

TOPOGRAPHY-RELATED VARIATION IN A NEOTROPICAL RAIN FOREST COMMUNITY ATTRIBUTES: INSIGHTS FROM A NEW 1-HA PLOT AT LOS TUXTLAS, MEXICO

IVÁN LEONARDO EK-RODRÍGUEZ¹, JORGE A. MEAVE², ROSAMOND COATES³,
 SANTIAGO SINACA-COLÍN³ AND GUILLERMO IBARRA-MANRÍQUEZ^{1*}

¹ Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Michoacán, Mexico.

² Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Coyoacán, Ciudad de México, Mexico.

³ Estación de Biología Tropical Los Tuxtlas, Universidad Nacional Autónoma de México, San Andrés Tuxtla, Veracruz, Mexico.

*Author for correspondence: gibarra@ies.unam.mx

Abstract

Background: The role of topography in the spatial variation of tropical rainforest (TRF) community attributes remains insufficiently understood. We analyze community attributes in a newly-established 1-ha plot located in the ‘Strongly dissected slopes’ land unit in a Neotropical TRF and compare them with those assessed in an older 1-ha plot located in the ‘Piedmont’ land unit.

Questions: What is the magnitude of topography-related spatial variation of TRF community attributes across a single locality? Does this variation influence the comparison of this TRF with similar forests worldwide?

Study Site and Years: Los Tuxtlas Tropical Biology Station (Veracruz, southern Mexico); 2018-2019.

Methods: We assessed community attributes (composition, structure, diversity) in the new plot by censusing all woody plants with DBH ≥ 1 cm.

Results: We recorded 4,375 individuals (basal area, 43.35 m²), 188 species, and 58 families. Fifteen families, including Arecaceae, Moraceae, and Meliaceae, accounted for a large proportion of species (57 %), individuals (86 %), and basal area (79 %). Most recorded plants (90 %) had DBH ≤ 10 cm. The evenness factor indicated high dominance in the community. The plots differed primarily in species and family composition, individual density, and vertical structure.

Conclusions: The community attributes of the TRF analyzed in plots located in different land units showed low variation. When compared with other TRFs worldwide, the Los Tuxtlas forest stands out for its low individual density and diversity but its higher basal area. Including the study site’s complex topography in this analysis did not significantly affect previous interregional comparisons.

Keywords: Community composition, forest structure, effective number of species, land units, relief.

Resumen

Antecedentes: El efecto de la topografía sobre la variación de los atributos comunitarios del bosque tropical húmedo (BTH) no se conoce adecuadamente. En 1 ha localizada sobre la unidad de terreno ‘laderas fuertemente disectadas’, se describen los atributos del BTH y se comparan con los evaluados previamente en una parcela de tamaño similar ubicada en un ‘Piedemonte’.

Preguntas: ¿Cuánto varían los atributos comunitarios del BTH entre ambas parcelas? ¿Esta variación afecta la comparación de este BTH con otros bosques del mundo?

Sitio y años de estudio: Estación de Biología Tropical Los Tuxtlas (Veracruz, México); 2018-2019.

Métodos: Cuantificamos los atributos comunitarios en la parcela nueva (composición, estructura y diversidad) mediante un censo de las plantas leñosas con DAP ≥ 1 cm

Resultados: Se registraron 4,375 individuos (área basal de 43,35 m²), 188 especies y 58 familias. Quince familias, incluidas Arecaceae, Moraceae y Meliaceae, representan una gran proporción de especies (57 %), individuos (86 %) y del área basal (79 %). El 90 % de las plantas tuvieron diámetros ≤ 10 cm. El factor de equitatividad indicó una alta dominancia. Las parcelas difirieron principalmente en su composición (especies y familias), densidad de individuos y estructura vertical.

Conclusiones: Los atributos comunitarios variaron poco entre parcelas. La comparación del BTH estudiado con bosques similares en el mundo mostró que el BTH de Los Tuxtlas presenta valores bajos de densidad de individuos y diversidad, pero altos de área basal. La incorporación de la topografía del sitio al análisis no modificó sustancialmente las comparaciones interregionales previas.

Palabras clave: Composición, estructura del bosque, número efectivo de especies, unidades terrestres, relieve.

This is an open access article distributed under the terms of the Creative Commons Attribution License CCBY-NC (4.0) international.

<https://creativecommons.org/licenses/by-nc/4.0/>



Identifying the factors responsible for the spatial variation of tropical rainforest community attributes remains a major challenge in vegetation science (Ch ave 2008, Zimmerman *et al.* 2008, Beech *et al.* 2017). Tropical rainforests (TRFs), which harbor the largest plant diversity among all terrestrial ecosystems, are distributed across the Earth's intertropical zone, in regions with low elevations ($< 1,000$ m), high annual precipitation ($> 1,500$ mm), and high temperatures ($20\text{--}25^\circ\text{C}$) (Whitmore 2008). Despite these environmental generalities, TRFs display substantial variation in community composition, structure, and diversity (Losos 2004, Ch ave 2008, Corlett & Primack 2011). By using plots of varying sizes (0.1–52 ha) worldwide (*e.g.*, Gentry 1982, 1988, Losos & Leigh 2004, Pitman *et al.* 2008), researchers have identified spatial patterns in TRF community attribute variation and revealed abiotic factors (soil properties, topography, and climate) as key drivers of this heterogeneity (John *et al.* 2007, Baldeck *et al.* 2013, Brown *et al.* 2013). Yet, a full understanding of the causes of spatial variation in TRF community attributes within regions and localities remains lacking.

Natural protected areas worldwide in the tropics are excellent scenarios for ecological TRF studies, as they offer invaluable yet often untapped opportunities to assess spatial variation in community attributes. For example, despite a long tradition of scientific research at the Los Tuxtlas Tropical Biology Station (LTBS), southern Mexico (Gonz alez Soriano *et al.* 1997, Reynoso *et al.* 2017), few studies have quantitatively characterized TRF community attributes at this site, with most of them being based in small sampling plots (< 1 ha) and relatively large size cutoffs (minimum diameter at breast height -DBH- from 2.5 to 10 cm) as criteria to include plants in vegetation surveys. Such a dearth of studies is worrisome, especially given the environmental heterogeneity observed in this biological reserve (Navarrete-Segueda *et al.* 2021, Miranda-Gallegos *et al.* 2023, Ek-Rodr guez *et al.* 2024), which can lead to substantial spatial variation in community attributes.

There are two important exceptions to the prevailing trend to use small plots for vegetation surveying at the LTBS. The first study was led by Frans Bongers and Jean Popma in the last decades of the 20th century (Bongers *et al.* 1988, Popma *et al.* 1988a), who examined the composition, structure, and diversity of woody and palm species ($\text{DBH} \geq 1$ cm) in one 1-ha plot and compared these attributes with reports from numerous TRF locations worldwide. Despite the important contribution of this early work to quantitative knowledge of the Los Tuxtlas TRF, this pioneer study has two important limitations. The first concerns incomplete species identification (a reflection of the limited botanical knowledge at that time), which hampers precise cross-site comparisons of floristic composition within the reserve. The second limitation is more important, as the study plot was established in a relatively flat area, a condition atypical of the terrain that mainly characterizes this biological reserve. According to the geopedological landscape stratification proposed by Navarrete-Segueda *et al.* (2021), the plot is located in the “Piedmont” land unit. More recently, Ek-Rodr guez *et al.* (2022) established another 1-ha plot to quantify liana community attributes; this new plot is relatively close to the older one but features a more complex topography. This new plot represents the “Strongly dissected slopes” land unit described by Navarrete-Segueda *et al.* (2021). For this study, we provide a detailed description of the TRF in this new plot, as this new information offers a good opportunity to examine the role of topography in the spatial variation of community attributes at this locality.

Topography has been recognized as the ultimate driver of TRF community attributes variation at both local (*e.g.*, Harms *et al.* 2001, Valencia *et al.* 2004, Gunatilleke *et al.* 2006, Baldeck *et al.* 2013, Guo *et al.* 2017, Rodrigues *et al.* 2019) and regional scales (*e.g.*, Clark & Clark 2000, Pitman *et al.* 2008, Bohlman *et al.* 2008, Brown *et al.* 2013, Jucker *et al.* 2018). Particularly for the LTBS, its location in a volcanic region has been proposed as the factor responsible for its high environmental heterogeneity (Mart n del Pozzo 1997). Earlier observations of physiognomic and compositional variation of vegetation among hilltops, lower topographic positions with mild slopes, and rocky sites with very shallow soils suggest that topography and related soil features are major drivers of such variation (Ibarra-Manr quez *et al.* 1997). Recent studies have examined the extent to which such environmental differences are reflected in TRF community attributes for big trees ($\text{DBH} \geq 10$ cm; Navarrete-Segueda *et al.* 2021), palms (Miranda-Gallegos *et al.* 2023), and lianas (Ek-Rodr guez *et al.* 2024), but information on the cross-land unit variability of the floristic composition, structure, and diversity of this forest is lacking. Such incomplete characterization of the TRF vegetation in the LTBS and its spatial variation call for new efforts to improve comparison of this forest with other TRFs worldwide.

To advance our understanding of the topography-related spatial variation in the TRF of the LTBS, we undertook this study with two main goals: (1) to provide a detailed characterization of TRF community attributes (floristic composition, structure, and diversity) in a recently established 1-ha plot located in a land unit characterized by a complex topography, and (2) to compare these attributes with those assessed through an older survey conducted in a same-sized plot located in a land unit with smoother topography. Taking advantage of this enhanced information, we re-examined the comparison of the Los Tuxtlas TRF community with similar forests worldwide. We hypothesized that topographic heterogeneity, as reflected in contrasting land units, is a major driver of variation in TRF community attributes, and thus expected substantial differences in composition, structure, and diversity between the two 1-ha plots located in different land units despite their close proximity.

Materials and methods

Study area. The Universidad Nacional Autónoma de México (UNAM) is the owner institution of the LTBS, a protected area and scientific research station located on the eastern slope of the San Martín Tuxtla Volcano, Veracruz State, southern Mexico (Figure 1A). The area of the LTBS (692 ha) encompasses an elevational range from ca. 150 to 650 m. The climate is Af(h), that is, hot and humid, according to the Köppen-Geiger climate classification (Kottek *et al.* 2006). Total annual precipitation is on average 3,433 mm, and the mean annual temperature is 24.2 °C. There is a period of relatively low precipitation in April and May, and another one of relatively low temperatures and winter rains (locally known as *nortes*) from November to February (Figure 1B). Overall, land formation in the Los Tuxtlas region has been dominated by fluvial processes and volcanic activity, with the lithology mainly consisting of Tertiary and Quaternary basaltic and igneous rocks. Accordingly, the predominant soils in the LTBS are derived from volcanic ashes with high nutrient and organic matter contents, along with shallow soils associated with recent basaltic lava flows (Nelson & Gonzalez-Caver 1992, Martín-del Pozzo 1997).

Unlike the situation regarding the regional floristic knowledge that prevailed for most of the 20th century, several tools now facilitate faster and more reliable identification of the more than 900 plant species in the reserve (*e.g.*, Cornejo-Tenorio *et al.* 2019, Ibarra-Manríquez *et al.* 2025). Thus, we were able to determine species identity for every single plant censused in the 1-ha plot. Ibarra-Manríquez *et al.* (1997) distinguished three variants in TRF physiognomy related to substrate and elevation: (1) TRF on deep soils, (2) TRF on young, shallow soils with high stoniness, and (3) TRF on high hilltops, such as El Vigía Hill (Figure 1C). They report two noteworthy features of the TRF in the LTBS: a high abundance of understory palms, lianas, and epiphytes, and upper-canopy trees with maximum heights of 30–40 m, with buttresses often measuring ≥ 0.5 m in height. Regarding leaf phenology, the forest is largely evergreen (Bongers *et al.* 1988, Ibarra-Manríquez *et al.* 1997), with only a few tree species shedding their foliage for a variable time between November and May.

