest age, with increasing elevation above the floors of valleys.

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Keywords
Karst, Mesoamerica, Maya Mountains, tree species diversity, elevation gradient.

INTRODUCTION

The flora of northern Mesoamerica conventionally has been thought to be derived from taxa that emigrated from South America around the time of the Great American Interchange (Gentry, 1982; Cronquist, 1988). Recently, however, this view of Mesoamerican floristics has been demonstrated to be an oversimplification. Studies evaluating floristic and paleobotanical evidence demonstrate complex multiple origins of the flora of northern Mesoamerica (Wendt, 1993; Burnham & Graham, 1999). One reason for the incomplete dominance of Amazonian-derived taxa in northern Mesoamerica may be the presence of soil types that are virtually absent from South America.

Northern Mesoamerica is unique for the continental Neotropics in being dominated by limestone substrata and karst terrain (Snead, 1980). Tropical, limestone outcrop soils are typically shallow and experience stronger seasonal drought than other soils of rain forest areas. They often have rapid drainage, high fertility, and have a relatively high pH and high organic matter content compared with many other tropical soils (Beard, 1944; Wright *et al.*, 1959; Furley & Newey, 1979; Richards, 1996). Consequently, limestone soils appear to be occupied by unique floras (Crowther, 1982; Proctor *et al.*, 1983; Wendt, 1993; Richards, 1996), but few studies have intensively investigated tropical forests over limestone because of the restricted distributions of this substrate and the difficulty of working in tropical karst terrain (Kelly *et al.*, 1988; Richards, 1996).

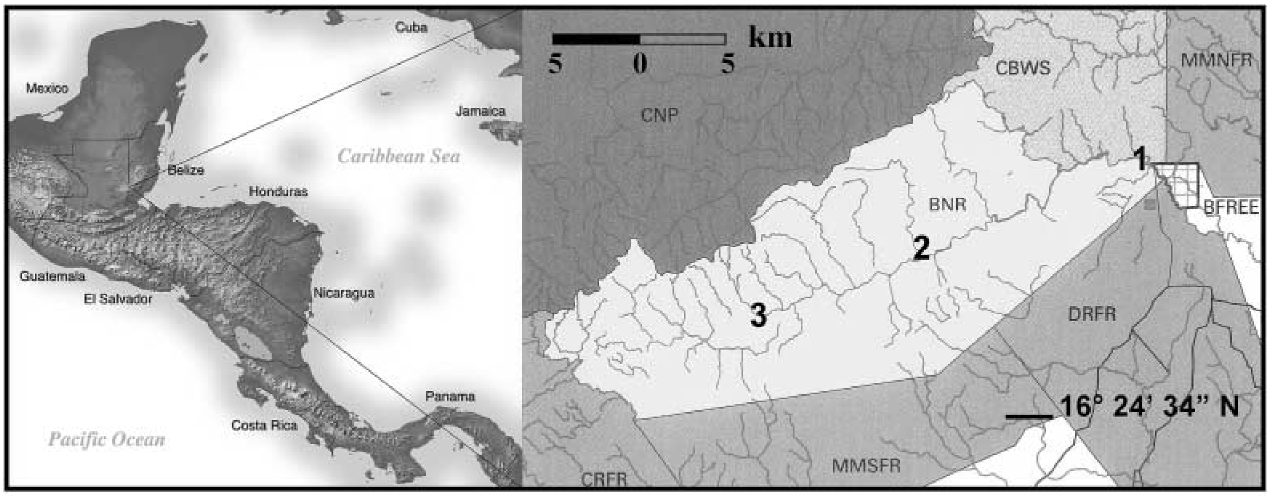
The forests of northern Mesoamerica remain largely undescribed, as research into the structure, composition, and dynamics of Neotropical forests has been concentrated mostly in southern Mesoamerica and South America (e.g. Gentry, 1988, 1990; Condit *et al.*, 1998; Dallmeier & Comiskey, 1998). A noteworthy exception is the well-known forest of Los Tuxtlas, Veracruz, México (González-Soriano *et al.*, 1997); this forest, however, is on a volcanic substrate. Most of the detailed studies of the floristics of tropical forests over limestone are from Malaysia and Indonesia (Chin, 1977; Crowther, 1982; Proctor *et al.*, 1983; Polak, 2000), China (Hua, 2002), or the Caribbean (Proctor, 1986; Kelly *et al.*, 1988; Borhidi, 1996; Rivera *et al.*, 2000).

Topography and associated changes in elevation are surrogate variables for many factors that determine plant growth and distribution, such as exposure to winds and disturbance, temperature, soil depth, water availability and drainage, and nutrient status. It is therefore not surprising that studies throughout the tropics consistently illustrate the influence of topography on the composition and distribution of tree species (Ashton, 1964; Basnett, 1992; Pitman *et al.*, 1999; Rennolls & Laumonier, 2000). Furthermore, species richness generally declines with elevation, but there are many exceptions (Rahbek, 1995), because elevation may represent multiple environmental gradients. Some observations indicate that slope forests in the Neotropics are more diverse than adjacent lowland or valley floor forests (French Guiana: Hallé *et al.*, 1978; Mexico: Wendt, 1993; Panama: Leigh, 1996; Bolivia: Foster, 1991; Smith & Killeen, 1998). To our knowledge, however, quantitative comparisons of the phytogeography and diversity of tree species among topographic positions have not been published for forests of northern Mesoamerica.

Given the strong effects of limestone on soils and drainage (Furley & Newey, 1979; King *et al.*, 1986), different topographic positions in karst terrain are expected to have different species composition and diversity, because small differences in elevation intensify the effects of seasonal drought. Wendt (1993) observed that compared with deeper soils nearby, limestone outcrops of southern Veracruz harbour a greater proportion of species that are endemic to northern Mesoamerica. Brewer & Webb (2002) found that the tree flora of a limestone valley floor in Belize was dominated by widespread Neotropical species and was unusually diverse for northern Mesoamerica. Based on these studies and preliminary observations, we hypothesized that with increasing elevation, tree species composition on limestone would increasingly include species restricted to northern Mesoamerica (northern species) and that species diversity would increase with elevation above the valley floors. We then conducted a study of the geographical distributions, and the richness and diversity, of tree species at different topographic positions on limestone in southern Belize.

Study area

Belize encompasses *c.* 22,275 km^2 of the base of the Yucatán Peninsula, between 15 and 19°N latitude. The geology of the wet, southern half of the country is dominated by the Maya Mountains, where the study area, the Bladen Nature Reserve (BNR), is located (16°24′34″–16°36′18″ N latitude). The climate of the area can be classified as tropical wet seasonal (Walsh, 1996), with an annual rainfall of 2500–3000 mm and a strong dry season from February to May. The BNR is *c.* 350 km^2 in area and encompasses the watershed of the Bladen Branch of the Monkey River, which runs from higher elevations in the south-west through the middle of the BNR to the north-east (Fig. 1). The south-east half of the watershed is composed of Coban (late Cretaceous) limestone, and the north-west half is composed of Bladen (Paleozoic) volcanic formations, with pockets of alluvium beside the river and its tributaries (Bateson & Hall, 1977). Evergreen forests (*sensu* Beard, 1944) grow on these pockets of alluvium and are surrounded by long and continuous, steep limestone slopes that rise *c.* 150–200 m from the floors of the valleys to



BFREE	**Belize Foundation for Research & Environmental Education**
BNR	**Bladen Nature Reserve**
CBWS	**Cockscomb Basin Wildlife Refuge**
CNP	**Chiquibul National Park**
CRFR	**Columbia Forest Reserve**
DRFR	**Deep River Forest Reserve**
MMNFR	**Maya Mountain North Forest Reserve**
MMSFR	**Maya Mountain South Forest Reserve**

Figure 1 The three study sites in Bladen Nature Reserve, in the Maya Mountains of Belize, Central America. Elevation ranges from valley floors to ridges at sites 1, 2 and 3 are 190, 180 and 160 m, respectively. Central America image courtesy of NASA/JPL/Caltech. Inset map © Belize Foundation for Research and Environmental Education, used with permission.

the ridges. Surrounding these slopes the topography is complex, including cone karst (knolls), rock outcrops, plateaus, shallow and deep sinkholes, etc. The alluvial soils are deep (≥ 1 m), fairly well-drained clay loams, and the soils on the slopes are shallow (mostly < 0.5 m) and rocky, very well-drained clay loams. The forest canopy is increasingly deciduous with elevation above the alluvial forests.

The last significant human occupation of the area was by the Maya on a relatively small scale in the valleys *c.* 1000 years before present (yr BP) (Abramiuk, 1999; P. Dunham, pers. comm.). As in most of the Neotropics, however, some mahogany (*Swietenia macrophylla* King) and cedar (*Cedrela odorata* L.) were removed from the area in more recent times. Approximately 120 yr BP a small mahogany logging operation was conducted in the north-east part of the watershed (Fowler, 1879), and *c.* 60 yr BP some trees were removed from the south-western part of the BNR (P. Dunham, pers. comm.), but large mahogany trees are not uncommon throughout the BNR (S. Brewer, pers. obs.).