Vegetation survey. The new 1-ha permanent plot was established on the eastern slope of the El Vigía Hill (hereafter referred to as the El Vigía or EVH plot; Figure 1C), ca. 0.5 km away from the older 1-ha plot established by the team lead by Frans Bongers and Jean Popma, hereafter referred to as the Lyell (LYE) plot (Bongers *et al.* 1988, Popma *et al.* 1988a), named after the Lyell trail that runs next to it. Mean elevation (± 1 SD) at the EVH plot is 131.1 ± 22.7 ($N = 188$), with a within-plot elevational drop of ca. 70 m and slopes ranging between 20° and 40° (Figure 1D).

To facilitate the vegetation survey, we subdivided the new 1-ha plot into 100 10 × 10-m quadrats (Figure 1E). We recorded and tagged all trees, shrubs, lianas, and palms with a stem diameter at breast height (1.3 m; DBH) ≥ 1 cm; multi-stemmed individuals were included if at least one stem met the inclusion criterion, *i.e.*, we adopted the by-tree inclusion method of de Souza *et al.* (2021). Epiphytic shrubs and trees, as well as hemi-epiphytic woody lianas, were excluded from the survey (*e.g.*, *Clusia flava* Jacq., Clusiaceae; *Coussapoa purpusii* Standl., Urticaceae; *Juanulloa mexicana* (Schltdl.) Miers, Solanaceae). In the case of strangler trees (*e.g.*, *Ficus* spp.), only individuals with true trunks rooted in the ground were included.

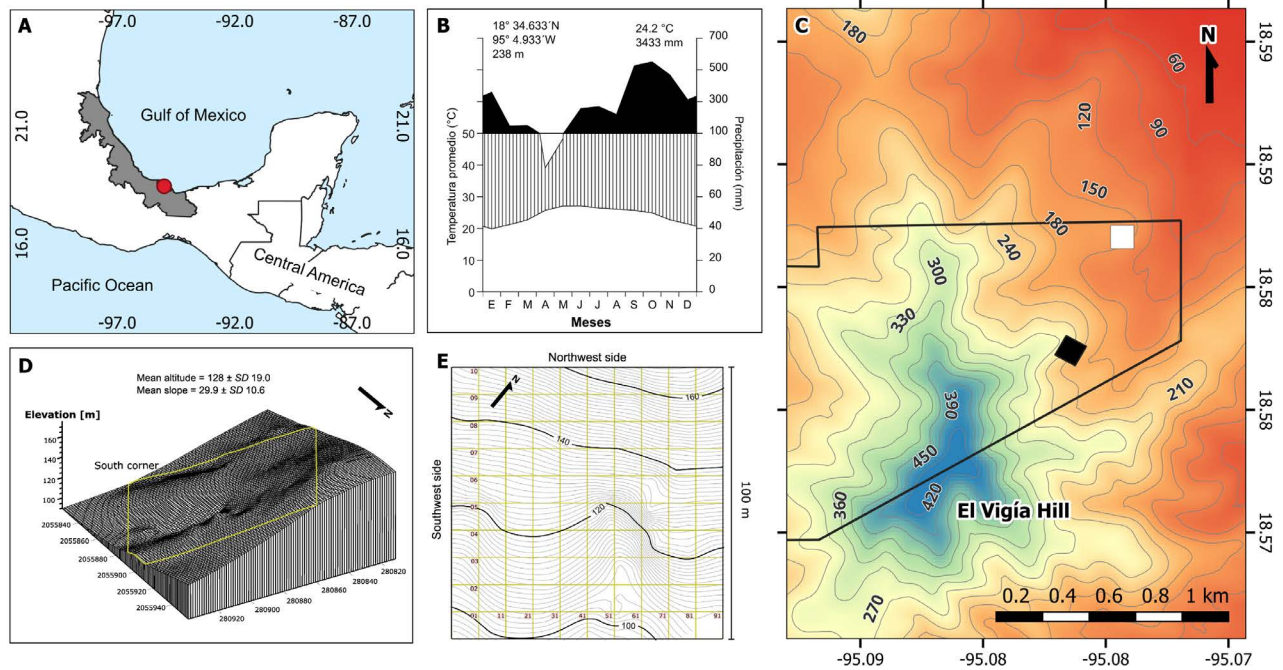


Figure 1. A. Location of the study site in the Los Tuxtlas Region (red circle), Veracruz State, Mexico. B. Ombrothermic diagram for the study site. C. Location of the study El Vigía Hill plot (black square) in the eastern sector of the Los Tuxtlas Tropical Biology Station. The location of the older (Lyell) plot studied by Bongers *et al.* (1988) and Popma *et al.* (1988a) is also shown (white square). D. Three-dimensional representation of the study plot showing its topographic complexity. E. Diagram plane of the grid (golden lines) in which the study plot was subdivided. Contour lines are also shown.

We measured the stem DBH of all plants with a diameter tape, except lianas, whose diameters were measured at the base of the rooting point (Burnham 2004). Trunk diameters of individuals having buttresses or irregular trunks were measured above these irregularities. Total height was measured for most individuals (excluding lianas) with a flexometer; the tallest individuals' heights were visually estimated by one of the authors (SSC).

Data analysis. Family classification followed APG (2016). To assess the relative contributions of families to community structure, we calculated a Family Importance Value (FIV) index for each family by summing its relative basal area, density, and species richness values (Mori *et al.* 1983). An Importance Value Index (IVI) was also calculated for each species as the sum of its relative basal area, density, and frequency values (Mueller-Dombois & Ellenberg 1974).

Plot-level diversity was quantified with the Hill numbers framework, by calculating the effective number of species (true diversity) of orders 0, 1, and 2, as follows (Jost 2006):

$${}^qD = (\sum p_i^q)^{1/(1-q)}$$

where, p_i = the proportion of individuals of the i_{th} species, qD = diversity of the order q . Increasing values of the q exponent represent greater weights given to species abundances in calculating the effective number of species. In the formula shown above, when $q = 1$ an undefined division emerges ($1/1-1$, i.e., $1/0$); thus, 1D is commonly approximated as the exponential of Shannon's entropy (H'). When $q = 0$ (0D or order 0 diversity), species abundances do not influence the diversity value (i.e., it represents species richness). As q increases, the influence of species abundances on diversity values becomes greater; if q tends to 1, species are weighted by their abundance, without giving disproportionate importance to rare or abundant species (this number is roughly indicative of common species); when $q = 2$ (2D or order 2 diversity), the species with the highest abundance, i.e., the dominant ones, have the largest influence on the diversity value. To further assess community dominance, we calculated the evenness factor (EF) as the ${}^2D/{}^0D$

ratio; EF values closer to 1 indicate a more even community, whereas values closer to 0 indicate strong dominance in the community (Jost 2010).

Comparing the floristic composition between the EVH and LYE plots (and other plots used in previous studies in the region) required standardizing taxonomic nomenclature and growth-form classification. This procedure allowed estimation of the number of shared species between the EVH and LYE plots and the calculation of a local overlap measure (qDS), which quantifies the proportion of non-shared species between the two assemblages for a given value of q (Jost *et al.* 2011).

Results

Floristic composition and structural importance of taxa in the EVH plot. In the EVH plot, we recorded 188 species representing 58 families ([Appendix 1](#)). Only 14 families, including Fabaceae (14 species), Bignoniaceae (10), Piperaceae (10), and Rubiaceae (9), accounted for 58.5 % of total species richness. By contrast, exactly one-half of the families (29) were represented by a single species ([Appendix 1](#), [Table 1](#)).

Table 1. Most speciose families in the El Vigía Hill 1-ha plot established on the “Steeply dissected slopes” land unit at the Los Tuxtlas Tropical Biology Station. S, number of species.

Trees/Shrubs/Palms		Lianas		All plants	
Families	S	Families	S	Families	S
Fabaceae	13	Bignoniaceae	9	Fabaceae	14
Piperaceae	10	Celastraceae	5	Bignoniaceae	10
Malvaceae	8	Malpighiaceae	3	Piperaceae	10
Moraceae	8	Menispermaceae	3	Rubiaceae	9
Rubiaceae	8	Vitaceae	3	Arecaceae	8
Arecaceae	7	Apocynaceae	2	Celastraceae	8
Lauraceae	7	Asteraceae	2	Malvaceae	8
Euphorbiaceae	6	Sapindaceae	2	Moraceae	8
Sapotaceae	6	Smilacaceae	2	Lauraceae	7
Annonaceae	5			Asteraceae	6
Meliaceae	5			Euphorbiaceae	6
Myrtaceae	5			Sapotaceae	6
Asteraceae	4			Annonaceae	5
Urticaceae	4			Meliaceae	5
Other 34	50	Other 10	11	Other 44	78
Total	146		42		188

The 15 most important families, *i.e.*, those having the largest FIV, accounted for 86 % of all individuals, 79 % of total basal area, and 57 % of 0D (total species richness; [Table 2](#)). Among these, Arecaceae had the highest FIV based on its extremely high density, whereas Moraceae and Meliaceae, which ranked second and third in FIV, respectively, stood out for their high basal area ([Table 2](#)). Fabaceae (rank 4th in FIV) was the most speciose family but had relatively low density (rank 14th) and basal area (8th). These 15 most important families were represented mainly by trees, except for Bignoniaceae and Celastraceae, which included both trees and lianas and ranked 14th and 15th, respectively, in the family ranking. The five families with the highest densities (Arecaceae, Moraceae, Piperaceae, Rubiaceae, and Urticaceae) comprised nearly 70 % of all individuals recorded in the EVH plot, while the five families with the largest basal area values (Anacardiaceae, Arecaceae, Euphorbiaceae, Meliaceae, and Moraceae) represented 48 % of total basal area.

Table 2. The 15 most important families sorted in decreasing order according to Family Importance Values (FIV) in the El Vigía Hill 1-ha plot at the Los Tuxtlas Tropical Biology Station. The relative contribution of each family to total density, basal area, and species richness is shown, and the highest value for each variable is indicated in bold typeface.

Families	Relative density	Relative basal area	Relative richness	FIV
Arecaceae	43.13	9.02	4.76	56.91
Moraceae	12.21	15.60	4.23	32.04
Meliaceae	2.65	10.37	2.65	15.67
Fabaceae	1.23	4.79	7.41	13.43
Urticaceae	6.90	4.32	2.12	13.34
Malvaceae	2.17	5.98	4.23	12.38
Euphorbiaceae	1.97	6.50	3.17	11.64
Rubiaceae	3.50	2.00	4.76	10.26
Piperaceae	3.70	0.85	5.29	9.84
Sapotaceae	1.26	4.28	3.17	8.71
Anacardiaceae	0.39	6.77	1.06	8.22
Metteniusaceae	1.65	5.84	0.53	8.01
Lauraceae	1.74	2.43	3.70	7.87
Bignoniaceae	2.15	0.35	5.29	7.79
Celastraceae	1.58	0.35	4.23	6.16
Other 43 families	13.78	20.57	43.39	77.74
Totals	100.00	100.00	100.00	300.00

Based on plant heights, the relative contributions of 13 families to density across different canopy strata in the forest were highly variable (Figure 2). In the lowest forest stratum (< 10 m; *i.e.*, the understory), five families were prominent (> 100 individuals ha^{-1}): Arecaceae (1,884 individuals whose heights were within this stratum), Moraceae (473), Urticaceae (292), Piperaceae (161), and Rubiaceae (145). Moraceae was also important in the middle canopy stratum (10-20 m, 38 individuals), followed by Malvaceae (30), Metteniusaceae (30), and Meliaceae (24). The upper canopy (> 20 m) was also dominated by Moraceae (23), Malvaceae (8), Euphorbiaceae (7), and Fabaceae (7). In turn, only six individuals surpassed 30 m in height, belonging to Fabaceae, Myristicaceae, Moraceae, and Apocynaceae.

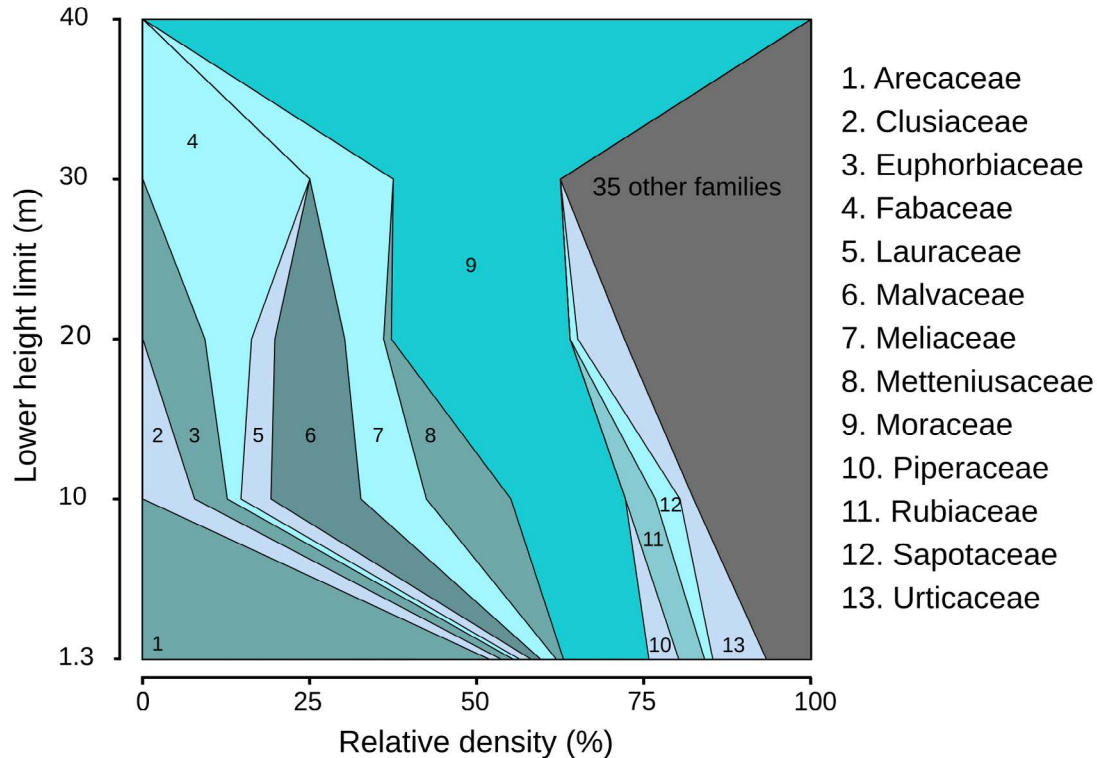


Figure 2. Family importance values by height classes (trees, shrubs and palms with DBH ≥ 1 cm).

The 15 most important species (*i.e.*, those with the largest IVIs) accounted for large fractions of total plant density (65 %), basal area (51.4 %), and frequency (40 %), although they only accounted for 8 % of the total species richness in the plot. The understory palm *Astrocaryum mexicanum* (Arecaceae) was the clear dominant as it had the largest IVI, which was more than threefold of those calculated for *Pseudolmedia glabrata* and *Guarea glabra*, which were second and third, respectively, in the species ranking (Figure 3). *Astrocaryum mexicanum* stood out both by its density and because this was the only species recorded in all 100 quadrats of the plot (*i.e.*, a 100 % frequency); its abundance ranged from 1-27 individuals per 10×10 m quadrat (mean, 14.8 individuals). Five species had high IVIs due to their large relative contributions to basal area (*Guarea glabra*, *Calatola uxpanapensis*, *Omphalea oleifera*, *Clarisia biflora*, and *Sideroxylum portoricensis* subsp. *minutiflorum*). In turn, the mid-canopy tree *Pseudolmedia glabrata* also had a high IVI, with all three structural variables contributing equally (Figure 3).

Community structure. In the EVH plot, we recorded 4,375 individuals (5,623 stems due to multi-stemming) and a total basal area of 43.95 m^2 . The species with the largest densities were *Astrocaryum mexicanum* (1,483 individuals ha^{-1}), *Myriocarpa longipes* (228), and *Trophis mexicana* (220), whereas those with the largest basal area values were *Guarea*

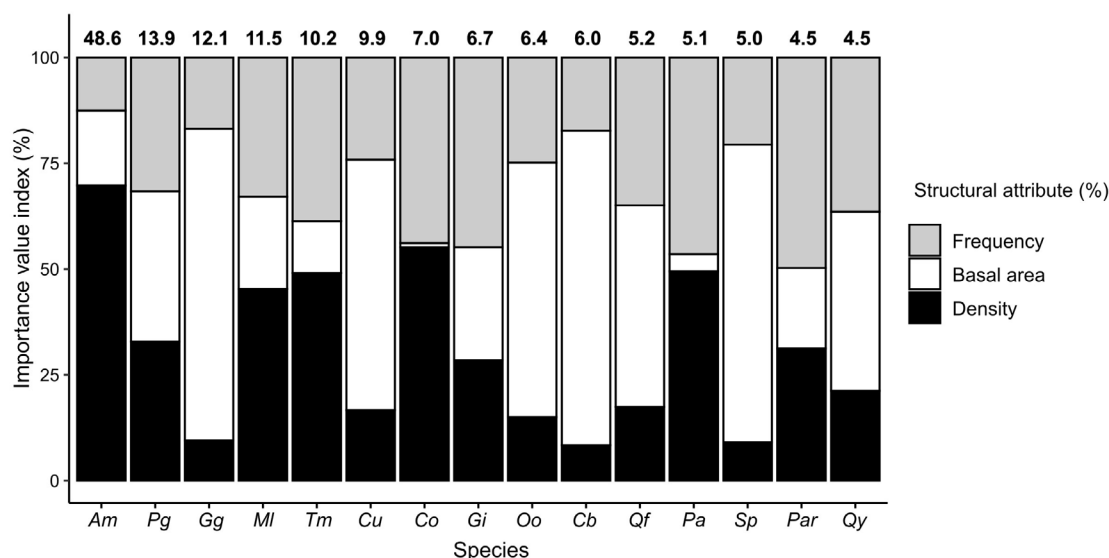


Figure 3. Relative contributions of plant density, basal area, and frequency to the Importance Value Index (IVI) of the 15 most important species, sorted from higher (left) to lower (right) IVI. Absolute IVI values for each species are shown above the bars. Species abbreviations: *Am* (*Astrocaryum mexicanum*, Arecaceae), *Pg* (*Pseudolmedia glabrata*, Moraceae), *Gg* (*Guarea glabra*, Meliaceae), *MI* (*Myriocarpa longipes*, Urticaceae), *Tm* (*Trophis mexicana*, Moraceae), *Cu* (*Calatola uxpanapensis*, Metteniusaceae), *Co* (*Chamaedorea oblongata*, Arecaceae), *Gi* (*Garcinia intermedia*, Clusiaceae), *Oo* (*Omphalea oleifera*, Euphorbiaceae), *Cb* (*Clarisia biflora*, Moraceae), *Qf* (*Quararibea funebris*, Malvaceae), *Pa* (*Piper aequale*, Piperaceae), *Sp* (*Sideroxylum portoricensis* subsp. *minutiflorum*, Sapotaceae), *Par* (*Poulsenia armata*, Moraceae) and *Qy* (*Quararibea yunckeri* subsp. *sessiliflora*, Malvaceae).

glabra (3.97 m² ha⁻¹), *Astrocaryum mexicanum* (3.84 m² ha⁻¹), and *Calatola uxpanapensis* (2.65 m² ha⁻¹). The largest recorded diameter (an individual of *Sideroxylum portoricense* subsp. *minutiflorum*) was 140 cm. Around 90 % of all individuals recorded in the plot had diameters < 10 cm, accounting for 88.7 % of all stems, but only for 3.6 % of the basal area in the plot (Table 3). Tree species made the largest contribution to total basal area, particularly trees with a large DBH (≥ 60 cm; 31 %), even though they represented a mere 0.7 % of total density (Table 4). In turn, palms significantly contributed to both density and basal area, particularly individuals with DBHs of 4–6 cm, whereas shrubs made the lowest contribution. With respect to lianas, only two individuals of *Pisonia aculeata* (Nyctaginaceae) had basal diameters ≥ 10 cm; lianas accounted for 9.1 % of total density but a much smaller proportion (1.5 %) of total basal area (Table 4).

Individuals with dissimilar heights contributed differentially to the vertical distribution of community variables. Individuals with height measurements (*i.e.*, all plants except lianas) ≥ 20 m represented ca. 10 % of total density, while contributing ca. 50 % of total basal area, as many of them had a DBH ≥ 60 cm (Figure 4A). By contrast, individuals with heights < 10 m made the highest contribution to density (90 %) but a much smaller contribution (ca. 21 %) to total basal area in the plot. In turn, almost one-third of the 146 self-standing species (28.8 %) did not have any individual exceeding 5 m in height, while 47.2 % of the species had maximum heights < 10 m (Figure 4B). Notably, only five individuals of different tree species had heights > 30 m: *Aspidosperma megalocarpon* (Apocynaceae), *Ficus yoponensis* (Moraceae), *Platymiscium dimorphandrum* (Fabaceae), *Styphnolobium parviflorum* (Fabaceae), and *Virola guatemalensis* (Myristicaceae). Among these species, all but *S. parviflorum* had individuals in smaller height classes, frequently < 5 m, with densities ranging from 2 to 24 individuals per plot (Appendix 1).

The rank-abundance curve revealed the strong dominance of a single species, the understory palm *A. mexicanum*, which accounted for 34 % of all individuals in the community; in fact, this proportion is higher than the sum values of the next nine species than that of the next five species combined (28.6 %; Figure 5, Appendix 1). A large proportion (68.6 %) of the 188 species recorded in the plot were represented by less than 10 individuals, whilst 12.2 % were doubletons (*i.e.*, represented by two individuals) and nearly one quarter (23.4 %) were singletons (*i.e.*, represented by one individual in the plot; Appendix 1).

Table 3. Number of taxa (families and species), stems, individuals and basal area recorded in the El Vigía Hill 1-ha plot located in the “Steeply dissected slopes” land unit at the Los Tuxtlas Tropical Biology Station. The figures were calculated for different lower cutoff diameters (DBH).

DBH (cm)	Families	Species	Stems	Individuals	Basal area (m ²)
≥ 1	58	188	5,623	4,375	43.95
≥ 2.5	56	167	3,842	3,117	43.59
≥ 5	51	134	2,564	2,199	42.37
≥ 10	35	81	636	460	36.91
≥ 20	28	55	265	218	32.79
≥ 30	24	43	168	132	28.52
≥ 40	19	32	95	78	23.09
≥ 50	17	25	62	50	18.70
≥ 60	13	19	37	29	13.77

Table 4. Contribution to total density and total basal area of each growth form by diameter classes in the El Vigía Hill 1-ha plot at the Los Tuxtlas Tropical Biology Station. For each growth form, the diameter class with the highest density or basal area is indicated with an asterisk. For the comparison of two or more growth forms within each diameter class, the highest values are indicated in bold typeface for each variable.