METHODS

Field methods and collections

Forests on valleys (alluvial forests on the floors of valleys, with < 5% inclination, indicated by a 'V' prefix in the analyses), lower slopes (forests on the lower third of the slopes next to the valley floor, 'L'), upper slopes (forests on the upper third of the slopes, 'U') and ridges (R) were sampled along elevational gradients at three sites in the watershed in 1999 and 2002 (Fig. 1). These topographic positions were selected because of their unambiguous definition, comparative ease in location, and their relation to soil moisture and other properties as reflected by previous studies in Belize (Furley & Newey, 1979 and references therein). As sample plots (SPs), belt transects, rather than regular plots, were best suited to following contours that represented the topographic positions and were more feasible for rapid sampling of the variation within and among the topographic positions in the difficult terrain of the BNR. The method used here was a modification of Gentry's (1982, 1988) method, which has become one standard for rapid sampling of plant diversity in tropical forests (Phillips & Miller, 2002). In the dry season of 1999, one transect 2 × 500 m (0.1 ha) was placed within each topographic position, along contour lines and skipping over treefall gaps in the canopy. While gaps are an important constituent of tropical forests, the irregular occurrence and highly variable physical structure of gaps would require an order of magnitude increase in the number of SPs to account for their effect on variation in diversity and composition. This was not justified given the objectives of the study. Orientation and percentage slope were measured at six points spaced evenly along each SP. The valley SPs were placed 50–60 m away from the base of the nearby slope, and the lower slope and upper slope SPs were placed in the middle of the lower and upper thirds of the slope face at each site, respectively. The precise location of the beginning of a given SP was determined haphazardly.

The three sites were 10 km apart and were located in the far north-eastern part of the BNR, where the Bladen Branch begins to emerge from the main gorge of the watershed (site 1; elevation range = 60–250 m), the approximate middle of the watershed (site 2; elevation range = 140–320 m), and the upper part of the watershed (site 3; elevation range = 240–400 m) (Fig. 1). The sites were chosen to reduce variability, other than topographic position and substrate, and were selected to: (1) represent separate, approximately equally spaced locations in the watershed, (2) consist of mature-phase forest, (3) have similar orientations of the slopes (all approximately north-facing), and (4) have slope faces that were of similar overall inclination and total elevation change from their respective valley forests. Trees that were within SPs were identified and their diameter measured at 130 cm above the soil surface (d.b.h. or diameter). A tree was counted if it had a d.b.h. ≥ 5 cm and if the centre of the base of its stem was within the SP. Trees included all woody, free-standing plants (including palms) ≥ 5 cm d.b.h. Palms with developed stems, regardless of diameter, were also included in the surveys. Lianas were not included in the surveys.

Voucher specimens were collected for all tree species, with the exceptions of species that were common and distinctive, and for which there was no confusion about their identity (e.g. *Schizolobium parahyba*, *Attalea cohune*; see Appendix 1 for species names and authorities). Morphospecies that could not be reliably separated from known species were included with the known species for the analyses (< 1% of all stems encountered). Morphospecies that could not be identified to family were included in the analyses of diversity; they represented < 3% of all species encountered and just five of nearly 1800 stems sampled. Less than 6% of all species (10 stems) could not be identified to species. Distributions of voucher specimens are available from the first author.

Data analyses

The species sampled in this study were classified into one of three major phytogeographical categories: (1) northern Mesoamerican species endemic to or primarily found in the area north of central Nicaragua (see Wendt, 1993 and Gentry, 1982 for discussions of what constitutes northern Central America), (2) species endemic to or primarily occurring throughout Mesoamerica, and (3) widespread species reaching South America, found in Amazonia or farther south. For these analyses, the very rare occurrence of a species just outside the periphery if its primary distribution as defined above (one or two collections compared with abundant collections elsewhere) did not warrant classifying it into a broader distribution category. Less than 5% of the species in this study had such distributions. Species distributions were determined from Neotropical floras such as *Flora Neotropica* and *Flora Mesoamericana*, online taxonomic data bases from the Missouri Botanical Garden (e.g. TROPICOS) and the New York Botanical Garden, and floristic lists or vegetation studies (see Table 2 for references).

Additionally, comparisons of species in this study were made with the compositions of nearby areas of northern Mesoamerica and the Caribbean, including the neighbouring states of México, the Petén of Guatemala, and Cuba, Jamaica, and Puerto Rico. For this study, we separated the Yucatán biotic province into two areas: the northern peninsula (Quintana Roo, Yucatán and Campeche) and the Petén of Guatemala. Comparisons of the forests in those areas and the forests of this study were made without statistical analysis due to differences in sampling methodology and differences in species density of each area. Nevertheless, such coarse comparisons allowed for examination of the relative floristic affinities of the topographic positions in the BNR with other areas of the region. Weaknesses of such comparisons included incomplete sampling of the forests of the Neotropics and splitting of poorly known taxa that should otherwise be lumped as one species of a broader range. Therefore, these comparisons may have been imprecise, but we believe that our conclusions about relative affinities were fairly robust.

Three statistical approaches were used to evaluate topographic effects on the phytogeography of species. First, regression analysis was employed to determine if relationships existed between the phytogeography of species and elevation above the valley floors, using the three broadly defined categories of distribution. Secondly, comparisons among topographic positions with respect to proportions of species by broad distribution category were performed using multivariate analysis of variance (MANOVA). Thirdly, the effects of geographical and elevational distances on compositional dissimilarities between sample plots (SPs) were evaluated using the Mantel test (McCune & Mefford, 1999; McCune & Grace, 2002).

Cluster analysis was used to classify SPs into groups based on the presence or absence, or relative abundance, of species present. The resulting dendrograms provided a visual means of assessing similarity among SPs, groups of SPs, and whether or not groupings of SPs were consistent with topography. Agglomerative cluster analysis of SPs (Ludwig & Reynolds, 1988) was employed (Podani, 1998). Two classes of distance measures among SPs were used in the analysis: the complement of Jaccard's index (J) (Jaccard, 1902) and chord Euclidean distance (CHD). The complement to Jaccard's index ($1-J$) is an expression of dissimilarity between individual SPs based on species presence/absence, and CHD is an expression of dissimilarity between SPs based on the proportional abundances of species. For the analyses, the abundance of trees was expressed as stem density.

Tree richness and diversity within the SPs were evaluated using Fisher's diversity index α (Fisher *et al.*, 1943) and species–individuals curves. Fisher's index was employed as a measure of tree species diversity that accounted for the number of individuals sampled, based on a log-series distribution of the species abundances. Fisher's α for each SP was calculated through an iterative procedure, using a program written by M. Rejmánek. This index varies less than species richness with sample size and has been increasingly used as an index of diversity in tropical forests (see Magurran, 1988; Condit *et al.*, 1998; Leigh, 1999 for discussions of the advantages of this index). Species–individuals curves allowed for the comparison of richness on a per-individual basis at different samples of individuals. Species–individuals curves were generated by resampling with PAST (Hammer *et al.*, 2001). The curves were cross-checked for consistency with cumulative species–individuals curves.

As an exploratory procedure, statistical comparisons of the topographic positions were conducted with respect to numbers of stems and Fisher's α. Analysis of variance (ANOVA) with site as a blocking factor was performed on numbers of stems and diversity indices, and *post-hoc* comparisons of means were performed with Bonferroni corrections to *P*-values. All proportions were angular-transformed, and numbers of stems were log-transformed to meet the assumptions of normality and homogeneity. Analyses of variance were executed with the SPSS 9.0 statistical software (SPSS, 1999).

RESULTS

Physical structure/size structure

The forests were evergreen on the valleys and lower slopes, semi-evergreen (25–50% deciduous trees) on the upper slopes, and semi-deciduous (50–75% deciduous trees) on the ridge (S. Brewer, pers. obs.). The slope forests had inclinations of 30–37%, and shallow soils (< 0.5 m), with occasional, exposed limestone rocks and boulders. The ridges had shallow soils and the most variable inclinations of the topographic positions, from 3% to 30%. The valley forests had inclinations of < 5% and deep soils (> 1 m).

Stem density increased significantly with elevation above the valleys ($R^2 = 0.76$, $P = 0.002$, d.f. = 9; quadratic function) (Table 1). For example, the average number of stems ≥ 5 cm on ridges was 70% greater than the number of stems on the upper slopes. Ridges had significantly more stems than the lower slope and valley positions and significantly more trees ≥ 10 cm d.b.h. than all other positions ($P < 0.05$, Table 1). Although not quantified by this study, the density and frequency of lianas were noticeably greater in the valley forests than in the slope and ridge forests. There are > 60 species of lianas in the forests on valley floors, while smaller numbers seem to be present on slopes and ridges forests (M. Rejmánek, unpubl. data). The proportions of trees < 10 cm d.b.h. were significantly negatively correlated with increase in elevation above the valley floors ($R^2 = 0.62$, $P = 0.002$, d.f. = 10; linear function) (see also Fig. 2, Table 1). The proportions of trees 10–20 cm d.b.h. were significantly positively correlated with increase in elevation above the valleys ($R^2 = 0.71$, $P = 0.001$, d.f. = 10; linear function). However, the proportions of stems ≥ 20 cm diameter (a rough estimate of canopy trees) were not significantly associated with elevation above the valleys ($R^2 = 0.10$, $P = 0.6$, d.f. = 10) and were not significantly different among the topographic positions ($F_{2,4} = 0.9$, $P = 0.8$). Differences among the topographic positions were most pronounced for trees in the smallest two size classes (Fig. 2). The slopes and valleys had similar distributions of medium-sized to large trees (≥ 50 cm d.b.h.) (Fig. 2), but < 1% of the ridge trees were ≥ 50 cm d.b.h.