Diameter class (cm)	Density (ind. ha ⁻¹)				Basal area (m ² ha ⁻¹)			
	Trees	Lianas	Palms	Shrubs	Trees	Lianas	Palms	Shrubs
1-2	532*	71	247	103*	0.11	0.02	0.04	0.05
2-4	481	166*	163	39	0.36	0.13	0.14	0.06*
4-6	235	89	1,059*	0	0.52	0.19	2.40*	0.00
6-8	156	55	410	0	0.69	0.21*	1.35	0.00
8-10	92	13	5	0	0.68	0.08	0.03	0.00
10-20	239	2	0	1	4.10	0.04	0.00	0.01
20-30	85	0	0	0	4.24	0.00	0.00	0.00
30-40	54	0	0	0	5.43	0.00	0.00	0.00
40-50	28	0	0	0	4.39	0.00	0.00	0.00
50-60	21	0	0	0	4.94	0.00	0.00	0.00
> 60	29	0	0	0	13.77*	0.00	0.00	0.00
Total (%)	1,952.0 (44.6)	396.0 (9.1)	1,884.0 (43.1)	142.0 (3.2)	39.21 (89.2)	0.66 (1.5)	3.96 (9.0)	0.11 (0.3)

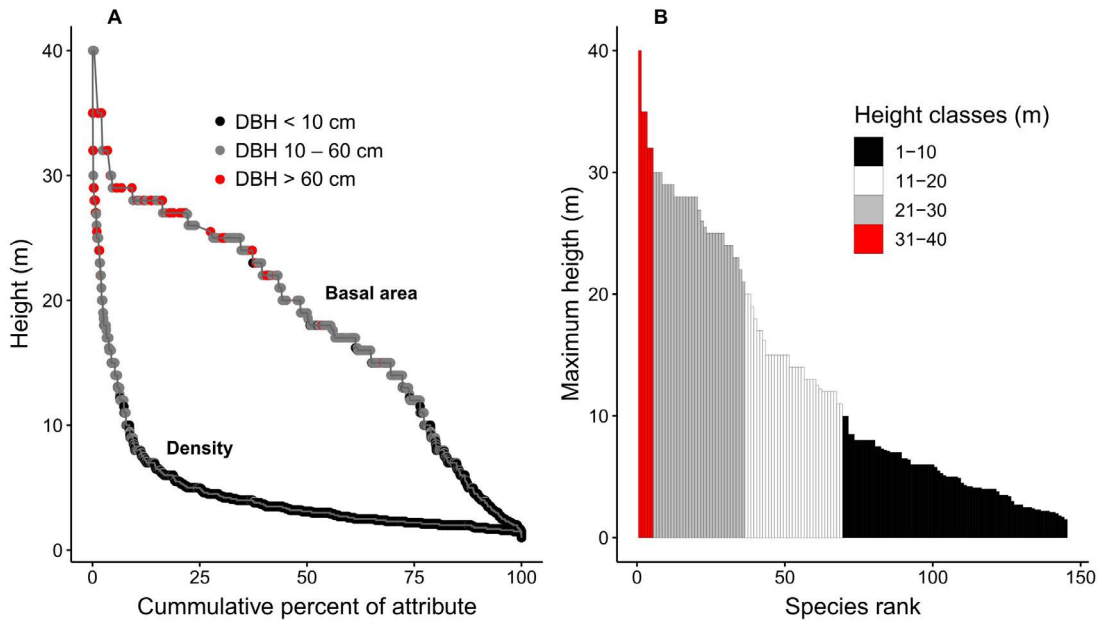


Figure 4. A. Vertical distribution of the cumulative plant density and basal area. B. Maximum height of each species (color bars) in the El Vigía Hill plot at the Los Tuxtlas Tropical Biology Station. Lianas were excluded in both cases.

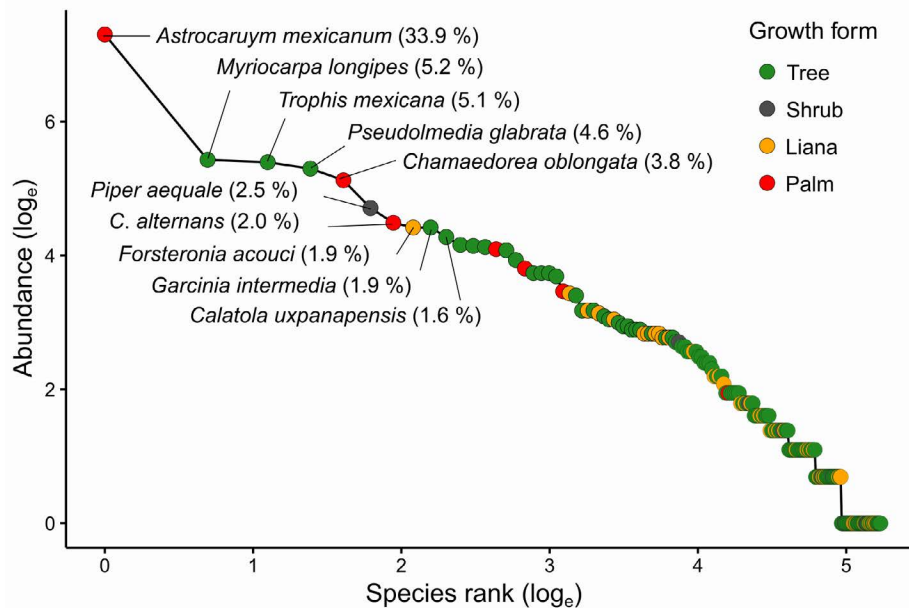


Figure 5. Rank-abundance curve of the species recorded in the El Vigía Hill 1-ha plot at the Los Tuxtlas Tropical Biology Station. Dot colors indicate different growth forms. The 10 most abundant species and their percent contributions to total abundance are indicated.

Community diversity. The large reduction in true diversity when increasing the diversity order from 0D (188 species) to 2D (7.8 species) revealed the strong dominance that characterized the floristic structure of this forest. When the analysis was performed separately for the different growth forms, the highest values for 1D and 2D were observed when palms were excluded, regardless of the minimum DBH used, reflecting the high dominance of this growth form (Table 5). Finally, when palms were included in the EF calculation, this ratio always approached zero (< 0.05). In contrast, the highest value (0.7) was observed for the subset containing only trees with a DBH ≥ 60 cm (Table 5).

The analysis of true diversity dissected by height classes (Figure 6) showed the largest 0D for heights < 10 m; below this threshold, 136 species (93 %) of all self-standing species were present. However, the high plant density in this height class was accompanied by a marked decline in diversity from 0D to 1D , and particularly to 2D . In general, 0D was inversely related to height, with decreases in this variable of 55.1 % and 76.4 % when moving from the lowest canopy stratum to the next two height classes (11–20 m and 21–30 m, respectively), while only six individuals of five species were emergent trees (> 30 m). Interestingly, however, 1D and 2D were higher for the intermediate height classes (11–20 and 21–30 m, respectively; Figure 6).

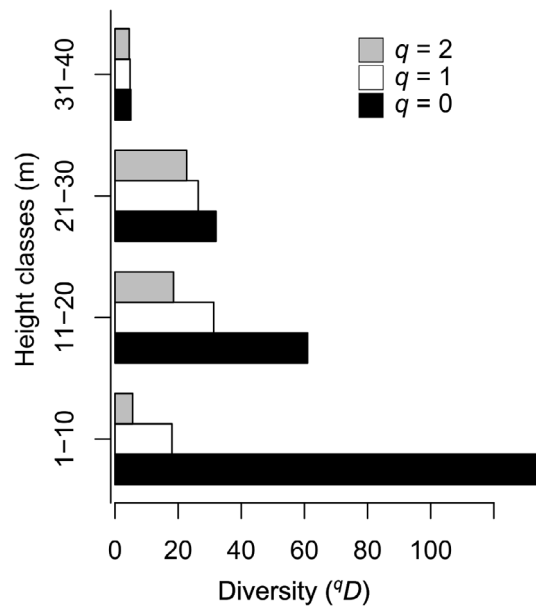


Figure 6. Vertical distribution of order 0 (0D), 1 (1D), and 2 (2D) true diversity for trees, shrubs, and palms with DBH $\geq$ 1 cm recorded in the El Vigía Hill plot at the Los Tuxtlas Tropical Biology Station.

The analysis of species richness by growth form (Table 5) showed that trees made the largest contribution to total 0D (69.1 %), followed by lianas (22.3 %), and, at a distance, by shrubs (5.3 %) and palms (3.7 %). Across the entire community, the effective number of species decreased strongly with increasing diversity order (EF = 0.06), indicating a highly uneven community (Figure 7A). However, when EF was estimated by growth form separately, the same trend was only observed for trees (EF = 0.16, Figure 7B), unlike liana diversity, which only decreased by 47.9 % for 1D and 68.2 % for 2D relative to 0D (42 species), indicating larger evenness (EF = 0.31) for this growth form. Although palms and shrubs are floristic subsets with a higher evenness than trees (EF = 0.22 and 0.18, respectively), both showed low values for all diversity orders (Figure 7B).

Discussion

In this study, we assessed TRF community attributes in a new 1-ha plot established on the “Strongly dissected slopes” land unit at the LTBS to shed new light on the effect of topography on the spatial variation of these attributes. In the following sections, we compare our findings with those from previous studies, particularly from a census conducted on a plot of the same size located on a nearby site with smoother topography (“Piedmont” land unit), also within the LTBS. Unlike our expectations, the vegetation in our plot showed strong similarities to that in the other plot, likely due to their proximity. Despite these similarities, some community attributes differed substantially, which is more in line with our prediction; the largest contrasts involved differences in species composition, plant density, community diversity, and vertical structure, particularly regarding the prevalence of different taxa across forest strata. By integrating our results with those reported in previous studies for the same locality, we confirm that the community

attributes of this TRF, located near the boreal limit of its Neotropical distribution, align with global patterns. Therefore, the undeniable role of topography as a primary driver of spatial variation in community attributes at the local scale does not appear to affect interregional comparisons.

Family composition and the most speciose families. Family composition was highly similar to that reported in previous studies in the study area. For the LYE plot, Bongers *et al.* (1988) reported Fabaceae, Lauraceae, Moraceae, and Rubiaceae among the most species-rich families, in line with the findings from the EVH plot, other studies in smaller plots (< 1 ha) from the Los Tuxtlas region (Table S1), as well as from other Neotropical localities (Gentry 1982, Ashton *et al.* 2004). Across the Neotropics, and even in some African TRFs, these families stand out for being the richest in tree species, along with other prominent families like Annonaceae, Arecaceae, Euphorbiaceae, Meliaceae, Myrtaceae, and Sapotaceae (Gentry 1988, Meave 1990, Valle-Doménech 2000, Zarco-Espinosa *et al.* 2010, Vázquez-Negrín *et al.* 2011).

Table 5. True diversity values of order 0 (0D), 1 (1D) and 2 (2D), for different growth forms and lower DBH cutoffs. In the evenness factor (EF) column, values very close to 0 (EF < 0.1) are indicated in bold.

Growth form	0D	1D	2D	EF ($^2D/^0D$)
<i>DBH ≥ 1 cm</i>				
Trees, shrubs, palms, and lianas	188	29.23	7.80	0.042
Trees, shrubs, and lianas	181	59.99	29.46	0.163
Trees, palms, and lianas	179	27.39	7.34	0.041
Trees, shrubs, and palms	145	21.54	6.49	0.045
Trees and liana	172	57.76	27.84	0.162
Trees and shrubs	138	43.13	22.08	0.160
Trees and palms	136	19.90	6.06	0.045
Trees	129	40.75	20.47	0.159
Lianas	43	21.88	13.20	0.307
Palms	7	2.31	1.58	0.226
Shrubs	9	2.43	1.62	0.180
<i>DBH ≥ 5 cm</i>				
Trees, shrubs, palms, and lianas	134	10.55	2.93	0.022
Trees, shrubs, and lianas	132	53.25	28.17	0.213
Trees, palms, and lianas	133	10.52	2.93	0.022
Trees, shrubs, and palms	110	8.48	2.65	0.024
Trees and lianas	131	53.03	28.11	0.215
Trees and shrubs	108	42.74	23.10	0.214
Trees and palms	109	8.45	2.64	0.024
Trees	107	42.54	23.05	0.215
Lianas	24	12.64	7.45	0.310
<i>DBH ≥ 10 cm</i>				
Trees and lianas	80	42.51	28.35	0.354
Trees (≥ 20)	55	31.53	20.50	0.373
Trees (≥ 30)	43	27.11	17.71	0.412
Trees (≥ 40)	32	22.82	15.68	0.490
Trees (≥ 50)	25	19.95	16.03	0.641
Trees (≥ 60)	19	16.24	13.79	0.726

The most important families and species. Although Bongers *et al.* (1988) did not report FIV values, the density of individuals, basal area, and species richness of the families with the highest FIV in our study are relatively similar. The structural prevalence of Arecaceae has been reported in previous studies carried out in the LTBS (Table S1). Specifically, in the LYE plot, Popma *et al.* (1988a) reported that *ca.* 62 % of all individuals censused were palms, all of which had heights ≤ 8 m, in agreement with our results. The relevance of Arecaceae regarding FIV has also been highlighted in other tropical forests from Mexico and Central America (Meave 1990, Milliken 1998, Valle-Doménech 2000, Zarco-Espinosa *et al.* 2010, Vázquez-Negrín *et al.* 2011, Table S1). In turn, the outstanding position of Moraceae in terms of FIV is primarily due to their cumulative basal area; however, in other sites, their importance may also be related to both species' richness and density (Table S1). Meliaceae, which ranked third in FIV, appears to be a particularity of the LTBS, as it has not been reported as an important component in other forests.

The family importance along the vertical gradient in our plot is not fully consistent with the findings in the LYE plot (Popma *et al.* 1988a). Although the prevalence of some understory families, such as Arecaceae and Rubiaceae, is likely a consistent feature of the LTBS forest, we also found a substantial contribution of Piperaceae and Urticaceae in the lowest stratum, with both families having species commonly associated with gap-phase regeneration stages (Martínez-Ramos 1985, Popma *et al.* 1988b). Similarly, Moraceae and Fabaceae were represented as conspicuous components of the middle and upper strata in both plots. The most outstanding differences between the two plots involved the high structural importance of Lauraceae in the upper canopy, as well as that of Araliaceae and Annonaceae in the middle stratum of the LYE plot, which were comparatively underrepresented in our study. With this information, the earlier idea put forward by Popma *et al.* (1988a) that the vertical structure of this forest cannot be readily generalized is now supported, even among adjacent sites, particularly for upper-canopy taxa.

Thus, the only pattern of vertical structure that can be identified is the threshold between the understory and canopy layers (about 8-10 m), as noted by Popma *et al.* (1988a), which can be explained by several factors. In part, this may reflect true habitat partitioning driven by microenvironmental height gradients (*e.g.*, temperature, light availability) and associated species' functional traits (Martínez-Ramos 1985, Popma *et al.* 1988b, 1992, Parker 1995, Poorter & Bongers 2006). In other cases, species may be restricted to a particular forest stratum due to ontogenetic constraints (Clark & Clark 1992, Poorter *et al.* 2006). Both cases -or even a combination of them- may result in vertical demographic bottlenecks, in which seedlings and young individuals establish in the understory but only a subset successfully transitions to higher forest strata, as occurs in *Brosimum alicastrum*, *Damburneya ambigens* (synonym

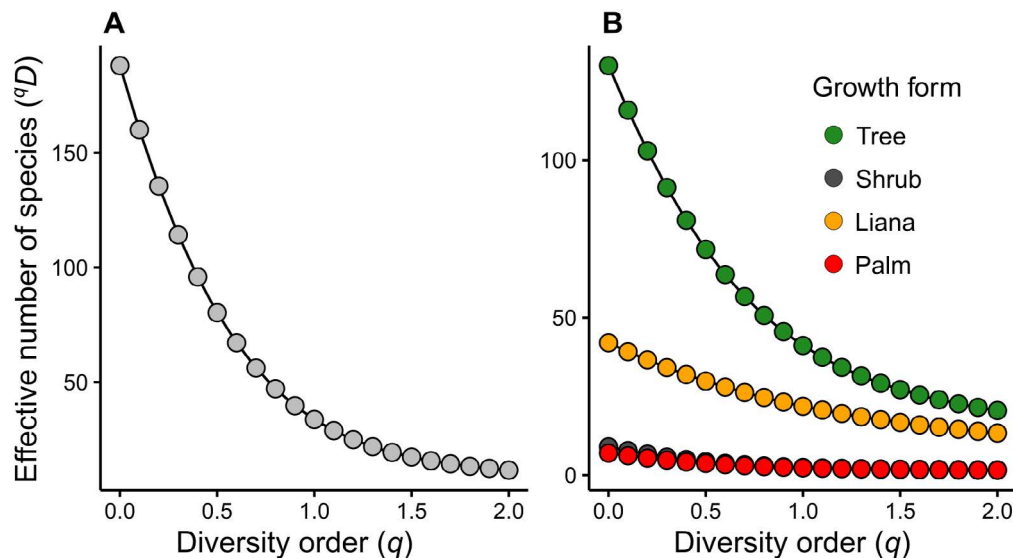


Figure 7. A. Mean diversity as a function of order q in the El Vigía Hill plot by growth forms categories. B. Comparison of diversity among growth forms as a function of order q .

Nectandra ambigens), and *Omphalea oleifera* (Dirzo *et al.* 1997, Dirzo & Mota-Bravo 1997, Rodríguez-Velázquez *et al.* 1997). Consequently, local species composition and environmental heterogeneity may play a key role in shaping vertical structure.

The three families with the highest FIV (Arecaceae, Moraceae, and Meliaceae) each had one species well represented with a high IVI (*Astrocaryum mexicanum*, *Pseudolmedia glabrata*, and *Guarea glabra*, respectively; [Table 3](#)). The former species was also dominant in the lowest stratum of the LYE plot (Bongers *et al.* 1988) and was also reported as the most dominant palm in five land units across the LTBS, with densities of at least 400 individuals per hectare (Miranda-Gallegos *et al.* 2023). Interestingly, there is evidence that *Astrocaryum mexicanum* density increased during the 1975–2013 period (Martínez-Ramos *et al.* 2016), with worrisome changes in tree community attributes. Those authors suggest that this phenomenon is mainly driven by anthropogenic disturbances, which increase canopy gap-opening rates in the forest and, in turn, increase understory light availability. The high density of this palm has several effects: (i) an increased production of *Astrocaryum mexicanum* fruits, (ii) a low predation rate of its fruits by mammals, (iii) seed rain interference and shading effect due to high palm density, and (iv) the physical damage to, or the death of, seedlings of other species caused by the fall of this palm's leaves. All these factors together may increase recruitment rates of *Astrocaryum mexicanum* seedlings, thereby excluding other plant species. However, and in contrast to this local-scale phenomenon, a negative effect of forest fragmentation on the abundance of this palm at a regional scale has been reported (Hernández-Ruedas *et al.* 2018). In turn, the importance of *Pseudolmedia glabrata* and *Guarea glabra*, both in terms of density and biomass, was also highlighted by Navarrete-Segueda *et al.* (2021) across the reserve, based on a vegetation survey restricted to individuals ≥ 10 cm in DBH. Such dominance suggests that these species are relatively unaffected by topographic variation at LTBS, a possibility that deserves further investigation.

Plant density and basal area patterns in the TRF community. The number of individuals recorded in this study (4,375 ind·ha⁻¹) represents the maximum per-hectare value reported to date for the LTBS, even after excluding the 396 liana individuals ([Table S2](#)). Unfortunately, the comparison of plant density for individuals with a DBH ≥ 1 cm between Los Tuxtlas and other studies is not straightforward, since such a diameter cutoff is seldom used and, more importantly, the reported values in other forests are highly variable (mean and SD for studies in Losos (2004), 6,645.1 $\pm$ 2,200.7 ind·ha⁻¹). From the studies shown in [Figure S1A](#), only one in South America (Cuyabeno, Ecuador; Valencia *et al.* 2004) and two in Mexico (Niños Héroes, Tabasco, 4,773 ind·ha⁻¹; Yaxchilán, Chiapas, 4,930 ind·ha⁻¹; Vázquez-Negrín *et al.* 2011, Valle-Doménech 2000), with minimum DBH cutoffs of 5, 2.5, and 1 cm, respectively, reported higher plant densities than that in the EVH plot. Conversely, among the TRF localities examined by Losos (2004), most have a higher mean density of individuals with DBH ≥ 1 cm (range 4,124–12,209 ind·ha⁻¹) than the values for the EVH and LYE plots (4,375 and 3,344 ind·ha⁻¹, respectively). Also, plant density for individuals with DBH ≥ 10 cm in the LTBS is generally lower than values from other forests worldwide (mean for EVH and LYE plots, 408 ind·ha⁻¹; mean for sites in [Figure S1B](#), 521.1 $\pm$ 108.9 ind·ha⁻¹), including most Mexican localities ([Figure S1B](#)). This comparison also holds for figures reported by Losos (2004) for different TRFs worldwide, even after excluding a locality with an exceptionally higher density (Nanjenshan, Taiwan, 1,052 ind·ha⁻¹; mean 554.22 $\pm$ 153.5 ind·ha⁻¹).

Therefore, we may conclude that plant density in the Los Tuxtlas TRF is at the lower end of the global range for this vegetation type, both for small (DBH ≥ 1 cm) and big trees (DBH ≥ 10 cm). This conclusion partially agrees with Bongers *et al.* (1988), who reported that the Los Tuxtlas TRF had a lower density of small individuals but a similar density of larger trees, based on comparisons of plant density assessed in the LYE plot with information available at the time for other forests. The lower density of individuals in the last plot was expected, as disturbance events are less frequent in sites with smoother topography (Martínez-Ramos 1985, Cushman *et al.* 2022) than in the EVH plot, which has a higher density and steeper topography. However, this local variation of individual density related to topographic heterogeneity does not affect comparisons with other TRF worldwide.

Despite its low plant density, the LTBS has a higher basal area than other TRFs, as previously noted by Bongers *et al.* (1988). The basal area in the EVH plot was slightly higher than that of the LYE plot ([Figure S1C](#)), both for

individuals with $\text{DBH} \geq 1 \text{ cm}$ (43.9 and 38.1 m^2 , respectively) and $\text{DBH} \geq 10 \text{ cm}$ (36.91 and 34.9 m^2 , respectively). Although the basal area differences between the two plots are small, they still suggest a greater number of individuals in the EVH plot (see above). The comparison of mean basal area values for Los Tuxtlas with those from other plots worldwide ([Figure S1C](#)) and those reported in Losos (2004) ($36.4 \text{ m}^2 \pm 4.7 \text{ ha}^{-1}$ for trees with a $\text{DBH} \geq 1 \text{ cm}$; $30.7 \text{ m}^2 \pm 5.1 \text{ ha}^{-1}$ for trees $\text{DBH} \geq 10 \text{ cm}$) indicate that the basal area recorded at the LTBS is generally higher, regardless of the diameter class being compared. This observation is consistent with pantropical TRF means reported by different authors, which range between 21 and 32 $\text{m}^2 \text{ ha}^{-1}$ (Rollet 1978, Hall & Swaine 1981). In conclusion, the LTBS TRF features a quite unique combination of a low plant density with a relatively large basal area, as previously stated by Bongers *et al.* (1988). Considering that trees having the thickest trunks make the largest contribution to total basal area in TRF communities ([Figure 4](#), [Table 4](#)), a likely explanation for this noteworthy pattern is that the LTBS may host, on average, thicker trees than most TRF localities worldwide (but see Kessler *et al.* 2005, Hamann *et al.* 1999, for some counterexamples). In addition, at Los Tuxtlas many trees with $\text{DBH} \geq 10 \text{ cm}$ are multi-stemmed (61 individuals in the EVH plot), which may further contribute to the higher total basal area in this community, which contrasts with its low plant density.

Community composition. At least 120 (63 %) of all species recorded in the EVH and LYE plots combined (*i.e.*, an approximate pooled richness of 248 species) were shared between them ($^qDS = 0.35$; [Figure S3](#)). These figures suggest that the spatial distribution of most species in this locality is unaffected by the area's topographic heterogeneity. However, this interpretation must be taken with caution for two considerations. First, the high number of morpho-species (*i.e.*, specimens that could not be identified) reported in Bongers *et al.* (1988) introduces uncertainty into the comparison of floristic composition between plots, likely resulting in low accuracy when estimating true compositional dissimilarity. Second, the large number of singletons in the two plots (EVH = 44, LYE ≈ 35), along with the low abundance of many other species, renders the detection of clear patterns difficult, as the presence of these rare species may result from isolated random dispersal and establishment events rather than representing systematic responses to environmental gradients (Hubbell 2013, 2015). Thus, claims about the influence of topography on species composition remain unsupported and warrant a larger sampling effort. We encourage more detailed studies to investigate how topography and other related environmental factors may cause differential species distributions in this TRF.