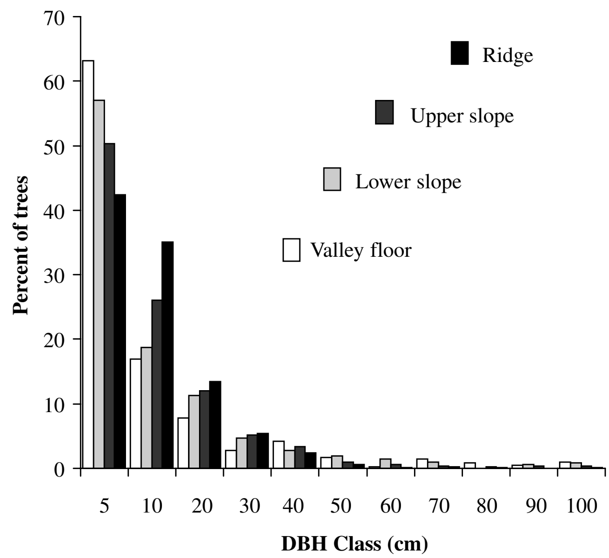


Figure 2 Distributions of stem diameters at the four topographic positions by diameter at breast height (d.b.h.) class (lower limit shown).

Table 1 Mean (SD) species richness, number of stems (*N*)*, and Fisher's diversity index α* for each of four topographic positions on limestone at two minimum sampling diameters, representing all trees (stems ≥ 5 cm) and excluding understory trees (stems ≥ 10 cm)

	Valley floor	Lower slope	Upper slope	Ridge
Species ≥ 5 cm	32.7 (2.1)	40.3 (4.0)	43.3 (6.1)	42.0 (2.6)
Species ≥ 10 cm	22.7 (0.6)	28.7 (3.8)	30.7 (4.5)	33.7 (0.6)
N ≥ 5 cm	112.3[a] (20.3)	110.7[a] (16.0)	136.3[a,b] (28.1)	236.0[b] (58.2)
N ≥ 10 cm	41.3[a] (6.8)	47.7[a,b] (9.3)	65.3[b] (7.6)	134.3[c] (21.0)
Fisher's α (stems ≥ 5 cm)	15.6[a] (1.1)	22.9[b] (1.4)	22.0[b] (2.0)	15.1[a] (1.1)
Fisher's α (stems ≥ 10 cm)	21.5[a,b] (4.0)	30.8[b] (2.0)	22.9[a,b] (5.2)	14.6[a] (1.7)

*Means in rows sharing the same superscript letter were not significantly different ($P > 0.05$, Bonferroni).

Phytogeography of the tree species

The ridges and valley floors were clearly distinct with respect to composition and phytogeography, while the slopes were transitional in these features. The highest percentages of species unique to a topographic position were found at the extremes of elevation: in the ridges and valleys, 61% and 39% of their species were unique to those positions, respectively, in contrast to 19% and 14% for the upper and lower slopes, respectively (Table 2). Slightly more than half (55.5%) of all species were found at only one of the four topographic positions (see also Table 2). Of these species, 49% were found on ridges, followed by valleys (26%), upper slopes (15%), and lower slopes (11%). Forty-one per cent of all species were found in only one of the 12 SPs.

Table 2 and Fig. 3 show how the Neotropical distributions of the sampled species varied with elevation above the valley floors. The proportions of species having northern distributions increased significantly with elevation above the valleys ($R^2 = 0.94$, $P < 0.001$) (Fig. 3a). No significant relationship between proportion of species of Mesoamerican distribution and elevation was detected ($R^2 = 0.026$, $P = 0.89$) (Fig. 3b). The proportions of sample species that have widespread distributions decreased significantly, however, with increasing elevation above the valley floors ($R^2 = 0.78$, $P = 0.001$) (Fig. 3c). Differences among the topographic positions in proportions of widespread ($F_{3,8} = 11.1$, $P < 0.01$) and northern species ($F_{3,8} = 54.9$, $P < 0.01$) were statistically significant. Ridges had more northern species than all topographic positions (all $P \le 0.02$), but fewer widespread species than all positions except upper slopes (all $P < 0.03$).

In general, all of the forests sampled were similar in their strong affinities for the Petén of Guatemala, sharing 89% of their species with that area. The forests also had strong affinities for neighbouring Mexican forests, although forests at greater elevations above the valleys had greater proportions of species that were also found on the Yucatán Peninsula (Table 2). Ridges, for example, had 68% of their species with distributions into the Yucatán Peninsula, compared with just 39% for the floors of valleys. Otherwise, no clear relationship between topography and proportion of species shared with the neighbouring Mexican areas was observed.

The proportion of species having distributions that reach the Greater Antilles was significantly, but weakly, positively correlated with increasing elevation above the valleys ($R^2 = 0.34$, $P = 0.049$; linear function, not shown) (Table 2). However, of the 10 most abundant species on the

Table 2 Summary of the phytogeographical affinities of the identified tree species within each of four topographic positions ($n = 3$ sample plots/position), at three scales of distribution. Percentage of species and percentage of stems (in parentheses) are provided. Unique species is the percentage of species in a position that were censused only in that position. Regional distributions (Greater Antilles and selected northern Mesoamerican) are not mutually exclusive, and therefore do not add to 100%. Neotropical distributions are mutually exclusive. The 'all positions' category represents all species censused at all topographic positions

	Valley	Lower slope	Upper slope	Ridge	All positions
Local					
Unique species	66 (39.4)	73 (14.3)	75 (19.0)	74 (61.3)	171 (55.5)
Regional					
Greater Antilles	21.2 (9.3)	23.3 (11.3)	25.3 (17.2)	33.8 (51.4)	29.8 (28.6)
Cuba*	10.6	13.5	19.2	23.0	20.5
Puerto Rico†	9.1	10.8	14.1	20.3	18.6
Jamaica‡	26.1	34.8	14.1	17.6	14.3
Mexico					
Yucatán§	39.4	48.6	51.3	67.6	55.9
Tabasco¶	43.9	45.9	47.4	41.9	46.6
Chiapas**	72.7	67.6	74.4	60.8	71.4
Guatemala					
Petén††	84.8	89.2	84.6	81.1	88.8
Neotropical					
Northern Mesoamerica	19.7 (54.3)	30.1 (44.2)	33.3 (47.4)	50.7 (69.3)	33.9 (56.7)
Mesoamerica	25.8 (15.5)	28.8 (29.6)	32.0 (27.5)	24.7 (14.7)	26.3 (20.6)
Widespread	54.5 (30.2)	41.1 (26.2)	34.7 (25.1)	24.7 (15.9)	39.8 (22.7)

*Borhidi (1996).
†Acevedo-Rodríguez & Axelrod (1999), Kartesz & Meacham (1999).
‡Kelly *et al.* (1988).
§Including Campeche, Yucatán and Quintana Roo: Sousa-Sánchez & Cabrera-Cano (1983), Tellez-Valdes & Cabrera-Cano (1987), Martínez-Salas *et al.* (2001).
¶Cowan (1983).
**Breedlove (1986).
††Standley *et al.* (1946–77), TROPICOS.

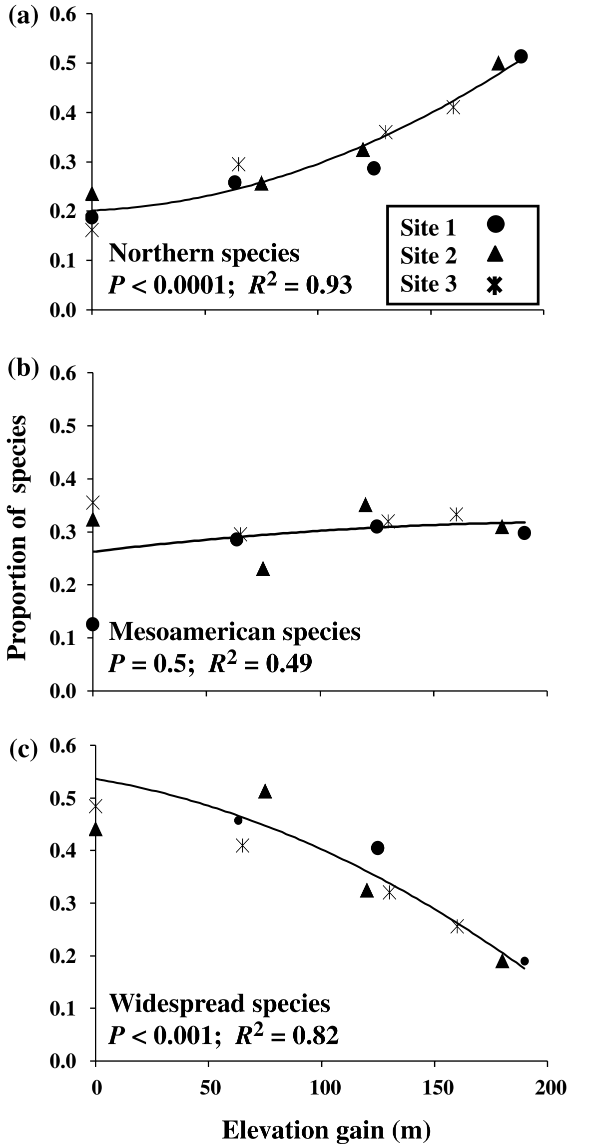


Figure 3 Regressions of proportions of species of three Neotropical distributions with elevations above the floors of valleys (statistics but not proportions of angular-transformed data shown). Distributions are (a) restricted to northern Mesoamerica, (b) of Mesoamerican distribution, or (c) widespread in the Neotropics (see text for explanation of distribution categories).

ridges, seven species (representing 40% of the stems) are commonly found in the Greater Antilles, including *Acacia scleroxyla*, a new species for Belize that is common in Hispaniola but appears to be quite rare in mainland Mesoamerica. In fact, half of the stems on ridges (51%) belong to species with distributions reaching the Greater Antilles, compared with just 9% of stems on the floors of the valleys. Of the widespread species, 42% are found in the Greater Antilles, but this proportion falls to 22% for northern Mesoamerican species.

Topographic effects on familial and species composition

There was no effect of geographical distance between SPs on their composition (Table 3). The effect of differences in absolute elevation was marginally significant. The effect of differences in relative elevations (above the valley floor at each location), however, was highly significant (Table 3). The compositional uniqueness of the ridge and valley forests was revealed by the agglomerative clustering of the SPs (Fig. 4a). Ridges and valleys consistently formed unique groups, regardless of the minimum tree diameter used (only results for trees ≥ 5 cm diameter shown). The upper and lower slopes, however, separated by site rather than by topographic position, when the analysis was based on species presence/absence (Fig. 4a). When species presence was weighted by abundance, topographic positions formed discrete groupings (Fig. 4b,c); such groupings followed topography more closely when understory trees (< 10 cm d.b.h.) were excluded (Fig. 4c). Groupings based on species abundance (via CHD) were more consistent with those based on species presence/absence (via $1-J$), when N rather than basal area was used as a measure of abundance (results for basal area not shown). Groupings formed by using trees ≥ 5 cm or ≥ 10 cm d.b.h. were very similar; however the groupings of slope SPs using the 5 cm d.b.h. minimum diameter conformed more closely to site than did groupings based on larger d.b.h. (results for trees ≥ 10 cm d.b.h. not shown).

A total of 181 species from 48 families were recorded from the SPs (1.2 ha total). The most speciose families on the ridges and upper slopes were the Rubiaceae, Sapotaceae and Fabaceae. The most speciose families on the lower slopes and valleys included the Moraceae, Sapotaceae, Rubiaceae and Arecaceae (Appendix 2). In abundance (N) of trees ≥ 5 cm diameter, the valleys and slopes were dominated by the Arecaceae, due to the high abundance of *Astrocaryum mexicanum*.

Three species, *Oxandra belizensis*, *Pseudolmedia spuria* and *Cryosophila stauracantha* were encountered on all topographic positions; these species were also well-represented among SPs (eight of 12). *Astrocaryum mexicanum* was the most abundant ($n = 331$) and frequent (nine SPs) species in this study, although it was absent from ridges. The ridges commonly shared only three of their 10 most abundant species with another position; *Pouteria reticulata*, *Protium copal* and *Nectandra coriacea* were shared with the upper slopes. The upper and lower slopes shared four species in their 10 most abundant: *Rinorea hummelii*, an understory tree, and the canopy trees *Oxandra belizensis*, *Drypetes brownii* and *Sebastiania tuerckheimiana*. Common but unique to valleys were *Protium confusum*, *Zanthoxylum riedelianum* and *Zanthoxylum ekmanii* (see also Appendix 1 for more details on species abundance).

During the course of this study, we collected 13 species not listed for Belize in Balick *et al.* (2000) (see Appendix 1), some of which have disjunct or limited distributions. One individual, collected in sterile condition, vegetatively matched *Chiangiodendron mexicanum* (Flacourtiaceae), a monotypic genus found in Mexico and recently discovered in

Table 3 Mantel correlations (r) of vegetation dissimilarity matrices with matrices of geographical distances and elevational differences (in metres). Only densities of stems ≥ 5 cm are used. Results of asymptotic approximation procedures and randomization tests are shown. Bonferroni levels of significance were set at $\alpha = 0.05/3 = 0.017$*, $0.01/3 = 0.0033$** and $0.001/3 = 0.00033$***

Matrices	r	Asymptotic approximation	Randomization tests
Jaccard dissimilarities			
Geographical distances	−0.08	n.s.	n.s.
Abs. elev. differences†	0.31	n.s.	*
Rel. elev. differences‡	0.77	***	***
Chord Euclidean distances			
Geographical distances	−0.09	n.s.	n.s.
Abs. elev. differences†	0.27	n.s.	n.s.
Rel. elev. differences‡	0.64	***	**
Euclidean distances			
Geographical distances	−0.12	n.s.	n.s.
Abs. elev. differences	0.24	n.s.	n.s.
Rel. elev. differences†	0.63	***	*

†Absolute elevation change.
‡Elevation changes (from the valley floor) at each location.

Costa Rica (T. Wendt, pers. comm.). *Acacia scleroxyla* (Fabaceae), previously known only from a few collections in Honduras but abundant in Hispaniola (D. Seigler, pers. comm.), was abundant on the ridges of two sites. *Ottoschulzia pallida* (Icacinaceae) and *Prunus lundelliana* (Rosaceae) were common only to limestone ridge tops in the study area and have been considered restricted to the Petén and southern Mexico. *Mortoniella pittieri* (Apocynaceae), listed in Balick *et al.* (2000), was common in the valley forest of site 1 (Brewer & Webb, 2002) but was known prior to 1997 only from small adjacent areas of Nicaragua and Costa Rica.

When evaluating only palms in the SPs, the ridges were characterized by a low number of species (three) and by the presence and high abundance of the clonal palm *Chamaedorea schippii*. The slopes were characterized by the presence of *Chamaedorea ernesti-augustii* (observed as uncommon but not sampled in the valleys) and by a relatively high abundance of *Cryosophila stauracantha*, and *Sabal mauritiiformis* (observed but not sampled in the valleys). The valley forests typically had relatively high abundance of *Attalea cohune*, *Bactris mexicana*, *Chamaedorea pinnatifrons*, *Chamaedorea tepejilote*, and *Geonoma interrupta*, the first two species being more abundant closer to major streams. *Astrocaryum mexicanum* was the most ubiquitous and abundant palm over all topographic positions and sites excluding the ridges, where it was absent. Other ubiquitous species were *Chamaedorea pinnatifrons*, *Cryosophila stauracantha*, *Bactris mexicana*, and *Desmoncus orthacanthos*. Site 3 in the upper watershed was unusual in its very high abundance of *Calyptrogyne ghiesbreghtiana*, which formed continuous cover < 1 m high in the valley forests and was abundant on the slopes. Site 3 was also unique because of the valley species *Synechanthus fibrosus*, a species not observed in the valleys of the other two sites.

Species richness and diversity

Species richness of trees increased significantly with increasing elevation above the valley until the ridge position, where richness declined slightly (Table 1; trees ≥ 5 and ≥ 10 cm, respectively: $R^2 = 0.63$, $P = 0.01$ and $R^2 = 0.72$, $P = 0.003$; quadratic functions). Using different minimum sampling diameters changed the order of richness among the topographic positions, however, with mean richness being slightly higher for upper slopes than ridges for trees ≥ 5 cm d.b.h. and lower than ridges for trees ≥ 10 cm d.b.h. (Table 1). Slopes were significantly more diverse than the ridges and valleys, respectively. The lower slopes were the most diverse position, with the valleys and ridges being significantly lower in diversity (all $P < 0.05$). Thus, Fisher's index could be explained by a quadratic function of diversity with elevation above the valleys ($R^2 = 0.86$, $P < 0.001$ for trees ≥ 5 cm d.b.h.), regardless of minimum diameter sampled. Species–individual curves showed that slopes have greater richness at all samples of individuals and have greater rates of accumulation of species with individuals sampled (Fig. 5). Ridges had greater initial rates of accumulation of species with individuals sampled than valleys; however, valleys surpassed ridges in richness in samples of 60 or more individuals.

DISCUSSION

Physical structure/size structure

Topography affects the physical structure of the forests over limestone in the BNR, despite small changes in elevation between topographic positions (< 250 m at the most). With increasing elevation above the valleys, trees 10–20 cm d.b.h. appear to take up the space that would otherwise be occupied by large trees on ridges, and by smaller, understory trees on slopes and ridges, probably due to the low number of individuals of *Astrocaryum mexicanum* at these positions. The stature of the forests becomes shorter from the valleys to the ridges, with fewer numbers of large trees, most likely because of increased edaphic drought enhanced by greater drainage and thinner soils at higher elevations (Furley & Newey, 1979), less access to groundwater, and greater exposure to desiccating winds in the dry season. The ridges may be more exposed to hurricanes, further reducing the

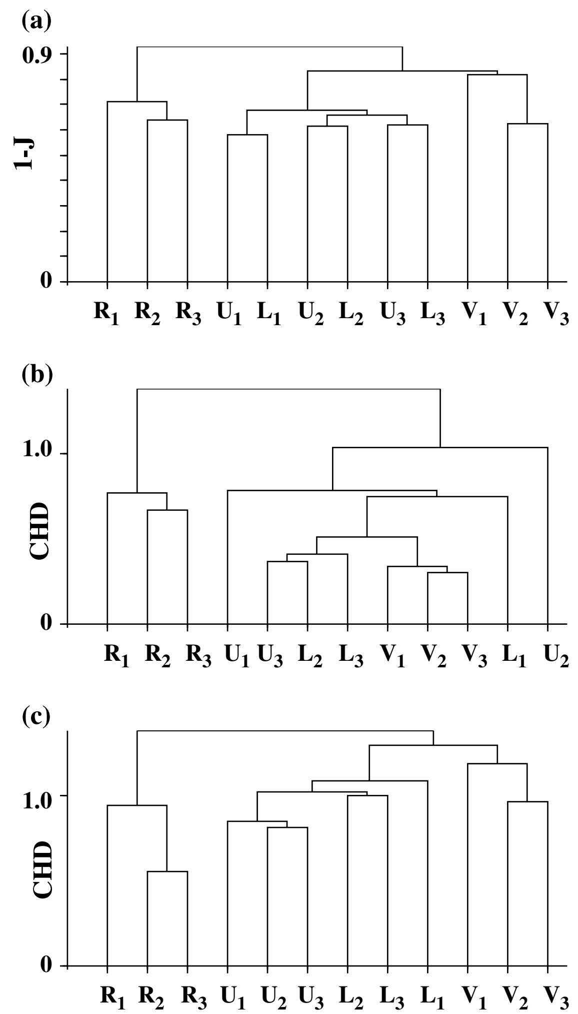


Figure 4 Agglomerative clustering of the sample plots (SPs) at four topographical positions (R, ridge; L, lower slope; U, upper slope; V, valley floor) within three sites (indicated by subscripts). The complement to Jaccard's index (1–*J*) is an expression of dissimilarity between individual SPs based on species presence/absence. Chord Euclidean distance (CHD) is an expression of distance between SPs based on the proportional abundances of species. Dendrograms are based on (a) trees ≥ 5 cm d.b.h., (b) trees ≥ 5 cm d.b.h. and (c) trees ≥ 10 cm d.b.h.