Is the Los Tuxtlas TRF among the least diverse in the world? Interestingly, despite differences in composition between the EVH and LYE plots, species richness (0D) is notably similar in both. Moreover, when 0D was compared with the number of species per unit area reported in previous studies in the LTBS, the figures were remarkably similar ([Figure S3](#)). In addition, previous studies found no significant differences in 0D across different land units for trees $\geq 10 \text{ cm}$ in DBH (Navarrete-Segueda *et al.* 2021), palms $> 1 \text{ m}$ in height (Miranda-Gallegos *et al.* 2023), and lianas $\geq 1 \text{ cm}$ in basal diameter (Ek-Rodríguez *et al.* 2024). Accordingly, we conclude that 0D is most likely unaffected by environmental differences across the study area. That said, when we compared species richness per hectare using the same diameter cutoffs and growth forms included in some studies worldwide, the LTBS had the lowest value in most cases ([Figure S2](#)), a result consistent with Bongers *et al.* (1988). These results support the notion that the location of the Los Tuxtlas TRF near the boreal margin of this vegetation type's continental distribution explains its low diversity. Although other authors have argued about the possible influence of factors such as disturbance level, soil fertility, or precipitation, the evidence supporting these possibilities is scarce (Gentry 1982, Bongers *et al.* 1988, Ashton *et al.* 2004).

Given the small plot sizes used in previous studies to analyze TRF community attributes at the LTBS, comparing 1D and 2D values from our study plot with those reported by those studies is not feasible. Moreover, few studies have estimated such values in other TRF worldwide ([Table S2](#)). However, considering the low species richness at Los Tuxtlas, and that 1D and 2D at the LTBS are generally lower than in other TRFs independently of the area ([Table S2](#)), we may conclude that true diversity in the Los Tuxtlas TRF is relatively low at all levels of q , *i.e.*, when considering species relative abundances. This result underscores the community's high dominance, particularly when palms are included in the assessment of community diversity ([Table 5](#)).

The present study advances our understanding of community attribute variation in the TRF of the LTBS, highlighting topography as a key driver of this variation. Our results show how topographic differences affect the spatial variation in community composition, plant density, and vertical structure. Admittedly, however, various community attributes (*e.g.*, species richness, family composition, total basal area, and diameter frequency distribution) are consistent with values reported in earlier studies despite the contrasting topography of our plot. In addition, and more importantly, we also showed that local-scale spatial variation in community attributes related to topographic heterogeneity does not introduce important biases in interregional comparisons of TRF structure and diversity.

Our results provide a more accurate image of the TRF vegetation in the study area and its spatial variation. This new information enables more meaningful regional comparisons of the Los Tuxtlas TRF with similar communities in other tropical regions. Like many other topographically complex tropical humid regions of the world, the Los Tuxtlas region encompasses a wide variety of land units. Unfortunately, given the degree of destruction of the TRF that still covered most of the region a little over half a century ago (Dirzo & Garcia 1992, Bonilla-Moheno & Aide 2020, von Thaden *et al.* 2020), it is nowadays impossible to determine what proportion of the original TRF in the region was more similar to either one of the two 1-ha plots compared here. The only conclusion that can be drawn with some level of confidence is that the extensive and less rugged areas of the region that are currently devoted to agriculture, but particularly to cattle ranching, hosted forests more similar to the one described in the LYE plot, whereas the forests in areas closer to the prominent volcanoes of the regions, where slopes become steeper and soils shallower, likely resembled more the forest described here in the EVH plot. Regardless of the magnitude of regional variation in the TRF across the Los Tuxtlas region and the high environmental heterogeneity of the LTBS landscape, we emphasize the need for additional studies to further explore spatial variation in community attributes and identify the underlying factors driving this variation. By doing so, we will gain new insights into the structure, diversity, dynamics, and functioning of these megadiverse forests.

Supplementary material

Supplemental data for this article can be accessed here: <https://doi.org/10.17129/botsci.3843>

Acknowledgments

This research was part of the first author's master's studies in the Posgrado en Ciencias Biológicas program at the Universidad Nacional Autónoma de México (UNAM). The first author also thanks SECIHTI (formerly Consejo Nacional de Humanidades, Ciencias y Tecnologías (CONAHCyT)) for a graduate scholarship.

Literature cited

- APG [Angiosperm Phylogeny Group]. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* **181**: 1-20. DOI: <https://doi.org/10.1111/boj.12385>
- Ashton PS, Brokaw N, Bunyavejchewin S, Condit R, Chuyong G, Co L, Dattaraja HS, Davies SJ, Esufali S, Ewango C, Foster R, Gunatilleke N, Gunatilleke S, Hart T, Hernandez C, Hubbell S, Itoh A, John R, Kanzaki M, Kenfack D, Kiratiprayon S, LaFrankie J, Lee HS, Liengola I, Lao S, Losos E, Makana JR, Manokaran N, Navarrete H, Ohkubo T, Pérez R, Pongpattananurak N, Samper C, Sringernyuang K, Sukumar R, Sun IF, Suresh HS, Tan S, Thomas D, Thompson J, Vallejo M, Villa Muñoz G, Valencia R, Yamakura T, Zimmerman, J. 2004. Floristics and vegetation of the forest dynamics plots. In: Losos EC, Leigh Jr. EG, eds. *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network*. Chicago: The University of Chicago Press. pp. 90-106. ISBN: 9780226493466
- Baldeck CA, Harms KE, Yavitt JB, John R, Turner BL, Valencia R, Navarrete H, Davies SJ, Chuyong GB, Kenfack

- D, Thomas DW, Madawala S, Gunatilleke N, Gunatilleke S, Bunyavejchewin S, Kiratiprayoon S, Yaacob A, Nur Supardi MN, Dalling JW. 2013. Soil resources and topography shape local tree community structure in tropical forests. *Proceedings of the Royal Society B: Biological Sciences* **280**: 20122532. DOI: <https://doi.org/10.1098/rspb.2012.2532>
- Beech E, Rivers M, Oldfield S, Smith PP. 2017. GlobalTreeSearch: The first complete global database of tree species and country distributions. *Journal of Sustainable Forestry* **36**: 454-489. DOI: <https://doi.org/10.1080/10549811.2017.1310049>
- Bohlman SA, Laurance WF, Laurance SG, Nascimento HEM, Fearnside PM, Andrade A. 2008. Importance of soils, topography and geographic distance in structuring central Amazonian tree communities. *Journal of Vegetation Science* **19**: 863-874. DOI: <https://doi.org/10.3170/2008-8-18463>
- Bongers F, Popma J, Meave del Castillo J, Carabias J. 1988. Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. *Vegetatio* **74**: 55-80. DOI: <https://doi.org/10.1007/BF00045614>
- Bonilla-Moheno M, Aide TM. 2020. Beyond deforestation: Land cover transitions in Mexico. *Agricultural Systems* **178**: 102734. DOI: <https://doi.org/10.1016/j.agsy.2019.102734>
- Brown C, Burslem DFRP, Illian JB, Bao L, Brockelman W, Cao M, Chang LW, Dattaraja HS, Davies S, Gunatilleke CVS, Gunatilleke IAUN, Huang J, Kassim AR, LaFrankie JV, Lian J, Lin L, Ma K, Mi X, Nathalang A, Noor S, Ong P, Sukumar R, Su SH, Sun IF, Suresh HS, Tan S, Thompson J, Uriarte M, Valencia R, Yap SL, Ye W, Law R. 2013. Multispecies coexistence of trees in tropical forests: spatial signals of topographic niche differentiation increase with environmental heterogeneity. *Proceedings of the Royal Society B: Biological Sciences* **280**: 20130502. DOI: <https://doi.org/10.1098/rspb.2013.0502>
- Burnham RJ. 2004. Alpha and beta diversity of lianas in Yasuní, Ecuador. *Forest Ecology and Management* **190**: 43-55. DOI: <https://doi.org/10.1016/j.foreco.2003.10.005>
- Chave J. 2008. Spatial variation in tree species composition across tropical forests: Pattern and process. In: Carson WP, Schnitzer SA, eds. *Tropical Forest Community Ecology*. Oxford: Wiley-Blackwell: pp. 9-11. ISBN: 978-1-4051-1897-2
- Clark DA, Clark DB. 1992. Life history diversity of canopy and emergent trees in a Neotropical rainforest. *Ecological Monographs* **62**: 315-344. DOI: <https://doi.org/10.2307/2937114>
- Clark DB, Clark DA. 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology and Management* **137**: 185-198. DOI: [https://doi.org/10.1016/S0378-1127\(99\)00327-8](https://doi.org/10.1016/S0378-1127(99)00327-8)
- Corlett R, Primack RB. 2011. *Tropical Rain Forests: an Ecological and Biogeographical Comparison*. Hoboken: Wiley-Blackwell. ISBN: 9781444392296. DOI: <https://doi.org/10.1002/9781444392296>
- Cornejo-Tenorio G, Ibarra-Manríquez G, Sinaca-Colín S. 2019. *Flora de los Tuxtlas: Guía Ilustrada*. Ciudad de México: Universidad Nacional Autónoma de México. ISBN: 978-607-30-1354-3
- Cushman KC, Detto M, García M, Müller-Landau C. 2022. Soils and topography control natural disturbance rates and thereby forest structure in a lowland tropical landscape. *Ecology Letters* **25**: 1126-1138. DOI: <https://doi.org/10.1111/ele.13978>
- de Souza CR, Coelho de Souza F, Maia VA, de Aguiar-Campos N, Coelho PA, Farrapo CL, Santos ABM, Araújo FC, Gianasi FM, Paula GGP, Morel JD, Fagundes NCA, Garcia, PO, Santos PF, Silva WB, Fontes MAL, Santos RM. 2021. Tropical forests structure and diversity: A comparison of methodological choices. *Methods in Ecology and Evolution* **12**: 2017-2027. DOI: <https://doi.org/10.1111/2041-210X.13670>
- Dirzo R, Garcia MC. 1992. Rates of deforestation in Los Tuxtlas, a Neotropical area in southeast Mexico. *Conservation Biology* **6**: 84-90. DOI: <https://doi.org/10.1046/j.1523-1739.1992.610084.x>
- Dirzo R, Ibarra-Manríquez G, Sánchez-Garduño C. 1997. *Nectandra ambigens* (laurel chilpatillo). In: González-Soriano E, Dirzo R, Vogt RC, eds. *Historia Natural de Los Tuxtlas*. México: Universidad Nacional Autónoma de México. pp. 124-129. ISBN: 968-36-5646-3
- Dirzo R, Mota-Bravo LM. 1997. *Omphalea oleifera* (corcho). In: González-Soriano E, Dirzo R, Vogt RC, eds. *Historia Natural de Los Tuxtlas*. México: Universidad Nacional Autónoma de México. pp. 130-133. ISBN: 968-36-5646-3