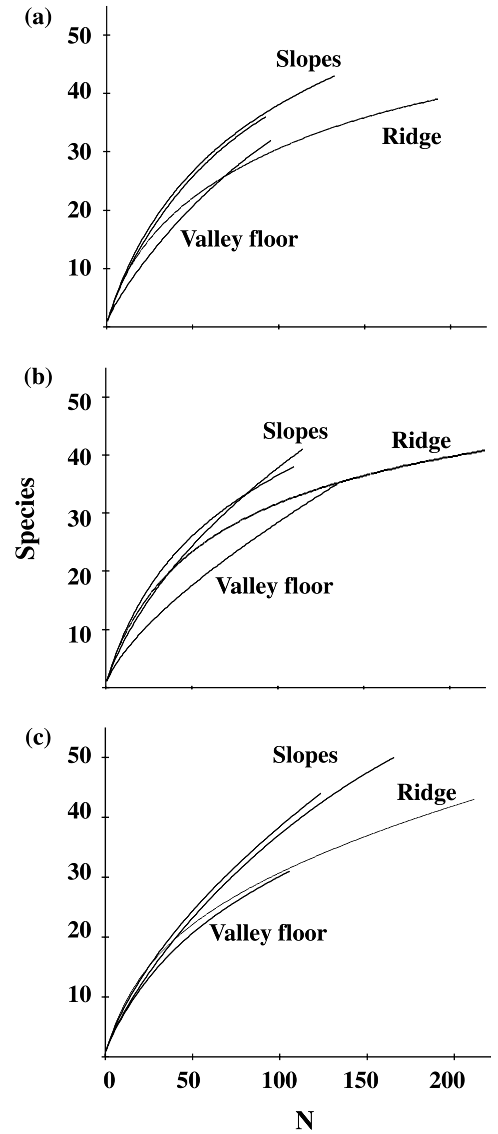


Figure 5 Species–individuals curves for four topographic positions (upper and lower slopes not differentiated with labels) within three sites (a, b, c correspond to sites 1, 2 and 3, respectively).

possibility of development of a tall forest (Bellingham, 1991; Brokaw & Grear, 1991; Everham & Brokaw, 1996), but our observations after Hurricane Iris in 2001 are more consistent with other studies that show greater resistance of ridge forest to hurricane damage (Scatena & Lugo, 1995).

Phytogeography of the tree species

Apparently driven by an interaction between topography and limestone geology, large-scale phytogeographical patterns are manifested at very local scales in the Bladen watershed. The limestone forests on the valleys and ridges are composed of tree species that have more restricted local distributions than those in the slope forests (Table 2). The relatively high local fidelity of the valley and ridge species reflects the unique species compositions of these positions compared with the slopes, which are transitional in their compositions. Species from northern Mesoamerica dominate the ridges, and Neotropically widespread species dominate the valleys, whether or not the measure is in stems or numbers of species represented (Table 2). Such phenomena are known in European literature as demonstrations of 'the Alechin's law of precedence' (pravilo predvareniia; Alekhin, 1950) or 'the Walter's law of the relative constancy of habitat' (das Gesetzmässigkeit der relativen Standortkonstanz; Walter, 1979).

The widespread Neotropical distributions of the tree species of the valleys may be due to a relatively mesic environment that is more conducive to colonization by vagile, generalist taxa that are better adapted to mesic conditions in the lowlands of South America. A large proportion of the lowland tree taxa in Amazonia are generalists with wide geographical ranges (Pitman *et al.*, 1999), and Gentry (1982) pointed out the preponderance of unusually wide-ranging taxa of South American origin in the lowland forests of Mesoamerica. The alluvial soils of the BNR are deeper and more prone to disturbance in the form of flooding, erosion and deposition than the well-drained slopes; therefore they are conducive to colonization by vagile taxa. Limestone, however, produces unique, well-drained soils and microtopography (Furley & Newey, 1979; Richards, 1996). Furthermore, karst landforms are common in northern Mesoamerica but are rare in southern Mesoamerica and South America (Sweeting, 1972; Snead, 1980). Local tree species, adapted to the drier edaphic and microclimatic conditions on limestone outcrops, should therefore be expected to have better recruitment and be better competitors in those environments than colonists from South America. Thus, compared with the other topographic positions, the ridges have a tree flora that is the most restricted in distribution when examined at small and large scales (Tables 1 and 2).

The ridges share a considerable proportion of their species with the Greater Antilles (34%), although this element is not as strong as the northern Mesoamerican element. Moreover, the floristic representation of the Greater Antilles in numbers of stems is much greater than would be expected from species alone (Table 2). Such an affinity might be expected given the dominance of outcrop limestone in the Greater Antilles and the associated drought-prone soils. The floristic comparisons of this study are made on a coarse level, however, and neighbouring forests of Mexico grow on both limestone and igneous substrata. Therefore, future studies of exposed limestone forests in the neighbouring parts of Mesoamerica may reveal similar floristic links to the Greater Antilles. Floristic links among limestone areas in this region may be driven more by water availability and substrate, via levels of edaphic drought, than by proximity (Estrada-Loera, 1991; Trejo-Torres & Ackerman, 2002).

Species richness and diversity

The high species richness of ridges can be explained simply by the fact that we sampled more stems at this position. High stem densities on ridges are associated with a low proportion of very small (< 10 cm d.b.h.) and large trees (> 50 cm d.b.h.). Higher species diversity on the slopes (as Fisher's α, Table 1) than valleys and ridges, however, is likely the result of the generation and/or maintenance of greater recruitment on slopes. A 'mass effect' (Shmida & Wilson, 1985) from nearby sources of species may be maintaining populations of species that might otherwise go locally extinct due to low and unstable population sizes. In addition, an intermediate physical position between two unique floras would cause the slopes to receive a higher diversity of seed inputs than the valleys and ridges; the greater overlap observed in the compositions of slopes with neighbouring positions may support this hypothesis.

Upon arrival, these propagules and resulting seedlings may have a greater probability of survival on slopes. The forests of valley floors appear to experience more intense seed predation by terrestrial mammals, especially small rodents (Brewer & Rejmánek, 1999), than occurs on the slopes (S. Brewer & M. Rejmánek, unpubl. data). Hallé *et al.* (1978) suggest that the discontinuous nature of the canopy on slopes, and the angled incidence of light, results in more light penetration through the canopy therefore promoting the survival of smaller, shade intolerant tree species. Small sample sizes in this study preclude a rigorous test of Hallé *et al.*'s (1978) hypothesis. On Barro Colorado Island, Panama, greater soil moisture on the slopes than the adjacent forests is believed to be a cause of higher tree diversity in those forests (Leigh, 1996). The soils on upper limestone slopes in Belize, however, produce stronger edaphic drought compared with valley soils (Wright *et al.*, 1959; Furley & Newey, 1979). The slopes occupy a broader moisture gradient and may have more microtopographic variation than the valleys and ridges, thus providing a greater variety of microhabitats for species with more restricted requirements for recruitment and/or more limited competitive ability.

Finally, greater age of forests on slopes, like some sites in Bolivia (Smith & Killeen, 1998), allows for greater net immigration of species over time. Valley forests were cleared and cultivated until *c.* 1000 yr BP (Abramiuk, 1999), a short time for long-lived trees (Chambers *et al.*, 1998), whereas the nearby slopes would be too steep and their soils too shallow for agriculture. Furthermore, the valley floor soils are likely subject to more frequent and stronger disturbance via changes in nearby watercourses and periodic, massive floods. Hurricanes may also have a greater impact on valleys than slopes, due to the shallow rooting of trees in valleys (Scatena & Lugo, 1995).

Conservation implications

Although limestone valley forests on alluvium in the BNR have neither unique floristics nor diversity when examined at the Neotropical scale – indeed, their composition is dominated by widespread Neotropical species – intact forests of this kind are rare in the region because of their valuable soils for agriculture and easy access for timber and wildlife extraction. On the other topographic extreme, ridge forests have the lowest diversity index, but they contain the most unusual floristic assemblage and have significant affinities for limestone forests in the Caribbean. Ridges also occupy a small proportion of the land area in the region and may serve as important sources of propagules for the recolonization of similar, restricted forests that have been disturbed by fire or hurricanes. Future vegetation studies should examine the phytogeography as well as diversity of the forests in the region, and should attempt to identify those variables, such as finer-scale topography and substrate type, that may be useful in the identification of forest types that require protection. One of the potential consequences of these findings for the conservation of biodiversity in northern Mesoamerica is that phytogeographical considerations in weighting the uniqueness of floristic composition – in addition to measures of diversity – must be considered in the delineation, prioritization, and management of potential protected areas. Thus, biodiversity surveys in this region may benefit from surrogate variables, such as topography, for phytogeographical elements of vegetation.