- Ek-Rodríguez IL, Coates R, Sinaca-Colín S, Ibarra-Manríquez G. 2022. Liana community attributes in one of the northernmost Neotropical rainforests. *Botanical Sciences* **100**: 353-369. DOI: <https://doi.org/10.17129/botsci.2955>
- Ek-Rodríguez IL, Meave JA, Navarrete-Segueda A, González-Arqueros ML, Ibarra-Manríquez G. 2024. Environmental heterogeneity influences liana community differentiation across a Neotropical rainforest landscape. *Ecology and Evolution* **14**: e11170. DOI: <https://doi.org/10.1002/ece3.1117>
- Gentry AH. 1982. Patterns of Neotropical plant species diversity. In: Hecht MK, Wallace B, Prance GT, eds. *Evolutionary Biology*. New York: Springer. pp. 1-84. DOI: https://doi.org/10.1007/978-1-4615-6968-8_1
- Gentry AH. 1988. Tree species richness of upper Amazonian forests. *Proceedings of the National Academy of Sciences of the United States of America* **85**: 156-159. DOI: <https://doi.org/10.1073/pnas.85.1.156>
- González Soriano E, Dirzo R, Vogt RC. eds. 1997. *Historia Natural de Los Tuxtlas*. México: Universidad Nacional Autónoma de México. ISBN: 968-36-5646-3
- Gunatilleke CVS, Gunatilleke IAUN, Esufali S, Harms KE, Ashton PMS, Burslem DFRP, Ashton PS. 2006. Species-habitat associations in a Sri Lankan dipterocarp forest. *Journal of Tropical Ecology* **22**: 371-384. DOI: <https://doi.org/10.1017/S0266467406003282>
- Guo Y, Wang B, Mallik AU, Huang F, Xiang W, Ding T, Wen S, Lu S, Li D, He Y, Li X. 2017. Topographic species-habitat associations of tree species in a heterogeneous tropical karst seasonal rain forest, China. *Journal of Plant Ecology* **10**: 450-460. DOI: <https://doi.org/10.1093/jpe/rtw057>
- Hall JB, Swaine MD. 1981. *Distribution and Ecology of Vascular Plants in a Tropical Rainforest: Forest vegetation in Ghana*. The Hague: Junk. ISBN-10: 906-193-681-0
- Hamann A, Barbon EB, Curio E, Madulid DA. 1999. A botanical inventory of a submontane tropical rainforest on Negros Island, Philippines. *Biodiversity & Conservation* **8**: 1017-1031. DOI: <https://doi.org/10.1023/A:1008847704539>
- Harms KE, Condit R, Hubbell SP, Foster RB. 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology* **89**: 947-959. DOI: <https://doi.org/10.1111/j.1365-2745.2001.00615.x>
- Hernández-Ruedas MA, Arroyo-Rodríguez V, Morante-Filho JC, Meave JA, Martínez-Ramos M. 2018. Fragmentation and matrix contrast favor understory plants through negative cascading effects on a strong competitor palm. *Ecological Applications* **28**: 1546-1553. DOI: <https://doi.org/10.1002/eap.1740>
- Hubbell SP. 2013. Tropical rain forest conservation and the twin challenges of diversity and rarity. *Ecology and Evolution* **3**: 3263-3274. DOI: <https://doi.org/10.1002/ece3.705>
- Hubbell SP. 2015. Estimating the global number of tropical tree species, and Fisher's paradox. *Proceedings of the National Academy of Sciences of the United States of America* **112**: 7343-7344. DOI: <https://doi.org/10.1073/pnas.1507730112>
- Ibarra-Manríquez G, Martínez-Ramos M, Dirzo R, Núñez-Farfán J. 1997. Vegetación. In: González-Soriano E, Dirzo R, Vogt RC, eds. *Historia Natural de Los Tuxtlas*. México: Universidad Nacional Autónoma de México. pp. 61-85. ISBN: 968-36-5646-3
- Ibarra-Manríquez G, Cornejo-Tenorio G, Sinaca-Colín S. 2025. Lo pasado, pasado: actualización taxonómica y distribución geográfica de la flora vascular de la Estación de Biología Tropical Los Tuxtlas, Veracruz, México. *Revista Mexicana de Biodiversidad* **96**: e965749. DOI: <https://doi.org/10.22201/ib.20078706e.2025.96.5749>
- John R, Dalling JW, Harms KE, Yavitt JB, Stallard RF, Mirabello M, Hubbell SP, Valencia R, Navarrete H, Vallejo M, Foster RB. 2007. Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences* **104**: 864-869. DOI: <https://doi.org/10.1073/pnas.0604666104>
- Jost L. 2006. Entropy and diversity. *Oikos* **113**: 363-375. DOI: <https://doi.org/10.1111/j.2006.0030-1299.14714.x>
- Jost L. 2010. The relation between evenness and diversity. *Diversity* **2**: 207-232. DOI: <https://doi.org/10.3390/d2020207>
- Jost L, Chao A, Chazdon R. 2011. Compositional similarity and beta diversity. In: Magurran, AE, McGill BJ, eds. *Biological Diversity: Frontiers in Measurement and Assessment*. New York: Oxford University Press. pp. 66-84. ISBN: 978-0-19-958066-8
- Jucker T, Bongalov B, Burslem DFRP, Nilus R, Dalponte M, Lewis SL, Phillips OL, Qie L, Coomes DA. 2018.

- Topography shapes the structure, composition and function of tropical forest landscapes. *Ecology Letters* **21**: 989-1000. DOI: <https://doi.org/10.1111/ele.12964>
- Kessler M, Keßler PJA, Gradstein SR, Bach K, Schmul M, Pitopang R. 2005. Tree diversity in primary forest and different land use systems in Central Sulawesi, Indonesia. *Biodiversity & Conservation* **14**: 547-560. DOI: <https://doi.org/10.1007/s10531-004-3914-7>
- Kottek M, Grieser J, Beck C, Rudolf B, Rubel F. 2006. World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift* **15**: 259-263. DOI: <https://doi.org/10.1127/0941-2948/2006/0130>
- Losos EC. 2004. The structure of tropical forests. In: Losos EC, Leigh Jr. EG, eds. *Tropical forest diversity and dynamism: Findings From a Large-Scale Plot Network*. Chicago: The University of Chicago Press. pp. 69-78. ISBN: 9780226493466
- Losos EC, Leigh EG. 2004. *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network*. Chicago: The University of Chicago Press. ISBN: 9780226493466
- Martín-del Pozzo AL. 1997. Geología. In: González-Soriano E, Dirzo R, Vogt RC, eds. *Historia Natural de Los Tuxtlas*. México: Universidad Nacional Autónoma de México. pp. 26-31. ISBN: 968-36-5646-3
- Martínez-Ramos M. 1985. Claros, ciclos vitales de los árboles tropicales y regeneración natural de las selvas altas perennifolias. In: Gómez-Pompa A, del Amo SR, eds. *Investigaciones Sobre la Regeneración de Selvas Altas en Veracruz, México*. Volumen II. México: Instituto Nacional de Investigaciones sobre Recursos Bióticos, Alhambra Mexicana. pp. 191-239. ISBN: 968-444-047-2
- Martínez-Ramos M, Ortiz-Rodríguez IA, Piñero D, Dirzo R, Sarukhán J. 2016. Anthropogenic disturbances jeopardize biodiversity conservation within tropical rainforest reserves. *Proceedings of the National Academy of Sciences* **113**: 5323-5328. DOI: <https://doi.org/10.1073/pnas.1602893113>
- Meave J. 1990. *Estructura y Composición de la Selva Alta Perennifolia de los Alrededores de Bonampak*. México: Instituto Nacional de Antropología e Historia. ISBN: 9686068678
- Milliken W. 1998. Structure and composition of one hectare of central Amazonian terra firme forest. *Biotropica* **30**: 530-537. DOI: <https://doi.org/10.1111/j.1744-7429.1998.tb00093.x>
- Miranda-Gallegos KV, Navarrete-Segueda A, Cortés-Flores J, González-Arqueros ML, Acosta-Pérez EE, Ibarra-Manríquez G. 2023. Landscape heterogeneity drives spatial distribution of palm community in a Neotropical rainforest reserve affected by defaunation. *Botanical Sciences* **101**: 654-669. DOI: <https://doi.org/10.17129/bots-ci.3204>
- Mori SA, Boom BM, de Carvalho AM, dos Santos TS. 1983. Southern Bahian moist forests. *The Botanical Review* **49**: 155-232. DOI: <https://doi.org/10.1007/BF02861011>
- Mueller-Dombois D, Ellenberg H. 1974. *Aims and Methods of Vegetation Ecology*. New York: John Wiley & Sons. ISBN: 0-471-62290-7
- Navarrete-Segueda A, Cortés-Flores J, Cornejo-Tenorio G, González-Arqueros ML, Torres-García M, Ibarra-Manríquez G. 2021. Timber and non-timber forest products in the northernmost Neotropical rainforest: Ecological factors unravel their landscape distribution. *Journal of Environmental Management* **279**: 111819. DOI: <https://doi.org/10.1016/j.jenvman.2020.111819>
- Nelson SA, Gonzalez-Caver E. 1992. Geology and K-Ar dating of the Tuxtla Volcanic Field, Veracruz, Mexico. *Bulletin of Volcanology* **55**: 85-96. DOI: <https://doi.org/10.1007/BF00301122>
- Parker GG. 1995. Structure and light environment of forest canopies. In: Lowman MD, Nadkarni NM, eds. *Forest canopies*. Academic Press. pp. 73-106. ISBN 0-12-457650-8
- Pitman NCA, Mogollón H, Dávila N, Ríos M, García-Villacorta R, Guevara J, Baker TR, Monteagudo A, Phillips OL, Vásquez-Martínez R, Ahuite M, Aulestia M, Cardenas D, Cerón CE, Loizeau P-A, Neill DA, Núñez VP, Palacios WA, Spichiger R, Valderrama E. 2008. Tree community change across 700 km of lowland Amazonian forest from the Andean foothills to Brazil. *Biotropica* **40**: 525-535. DOI: <https://doi.org/10.1111/j.1744-7429.2008.00424.x>
- Popma J, Bongers F, Meave del Castillo J. 1988a. Patterns in the vertical structure of the tropical lowland rain forest of Los Tuxtlas, Mexico. *Vegetatio* **74**: 81-91. DOI: <https://doi.org/10.1007/BF00045615>

- Popma J, Bongers F, Martínez-Ramos M, Veneklaas E. 1988b. Pioneer species distribution in treefall gaps in Neotropical rain forest; a gap definition and its consequences. *Journal of Tropical Ecology* **4**: 77-88. DOI: <https://doi.org/10.1017/S0266467400002534>
- Popma J, Bongers F, Werger MJA. 1992. Gap-dependence and leaf characteristics of trees in a tropical lowland rain forest in Mexico. *Oikos* **63**: 207-214. DOI: <https://doi.org/10.2307/3545380>
- Poorter L, Bongers F. 2006. Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* **87**: 1733-1743. DOI: [https://doi.org/10.1890/0012-9658\(2006\)87\[1733:LTAGPO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1733:LTAGPO]2.0.CO;2)
- Poorter L, Bongers L, Bongers F. 2006. Architecture of 54 moist-forest tree species: traits, trade-offs, and functional groups. *Ecology* **87**: 1289-1301. DOI: [https://doi.org/10.1890/0012-9658\(2006\)87\[1289:AOMTST\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1289:AOMTST]2.0.CO;2)
- Reynoso VH, Coates RI, Vázquez Cruz ML. eds. 2017. *Avances y Perspectivas en la Investigación de los Bosques Tropicales y sus Alrededores: La región de Los Tuxtlas*. Ciudad de México: Universidad Nacional Autónoma de México. ISBN: 978-607-02-9882-0
- Rodrigues AC, Villa PM, Neri AV. 2019. Fine-scale topography shape richness, community composition, stem and biomass hyperdominant species in Brazilian Atlantic forest. *Ecological Indicators* **102**: 208-217. DOI: <https://doi.org/10.1016/j.ecolind.2019.02.033>
- Rodríguez-Velázquez J, Martínez-Ramos M, Dyer-Leal G. 1997. *Brosimum alicastrum* (Ojoche). In: González-Soriano E, Dirzo R, Vogt RC, eds. *Historia Natural de Los Tuxtlas*. México: Universidad Nacional Autónoma de México. pp. 97-100. ISBN: 968-36-5646-3
- Rollet B. 1978 Description, functioning and evolution of tropical forest ecosystems. 5. Organization. In: *Tropical Forest Ecosystems; a State of Knowledge*. Paris: UNESCO. pp. 112-142. ISBN: 92-3-101507-9
- Valencia R, Foster RB, Villa G, Condit R, Svenning J-C, Hernández C, Romoleroux K, Losos E, Magård E, Balslev H. 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. *Journal of Ecology* **92**: 214-229. DOI: <https://doi.org/10.1111/j.0022-0477.2004.00876.x>
- Valle-Doménech A. 2000. *Análisis estructural de una hectárea de selva alta perennifolia en el monumento natural Yaxchilán (Chiapas), México*. BSc Thesis. Universidad Nacional Autónoma de México.
- Vázquez-Negrín I, Castillo-Acosta O, Valdez-Hernández JI, Zavala-Cruz J, Martínez-Sánchez JL. 2011. Estructura y composición florística de la selva alta perennifolia en el ejido Niños Héroes Tenosique, Tabasco, México. *Polibotánica* **32**: 41-61.
- von Thaden JJ, Laborde J, Guevara S, Mokondoko-Delgadillo P. 2020. Dinámica de los cambios en el uso del suelo y cobertura vegetal en la Reserva de la Biosfera Los Tuxtlas (2006-2016). *Revista Mexicana de Biodiversidad* **91**: e913190. DOI: <https://doi.org/10.22201/ib.20078706e.2020.91.3190>
- Whitmore TC. 2008. *An Introduction to Tropical Rain Forests*. Oxford: Oxford Univ. Press. ISBN: 978-0198501473
- Zarco-Espinosa V, Valdez-Hernández JI, Ángeles-Pérez G, Castillo-Acosta O. 2010. Estructura y diversidad de la vegetación arbórea del parque estatal Agua Blanca, Macuspana, Tabasco. *Universidad y Ciencia* **26**: 1-17.
- Zimmerman JK, Thompson J, Brokaw N. 2008. Dynamics plots: Testing explanations for the maintenance of species diversity. In: Carson WP, Schnitzer SA. eds. *Tropical Forest Community Ecology*. Oxford: Wiley-Blackwell, pp. 98-117. ISBN: 978-1-4051-1897-2

Associate editor: Alejandro Zavala Hurtado

Author contributions: ILER: conceptualization, data collection, curation, and analysis, writing-original draft, writing-review and editing. JAM: conceptualization, supervision, curation, and analysis, writing-original draft, writing-review and editing. RC: data collection, writing review, and editing. SSC: data collection. GIM: conceptualization, data collection and analysis, supervision, writing-original draft, writing-review and editing.