Although Belize is one of the least populated countries in the Neotropics, the recent construction of a paved highway through southern Belize will certainly lead to growth in human populations that will extract many kinds of resources from the forests of the Maya Mountains. Limestone areas are particularly valuable sources of minerals and rich agricultural land, and for this reason have become increasingly vulnerable to human activity (e.g. Day, 1993). Future decisions about the delimitation and management of protected areas in this region will require a better understanding of the patterns and composition of the biodiversity of limestone forests.

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BIOSKETCHES

Steven W. Brewer is interested in testing hypotheses about landscape patterns of tree diversity and phytogeography, examining the dynamics of seed predation and dispersal in plant recruitment, and the conservation of plant communities.

Marcel Rejmánek conducts research on predicting and quantifying the risk of invasions by plants, plant community classification and dynamics, and the ecology of seed dispersal and regeneration of tropical forests.

Molly A. H. Webb is an Assistant Professor of research at Oregon State University, where she studies the reproductive physiology and endocrinology of sturgeon.

Paul V. A. Fine is finishing his dissertation on habitat specialization of Amazonian trees. He is especially interested in the effects herbivores may have on the origin and maintenance of patterns of high beta-diversity across different soil types.

Appendix 1 Abundance (number of stems) of taxa recorded in the transects on limestone by transect (subscript) within four topographic positions

Taxon	Valley floor						Lower slope						Upper slope						Ridge					
	BA_1	N_1	BA_2	N_2	BA_3	N_3	BA_1	N_1	BA_2	N_2	BA_3	N_3	BA_1	N_1	BA_2	N_2	BA_3	N_3	BA_1	N_1	BA_2	N_2	BA_3	N_3
Actinidiaceae																								
Saurauia yasicae Loes.	0	0	0	0	0	0	0	0	0.002	1	0.008	1	0	0	0	0	0.006	1	0	0	0	0	0	0
Anacardiaceae																								
Astronium graveolens Jacq.	0	0	0	0	0	0	0.442	1	0	0	0	0	0	0	0	0	0	0	0.082	2	0	0	0	0
Comocladia guatemalensis Donn. Sm.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.210	3
Metopium brownei (Jacq.) Urb.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.074	5	1.820	12	0.570	8
Spondias mombin L.	0.177	3	0	0	0.509	3	0	0	0.297	1	0.012	1	0	0	0	0	0	0	0	0	0	0	0	0
Annonaceae																								
Annona primigenia Standl. & Steyerm.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.017	1	0	0	0	0
Annona scleroderma Saff.	0	0	0	0	0	0	0	0	0	0	0.048	1	0	0	0	0	0.046	1	0	0	0	0	0	0
Cymbopetalum mayanum Lundell	0.061	1	0.038	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mosannona depressa (Baill.) Chatrou	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.004	1	0	0
Oxandra belizensis (Lundell) Lundell*	0	0	0.164	1	0	0	0.073	4	0.041	1	0.261	7	0.081	11	0.014	3	0.017	3	0.047	2	0	0	0	0
Stenanona stenopetala (Donn. Sm.) G.E. Schatz	0	0	0	0	0	0	0	0	0	0	0.004	1	0	0	0	0	0.003	1	0	0	0	0	0	0
Apocynaceae																								
Aspidosperma megalocarpon Müll. Arg.	0	0	0.693	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aspidosperma spruceanum Benth. ex Müll. Arg.	0	0	0	0	0	0	0.884	2	0.004	1	0.011	1	0.129	6	0.047	1	0.038	2	0	0	0	0	0.002	1
Mortoniella pittieri Woodson	0.166	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plumeria obtusa L.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.011	1	0	0
Stemmadenia donnell-smithii (Rose) Woodson	0.191	2	0.012	1	0.065	1	0	0	0.014	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Araliaceae																								
Dendropanax arboreus (L.) Decne. & Planch.	0	0	0	0	0	0	0.016	1	0.029	3	0.264	1	0	0	0.021	2	0.184	2	0	0	0	0	0	0
Arecaceae																								
Astrocaryum mexicanum Liebm.	0.108	44	0.128	65	0.081	41	0.026	17	0.065	33	0.063	32	0.010	20	0.016	8	0.118	60	0	0	0	0	0	0
Attalea cohune Mart.	0.212	2	0.178	1	0	0	0	0	0	0	0.156	1	0	0	0	0	0	0	0	0	0	0	0	0
Cryosophila stauracantha (Heynh.) R. Evans	0	0	0.035	2	0	0	0	0	0.035	2	0.035	2	0.106	6	0.088	5	0.124	7	0	0	0.012	5	0.008	2
Sabal mauritiiformis (H. Wendl. ex H. Karst.) Griseb. & H. Wendl.	0	0	0	0	0	0	0.031	1	0	0	0.085	2	0.147	3	0	0	0.074	2	0	0	0	0	0	0
Bignoniaceae																								
Tabebuia ochracea (Cham.) Standl.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.010	1
Bombacaceae																								
Ceiba pentandra (L.) Gaertn.	0	0	3.142	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudobombax ellipticoideum A. Robyns	0	0	0	0	0	0	0.242	1	0	0	0	0	0.002	1	0	0	0	0	0.356	6	0	0	0.229	1
Quararibea funebris (La Llave) Vischer	0	0	0	0	0.018	1	0.191	14	0	0	0.169	6	0.055	2	0	0	0.097	5	0	0	0	0	0	0
Burseraceae																								
Bursera simaruba (L.) Sarg.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.212	8	0.087	6	0.202	4
Protium copal (Schltdl. & Cham.) Engl.	0	0	0	0	0	0	0.060	2	0.010	2	0	0	0.061	3	0.005	1	0.008	2	0.368	15	0.264	11	0.098	5
Protium confusum (Rose) Pittier	0.156	9	0.074	6	0.051	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capparaceae																								
Capparis discolor Donn. Sm.*	0	0	0.009	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caricaceae																								
Jacaratia dolichaula (Donn. Sm.) Woodson	0	0	0.003	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Celastraceae																								
Crossopetalum parviflorum (Hemsl.) Lundell	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.004	1	0	0	0	0	0	0	0	0

Maytenus schippii Lundell	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.532	13	0	0	0	0
Wimmeria bartlettii Lundell	0	0	0	0	0	0	0	0	0	0	0.021	1	0.520	2	0.026	2	0.008	1	0	0	0.035	4	0.047	1
Celtidaceae																								
Celtis schippii Standl.	0.003	1	0	0	0.116	2	0	0	0.008	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chrysobalanaceae																								
Hirtella racemosa Lam.	0	0	0	0	0	0	0	0	0	0	0	0	0.007	1	0	0	0	0	0.030	1	0	0	0	0
Hirtella triandra Sw.	0.005	1	0	0	0	0	0	0	0.003	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clusiaceae																								
Calophyllum brasiliense Cambess.	0	0	0	0	0	0	0.184	1	0	0	0.003	1	0	0	0	0	0	0	0	0	0	0	0	0
Clusia massoniana Lundell	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.032	2	0.179	6
Clusia rosea Jacq.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.158	4	0	0
Garcinia intermedia (Pittier) Hammel	0	0	0.040	1	0.013	1	0.063	2	0.014	1	0	0	0.023	3	0	0	0.038	2	0	0	0	0	0	0
Combretaceae																								
Bucida buceras L.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.109	1	1.793	3	0	0
Terminalia amazonia (J. Gmel.) Exell	0.067	1	0	0	2.149	3	0	0	0.013	1	0.118	1	0	0	0.116	1	2.178	2	0	0	0	0	0	0
Terminalia oblonga (Ruiz & Pav.) Steud.	0	0	0	0	0	0	0	0	0	0	0.015	1	0	0	0	0	0	0	0	0	0	0	0	0
Ebenaceae																								
Diospyros digyna Jacq.	0.008	1	0	0	0	0	0.006	1	0	0	0	0	0.012	2	0	0	0	0	0	0	0	0	0	0
Diospyros salicifolia Humb. & Bonpl. ex Willd.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.044	2	0.138	5	0.014	1
Euphorbiaceae																								
Alchornea latifolia Sw.	0	0	0	0	0.349	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Croton arboreus Millsp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.005	2	0.014	2	0	0
Drypetes brownii Standl.	0.011	2	0	0	0	0	0.442	3	0.496	5	0.130	2	0.577	6	0.013	2	0.322	4	0	0	0	0	0	0
Drypetes lateriflora (Sw.) Krug & Urb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.046	3	0	0
Gymnanthes lucida Sw.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.091	10	0.100	10	0.057	3
Sebastiania tuerckheimiana (Pax & K. Hoffm.) Lundell	0	0	0	0	0	0	0.035	3	0.060	3	0.284	5	0.062	1	0.422	9	0.391	5	0	0	0	0	0.051	2
Fabaceae																								
Acacia cookii Saff.	0	0	0	0	0	0	0	0	0	0	0.011	1	0.072	3	0	0	0.008	1	0.017	1	0	0	0	0
Acacia cornigera (L.) Willd.	0	0	0	0	0	0	0.015	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acacia scleroxyla Tussac	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.703	9	1.578	11
Bauhinia divaricata L.	0	0	0	0	0	0	0	0	0	0	0	0	0.269	1	0	0	0	0	0	0	0	0	0.067	1
Caesalpinia aff. *violacea* (Mill.) Standl.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.044	1	0	0	0	0
Cojoba arborea (L.) Britton & Rose	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.593	1	0	0	0	0	0	0
Cynometra retusa Britton & Rose	0	0	0	0	0	0	0	0	0	0	0.047	2	0	0	0	0	0.008	2	0	0	0	0	0	0
Dialium guianense (Aubl.) Sandwith	0	0	0.703	2	0.515	3	0.426	2	0	0	0.289	2	0.005	1	0.338	2	0	0	0	0	0	0	0	0
Erythrina sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.008	1	0	0	0	0
Inga sapindoides Willd.	0	0	0	0	0.007	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lonchocarpus heptaphyllus (Poir.) DC.	0.231	3	0	0	0	0	0	0	0	0	0	0	0.025	1	0	0	0	0	0	0	0	0	0	0
Lysiloma latisiliquum (L.) Benth.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.034	2	0	0	0	0
Platymiscium dimorphandrum Donn. Sm.	0	0	0	0	0.043	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pterocarpus rohrii Vahl	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.091	2	0.179	3	0	0	0	0
Schizolobium parahyba (Vell.) S.F. Blake	0.442	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Swartzia cubensis (Britton & P. Wilson) Standl.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.047	1	0	0	0.162	1	0	0	0	0
Swartzia simplex var. *ochnacea* (DC.) R.S. Cowan	0.005	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zygia confusa L. Rico	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.004	1

Appendix 1 *continued*

Taxon	Valley floor BA₁						Lower slope						Upper slope						Ridge					
	BA_1	N_1	BA_2	N_2	BA_3	N_3	BA_1	N_1	BA_2	N_2	BA_3	N_3	BA_1	N_1	BA_2	N_2	BA_3	N_3	BA_1	N_1	BA_2	N_2	BA_3	N_3
Flacourtaceae																								
Casearia bartlettii Lundell	0	0	0	0	0	0	0	0	0.003	1	0.037	1	0	0	0.003	1	0.006	1	0	0	0	0	0	0
Casearia tremula (Griseb.) Griseb. ex C. Wright	0	0	0	0	0	0	0	0	0.004	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
aff. *Chiangiodendron mexicanum* T. Wendt*	0	0	0	0	0	0	0.003	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laetia thamnia L.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.027	3	0	0	0.004	1	0.117	25	0.060	11
Lunania mexicana Brandegee	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.010	1	0	0
Pleuranthodendron lindenii (Turcz.) Sleumer	0	0	0.181	1	0.072	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Icacinaceae																								
Ottoschulzia pallida Lundell*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.002	1	0	0	0.441	23	0.611	32	0.392	14
Lauraceae																								
Cinnamomum aff. *triplinerve* (Ruiz & Pav.) Kosterm.	0.009	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Licaria areolata Lundell*	0	0	0	0	0	0	0	0	0.013	1	0	0	0	0	0.091	2	0	0	0	0	0	0	0	0
Licaria peckii (I.M. Johnst.) Kosterm.	0.006	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nectandra coriacea (Sw.) Griseb.	0	0	0	0	0	0	0	0	0.003	1	0	0	0.028	2	0.038	1	0.006	1	0.012	1	0.064	8	0.096	9
Nectandra lundellii C. K. Allen	0	0	0	0	0.157	3	0.012	1	0.012	1	0	0	0	0	0	0	0.021	1	0	0	0	0	0	0
Ocotea cernua (Nees) Mez	0.024	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
aff. *Ocotea veraguensis* (Meisn.) Mez*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.010	1
Malpighiaceae																								
Bunchosia nitida (Jacq.) DC.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.003	1	0	0	0	0	0	0
Bunchosia polystachia (Andrews) DC.	0	0	0	0	0.017	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bunchosia swartziana Griseb.	0	0	0	0	0	0	0.017	1	0	0	0	0	0	0	0.002	1	0	0	0	0	0	0	0	0
Malpighia souzae Miranda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.026	6	0	0
Malpighiaceae	0	0	0	0	0	0	0	0	0.028	1	0	0	0	0	0	0	0	0	0	0	0	0	0.002	1
Melastomataceae																								
Miconia fulvostellata L.O. Williams	0	0	0	0	0	0	0	0	0	0	0.021	1	0	0	0	0	0	0	0	0	0	0	0	0
Miconia impetiolaris (Sw.) D. Don ex DC.	0	0	0	0	0.005	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mouriri exilis Gleason	0	0	0.003	1	0.004	1	0	0	0	0	0.007	1	0	0	0	0	0	0	0	0	0	0	0	0
Meliaceae																								
Guarea glabra Vahl	0.010	1	0.166	5	0.040	4	0.022	2	0.024	2	0.006	1	0.006	2	0	0	0	0	0	0	0	0	0	0
Guarea grandifolia DC.	0	0	0.096	3	0.025	1	0	0	0.018	2	0.115	1	0	0	0.029	1	0	0	0	0	0	0	0	0
Swietenia macrophylla King	0	0	0	0	0	0	0	0	0	0	0.004	1	0.067	1	0	0	0	0	0	0	0	0	0	0
Trichilia erythrocarpa Lundell	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.004	2
Trichilia martiana C. DC.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.008	1	0	0	0	0	0	0
Trichilia minutiflora Standl.	0	0	0	0	0	0	0	0	0	0	0	0	0.035	3	0	0	0	0	0.085	6	0	0	0.004	1
Trichilia moschata Sw.	0	0	0.004	1	0	0	0.171	2	0.028	1	0.259	2	0.080	1	0	0	0	0	0	0	0	0	0	0
Trichilia pallida Sw.	0	0	0	0	0	0	0	0	0	0	0	0	0.003	1	0	0	0	0	0	0	0	0	0	0
Menispermaceae																								
Hyperbaena mexicana Miers	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.019	2	0	0
Moraceae																								
Brosimum alicastrum Sw.	1.131	1	1.090	3	0	0	0.055	1	0.555	2	2.013	5	0.017	1	0.674	4	0.819	2	0	0	0	0	0	0
Castilla elastica Sessé ex Cerv.	0.164	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coussapoa oligocephala Donn. Sm	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.121	3	0	0	0	0
Ficus colubrinae Standl.	0	0	0	0	0	0	0	0	0	0	0.031	1	0	0	0	0	0	0	0	0	0	0	0.053	1

Ficus guajavoides Lundell	0	0	0.004	1	0.006	2	0.028	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ficus insipida Willd.	0.004	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Poulsenia armata (Miq.) Standl.	0	0	0.778	14	0.286	5	0	0	0.416	5	0.449	3	0	0	0	0	0	0	0	0	0	0	0	0
Pourouma bicolor Mart.	0	0	0	0	0.059	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudolmedia spuria (Sw.) Griseb.	0.011	1	0	0	0	0	0.008	2	0.018	3	0.005	1	0.166	10	0.210	9	0.251	9	0	0	0.004	2	0	0
Trophis mexicana (Liebm.) Bureau	0	0	0.007	1	0	0	0.042	2	0	0	0	0	0.023	1	0.004	1	0	0	0	0	0	0	0	0
Trophis racemosa (L.) Urb.	0.009	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myristicaceae																								
Compsoneura mexicana (Hemsl.) Janovec	0	0	0.004	1	0	0	0	0	0	0	0	0	0	0	0	0	0.005	1	0	0	0	0	0	0
Virola koschnyi Warb.	0	0	0	0	0.088	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myrsinaceae																								
Ardisia compressa Kunth	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.003	1
Myrtaceae																								
Eugenia aeruginea DC.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.316	29	0.069	12	0.183	32
Eugenia trikii Lundell	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.038	8	0	0	0.125	8
Nyctaginaceae																								
Neea fagifolia Heimerl*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.008	1	0	0
Neea psychotrioides Donn. Sm.	0	0	0	0	0	0	0	0	0	0	0	0	0.073	2	0	0	0.017	1	0.014	2	0.005	2	0.107	2
Ochnaceae																								
Ouratea insulae L. Riley	0	0	0	0	0	0	0.003	1	0	0	0	0	0	0	0	0	0	0	0	0	0.002	1	0	0
Olacaceae																								
Heisteria media S.F. Blake	0	0	0.006	1	0.010	1	0.020	4	0.181	9	0.173	4	0.081	3	0.035	4	0.073	2	0	0	0	0	0	0
Oleaceae																								
Chionanthus oblanceolatus (B.L. Rob.) P.S. Green	0	0	0	0	0	0	0	0	0.018	3	0.005	1	0.017	2	0.014	3	0.005	2	0	0	0	0	0	0
Chionanthus panamensis (Standl.) Stearn	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.047	3	0.024	1
Piperaceae																								
Piper schippianum Trel. & Standl.	0	0	0	0	0	0	0	0	0.002	1	0	0	0.002	1	0	0	0.002	1	0	0	0	0	0	0
Polygonaceae																								
Coccoloba acapulcensis Standl.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.051	1	0	0
Coccoloba diversifolia Jacq.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.306	14	1.174	45	0.653	23
Coccoloba tuerckheimii Donn. Sm.	0	0	0	0	0.004	1	0	0	0	0	0.817	1	0	0	0	0	0	0	0	0	0	0	0	0
Rhamnaceae																								
cf. *Colubrina* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.089	5	0.192	10
Rosaceae																								
Prunus lundelliana Standl.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.012	1	0	0	0.072	3	0.212	8	0	0
Rubiaceae																								
Alseis yucatanensis Standl.	0.088	1	0	0	0	0	0.123	4	0.131	6	0.005	1	0.059	1	0.106	4	0.127	2	0	0	0	0	0	0
Chione venosa (Sw.) Urb.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.017	1
Exostema mexicanum A. Gray	0	0	0	0	0	0	0	0	0.004	1	0	0	0.010	1	0	0	0	0	0.004	1	0	0	0	0
Faramea occidentalis (L.) A. Rich.	0	0	0	0	0	0	0	0	0.003	1	0.008	1	0	0	0.002	1	0	0	0	0	0	0	0	0
Glossostipula concinna (Standl.) Lorence*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.263	3	0.701	12	0	0
Guettarda combsii Urb.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.002	1	0.126	3
Guettarda elliptica Sw.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.035	6	0	0
Guettarda macrosperma Donn. Sm.	0	0	0.036	1	0.004	1	0.002	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Posoqueria latifolia (Rudge) Roem. & Schult.	0	0	0	0	0	0	0	0	0	0	0	0	0.027	1	0	0	0	0	0	0	0	0	0	0
Psychotria chiapensis Standl.	0.006	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.006	1	0	0	0	0	0	0

Appendix 1 *continued*

Taxon	Valley floor						Lower slope						Upper slope						Ridge					
	BA_1	N_1	BA_2	N_2	BA_3	N_3	BA_1	N_1	BA_2	N_2	BA_3	N_3	BA_1	N_1	BA_2	N_2	BA_3	N_3	BA_1	N_1	BA_2	N_2	BA_3	N_3
Psychotria pubescens Sw.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.006	1	0	0	0	0	0	0	0	0
Psychotria simiarum Standl.	0	0	0.010	1	0.049	7	0	0	0	0	0.035	5	0	0	0	0	0.007	2	0	0	0	0	0	0
Randia aculeata L.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.005	2	0	0
Randia armata (Sw.) DC.	0	0	0.005	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Randia genipifolia (Standl. & Steyerm.) Lorence	0	0	0.003	1	0	0	0	0	0	0	0.003	1	0	0	0	0	0.006	2	0	0	0	0	0	0
Rondeletia belizensis Standl.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.199	9	0.337	7
Stenostomum lucidum (Sw.) C.F. Gaertn.	0	0	0	0	0	0	0.060	4	0	0	0	0	0.147	4	0.299	4	0.282	2	0.003	1	0	0	0	0
Rutaceae																								
Amyris elemifera L.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.011	1	0	0	0	0	0	0
Zanthoxylum acuminatum ssp. *juniperinum* (Poepp.) Reynel	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.057	2	0.065	3	0.027	1
Zanthoxylum ekmanii (Urb.) Alain	0.270	1	0.337	1	0.215	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zanthoxylum riedelianum Engl.	0.020	2	0.016	1	0.025	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sapindaceae																								
Allophylus camptostachys Radlk.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.003	1
Allophylus psilospermus L.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.003	1
Cupania belizensis Standl.	0	0	0	0	0	0	0	0	0	0	0	0	0.028	2	0	0	0.005	1	0	0	0	0	0	0
Exothea paniculata (Juss.) Radlk.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.088	8	0.077	2
Matayba apetala Radlk.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.022	1	0	0	0	0	0	0
Sapindaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.005	2	0	0	0	0
Sapindus saponaria L.	0	0	0	0	0	0	0	0	0.050	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sapotaceae																								
Chrysophyllum venezuelanense (Pierre) T.D. Penn.	0	0	0	0	0	0	0	0	0	0	0.294	1	0	0	0	0	0.232	1	0	0	0	0	0	0
Manilkara chicle (Pittier) Gilly	0.046	3	0	0	0	0	0	0	0.007	2	0	0	0	0	0	0	0	0	0.054	4	0	0	0	0
Manilkara staminodella Gilly	0	0	0	0	0	0	0	0	0	0	0	0	1.435	4	0.104	3	0	0	0.066	1	0.003	1	0.189	5
Manilkara zapota (L.) P. Royen	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.011	1	0	0	0	0	0	0
Pouteria amygdalina (Standl.) Baehni	0	0	0	0	0	0	0.032	2	0	0	0	0	0.247	3	0.009	3	0.005	1	0.025	3	0	0	0.015	2
Pouteria campechiana (Kunth) Baehni	0	0	0.002	1	0	0	0	0	0.021	1	0	0	0.032	3	0	0	0	0	0	0	0	0	0	0
Pouteria durlandii Standl. (Baehni)	0.014	2	0.035	1	0	0	0	0	0.056	1	0	0	0.103	1	0.125	5	0.002	1	0	0	0	0	0	0
Pouteria izabalensis (Standl.) Baehni	0	0	0.342	8	0.145	1	0	0	0	0	0	0	0	0	0	0	0.009	1	0	0	0	0	0	0
Pouteria reticulata (Engl.) Eyma	0	0	0	0	0	0	0.074	2	0.010	1	0	0	0.219	5	0.320	13	0.006	2	0.112	7	0.231	19	0.375	19
Sideroxylon floribundum ssp. *belizense* (Lundell) T.D. Penn.	0	0	0	0	0	0	0	0	0	0	0.011	1	0	0	0	0	0	0	0.140	2	0.130	5	0	0
Sterculiaceae																								
Guazuma ulmifolia Lam.	0	0	0	0	0	0	0	0	0.126	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Theophrastaceae																								
Deherainia smaragdina (Planch. ex Linden) Decne.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.003	1	0	0	0	0	0	0
Jacquinia longifolia Standl.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.028	1	0	0
Tiliaceae																								
Heliocarpus americanus L.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.045	1	0	0	0.011	2	0	0
Mortoniodendron vestitum Lundell*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.016	1	0	0	0	0	0	0	0	0

Trichospermum grewiifolium (A. Rich.) Kosterm.	0.181	1	0	0	0	0	0.116	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ulmaceae																								
Ampelocera hottlei (Standl.) Standl.	0.004	1	0.048	1	0	0	0.004	1	0	0	0.103	2	0.339	5	0.095	1	0	0	0	0	0	0	0	0
Urticaceae																								
Verbenaceae																								
Vitex gaumeri Greenm.	0	0	0	0	0	0	0	0	0	0	1.327	1	0	0	0	0	0	0	0	0	0	0	0	0
Violaceae																								
Rinorea hummelii Sprague	0	0	0.003	1	0.005	1	0.011	3	0.032	8	0.069	15	0	0	0.008	3	0.066	15	0	0	0	0	0	0
Indet.																								
Indet. 1	0	0	0	0	0	0	0.045	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Indet. 2	0	0	0	0	0	0	0	0	0.137	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Indet. 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.129	1	0	0
Indet. 4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.116	1
Indet. 5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.023	1

BA, basal area (m^2); *N*, number of stems. *Not previously published (in Balick *et al.*, 2000) for Belize.

Appendix 2 The top 25 families on the topographic positions as ranked by number of species

Valley			Lower slope			Upper slope			Ridge		
Family	*S*	*N*	Family	*S*	*N*	Family	*S*	*N*	Family	*S*	*N*
Moraceae	9	33	Rubiaceae	7	25	Rubiaceae	9	26	Fabaceae	9	31
Rubiaceae	6	14	Sapotaceae	7	11	Sapindaceae	8	47	Rubiaceae	8	46
Fabaceae	6	12	Moraceae	6	24	Fabaceae	8	15	Sapotaceae	5	68
Sapotaceae	4	16	Arecaceae	4	90	Meliaceae	7	10	Euphorbiaceae	4	32
Lauraceae	4	7	Meliaceae	4	14	Arecaceae	3	111	Sapindaceae	4	14
Arecaceae	3	166	Fabaceae	4	8	Moraceae	3	37	Anacardiaceae	3	30
Meliaceae	3	15	Annonaceae	3	14	Annonaceae	3	19	Moraceae	3	6
Apocynaceae	3	7	Flacourtiaceae	3	4	Lauraceae	3	7	Anacardiaceae	3	4
Rutaceae	2	8	Lauraceae	3	4	Euphorbiaceae	2	27	Myrtaceae	2	89
Myristicaceae	2	6	Bombacaceae	2	21	Olacaceae	2	16	Polygonaceae	2	83
Euphorbiaceae	2	5	Euphorbiaceae	2	21	Bombacaceae	2	8	Burseraceae	2	49
Melastomataceae	2	4	Apocynaceae	2	5	Celastraceae	2	5	Flacourtiaceae	2	38
Annonaceae	2	3	Clusiaceae	2	5	Flacourtiaceae	2	5	Lauraceae	2	19
Bombacaceae	2	2	Anacardiaceae	2	3	Sapindaceae	2	4	Celastraceae	2	18
Burseraceae	1	20	Combretaceae	2	3	Malpighiaceae	2	2	Clusiaceae	2	12
Anacardiaceae	1	6	Malpighiaceae	2	2	Tiliaceae	2	2	Meliaceae	2	9
Combretaceae	1	4	Melastomataceae	2	2	Violaceae	1	18	Malpighiaceae	2	7
Celtidaceae	1	3	Violaceae	1	26	Apocynaceae	1	9	Nyctaginaceae	2	7
Clusiaceae	1	2	Olacaceae	1	21	Burseraceae	1	6	Apocynaceae	2	2
Flacourtiaceae	1	2	Araliaceae	1	5	Ulmaceae	1	6	Icacinaceae	1	69
Olacaceae	1	2	Burseraceae	1	4	Clusiaceae	1	5	Rhamnaceae	1	15
Ulmaceae	1	2	Oleaceae	1	4	Araliaceae	1	4	Rosaceae	1	11
Violaceae	1	2	Ulmaceae	1	3	Combretaceae	1	3	Ebenaceae	1	8
Capparidaceae	1	1	Actinidiaceae	1	2	Nyctaginaceae	1	3	Arecaceae	1	7
Caricaceae	1	1	Celastraceae	1	1	Ebenaceae	1	2	Bombacaceae	1	7
Total	66	348		75	332		78	408		77	704

S, number of species; *N*, number of stems ≥ 5 cm d.b.h.