Supporting Agencies: Not applicable.

Conflict of interests: The authors declare that there is no conflict of interest, financial or personal, in the information, presentation of data, and results of this article.

Appendix 1. List of species recorded in a 1-ha plot at the Los Tuxtlas Tropical Biology Station, established in the “Steeply dissected slopes” land unit. Species names are listed in alphabetical order by the family to which they belong (in bold typeface), following the APG IV (2016) classification system. Species number in each family is indicated in parentheses next to its name. Density is provided by individuals and stems (separated by a slash). Maximum height is given only for self-standing species (i.e., excluding lianas).

Families/Species	Growth form	Density (ha⁻¹)	Basal area (cm² ha⁻¹)	Maximum height (m)
ACTINIDIACEAE (1)				
<i>Saurauia yasicae</i> Loes.	Tree	7/22	13,142.18	20.0
ANACARDIACEAE (2)				
<i>Spondias radlkoferi</i> Donn. Sm.	Tree	7/0	15,630.40	29.0
<i>Tapirira mexicana</i> Marchand	Tree	10/15	14,135.55	28.0
ANNONACEAE (5)				
<i>Annona mucosa</i> Jacq.	Tree	1/3	27.68	3.5
<i>Cymbopetalum baillonii</i> R.E. Fr.	Tree	15/0	8,870.25	25.0
<i>Desmopsis ibarrarum</i> G.E. Schatz ex Ortíz-Rodr.	Tree	6/0	69.05	4.0
<i>Desmopsis trunciflora</i> (Schltdl. & Cham.) G.E. Schatz	Tree	3/6	156.04	8.5
<i>Tridimeris tuxtensis</i> G.E. Schatz	Tree	1/0	52.81	6.0
APOCYNACEAE (4)				
<i>Aspidosperma megalocarpon</i> Müll. Arg.	Tree	4/0	3,613.31	35.0
<i>Forsteronia acouci</i> (Aubl.) A. DC.	Liana	83/92	1,757.26	NA
<i>Prestonia clandestina</i> J.F. Morales	Liana	1/0	2.07	NA
<i>Tabernaemontana donnell-smithii</i> Rose	Tree	4/0	1,569.77	15.0
ARALIACEAE (1)				
<i>Dendropanax arboreus</i> (L.) Decne. & Planch.	Tree	16/18	6,082.85	28.0
ARECACEAE (8)				
<i>Astrocaryum mexicanum</i> Liebm. ex Mart.	Palm	1,483/0	37,794.99	8.5
<i>Bactris mexicana</i> Mart.	Palm	7/13	64.88	4.0
<i>Chamaedorea alternans</i> H. Wendl.	Palm	89/0	459.32	5.1
<i>Chamaedorea ernesti-augusti</i> H. Wendl.	Palm	45/0	84.84	4.0
<i>Chamaedorea oblongata</i> Mart.	Palm	168/0	297.87	7.3
<i>Chamaedorea pinnatifrons</i> (Jacq.) Oerst.	Palm	32/0	42.54	3.5
<i>Chamaedorea tepejilote</i> Liebm	Palm	60/133	871.08	6.5
<i>Desmoncus orthacanthos</i> Mart.	Liana	3/11	25.22	NA

Topography-related variation of rainforest attributes

Families/Species	Growth form	Density (ha ⁻¹)	Basal area (cm ² ha ⁻¹)	Maximum height (m)
ARISTOLOCHIACEAE (1)				
<i>Aristolochia ovalifolia</i> Duch.	Liana	6/0	63.13	NA
ASTERACEAE (6)				
<i>Critonia daleoides</i> DC.	Shrub	2/0	7.98	4.0
<i>Koanophyllon galeottii</i> (B.L. Rob.) R.M. King & H. Rob.	Tree	3/0	157.29	7.5
<i>Mikania hookeriana</i> DC.	Liana	4/0	48.63	NA
<i>Neurolaena lobata</i> (L.) Cass.	Tree	11/12	156.34	7.0
<i>Tuxtla pittieri</i> (Greenm.) Villaseñor & Strother	Liana	3/0	115.61	NA
<i>Vernonanthura patens</i> (Kunth) H. Rob.	Shrub	3/0	3.04	2.2
BIGNONIACEAE (10)				
<i>Amphitecna tuxtlensis</i> A.H. Gentry	Tree	5/7	100.35	8.0
<i>Anemopaegma chrysanthum</i> Dugand	Liana	9/0	55.55	NA
<i>Dolichandra unguis-cati</i> (L.) L.G. Lohmann	Liana	1/3	16.89	NA
<i>Fridericia candicans</i> (Rich.) L.G. Lohmann	Liana	9/10	196.46	NA
<i>Fridericia chica</i> (Bonpl.) L.G. Lohmann	Liana	4/0	43.39	NA
<i>Fridericia florida</i> (DC.) L.G. Lohmann	Liana	2/0	22.51	NA
<i>Fridericia schumanniana</i> (Loes.) L.G. Lohmann	Liana	6/0	123.43	NA
<i>Mansoa verrucifera</i> (Schltdl.) A.H. Gentry	Liana	17/0	255.21	NA
<i>Stizophyllum riparium</i> (Kunth) Sandwith	Liana	24/41	255.25	NA
<i>Tanaecium pyramidatum</i> (Rich.) L.G. Lohmann	Liana	17/20	454.83	NA
CORDIACEAE (1)				
<i>Cordia megalantha</i> S.F. Blake	Tree	1/0	4,447.16	28.0
BURSERACEAE (1)				
<i>Bursera simaruba</i> (L.) Sarg.	Tree	9/0	16,258.98	29.0
CANNABACEAE (1)				
<i>Trema micrantha</i> (L.) Blume	Tree	9/0	1,282.26	14.0
CAPPARACEAE (3)				
<i>Capparidastrium mollicellum</i> (Standl.) Cornejo & Iltis	Tree	7/0	507.19	15.0
<i>Capparidastrium tuxtlense</i> Cornejo & Iltis	Tree	1/2	53.45	7.0
<i>Crateva tapia</i> L.	Tree	2/0	31.95	5.0

Families/Species	Growth form	Density (ha ⁻¹)	Basal area (cm ² ha ⁻¹)	Maximum height (m)
CARICACEAE (1)				
<i>Carica papaya</i> L.	Tree	2/0	36.47	4.3
CELASTRACEAE (8)				
<i>Crossopetalum parviflorum</i> (Hemsl.) Lundell	Tree	1/2	4.21	3.0
<i>Haydenoxylon calzadae</i> (Lundell) Biral	Tree	6/9	727.94	10.0
<i>Hippocratea volubilis</i> L.	Liana	1/0	2.24	NA
<i>Monteverdia purpusii</i> (Lundell) Biral	Tree	2/0	59.31	7.2
<i>Pristimera caribaea</i> (Urb.) A.C. Sm.	Liana	17/19	135.35	NA
<i>Pristimera celastroides</i> (Kunth) A.C. Sm.	Liana	5/6	64.69	NA
<i>Salacia cordata</i> (Miers) Mennega	Liana	31/36	474.46	NA
<i>Salacia multiflora</i> (Lam.) DC.	Liana	6/8	49.26	NA
CLUSIACEAE (1)				
<i>Garcinia intermedia</i> (Pittier) Hammel	Tree	83/84	7,849.00	18.0
COMBRETACEAE (1)				
<i>Combretum laxum</i> Jacq.	Liana	23/27	505.68	NA
CONNARACEAE (1)				
<i>Connarus schultesii</i> Standl.	Liana	16/20	213.99	NA
CONVOLVULACEAE (1)				
<i>Ipomoea philomega</i> (Vell.) House	Liana	16/17	115.28	NA
DILLENIACEAE (1)				
<i>Tetracera volubilis</i> L.	Liana	1/5	32.69	NA
EBENACEAE (1)				
<i>Diospyros nigra</i> (J.F. Gmel.) Perr.	Tree	3/0	32.77	3.4
EUPHORBIACEAE (6)				
<i>Acalypha diversifolia</i> Jacq.	Shrub	19/48	130.39	4.1
<i>Alchornea latifolia</i> Sw.	Tree	14/0	5,787.28	25.0
<i>Croton schiedeana</i> Schltldl.	Tree	7/15	1,238.91	15.0
<i>Omphalea oleleifera</i> Hemsl.	Tree	42/43	16,865.64	28.0
<i>Sapium lateriflorum</i> Hemsl.	Tree	1/0	1.68	2.3
<i>Tetrorchidium rotundatum</i> Standl.	Tree	3/0	4,552.84	22.0

Topography-related variation of rainforest attributes

Families/Species	Growth form	Density (ha ⁻¹)	Basal area (cm ² ha ⁻¹)	Maximum height (m)
FABACEAE (14)				
<i>Erythrina folkersii</i> Krukoff & Moldenke	Tree	3/0	159.10	8.0
<i>Inga acrocephala</i> Steud.	Tree	11/0	1,465.01	14.0
<i>Inga mexicana</i> (T.D. Penn.) M. Sousa	Tree	3/7	7.67	2.5
<i>Inga paterno</i> Harms	Tree	7/0	76.67	8.0
<i>Inga pavoniana</i> G. Don	Tree	2/0	11.97	4.5
<i>Inga semialata</i> (Vell.) Mart.	Tree	1/2	1.66	2.0
<i>Lonchocarpus guatemalensis</i> Benth.	Tree	4/0	720.09	25.0
<i>Lonchocarpus septentrionalis</i> M. Sousa	Tree	1/2	82.16	4.2
<i>Machaerium floribundum</i> Benth.	Liana	5/7	108.83	NA
<i>Platymiscium dimorphandrum</i> Donn. Sm.	Tree	2/0	6,160.44	32.0
<i>Pterocarpus rohrii</i> Vahl	Tree	12/14	11,214.82	29.0
<i>Styphnolobium parviflorum</i> M. Sousa & Rudd	Tree	1/0	1,007.15	32.0
<i>Vachelia mayana</i> Lundell	Tree	1/0	16.05	6.0
<i>Vatairea lundellii</i> (Standl.) Killip ex Record	Tree	1/0	8.44	4.0
ICACINACEAE (1)				
<i>Mappia multiflora</i> Lundell	Tree	1/0	225.22	8.0
LACISTEMATAACEAE (1)				
<i>Lacistema aggregatum</i> (P.J. Bergius) Rusby	Tree	1/0	2.68	2.7
LAMIACEAE (1)				
<i>Aegiphila costaricensis</i> Moldenke	Tree	7/0	105.24	6.0
LAURACEAE (7)				
<i>Damburneya ambigens</i> (S.F. Blake) Trofimov	Tree	12/19	4,932.45	24.0
<i>Damburneya gentlei</i> (Lundell) Trofimov	Tree	24/26	2,175.22	25.0
<i>Damburneya inconspicua</i> (van der Werff) Trofimov	Tree	2/0	48.14	2.1
<i>Damburneya salicifolia</i> (Kunth) Trofimov & Rohwer	Tree	4/6	690.70	12.0
<i>Licaria velutina</i> van der Werff	Tree	30/39	2,757.00	17.0
<i>Ocotea heydeana</i> (Mez & Donn. Sm.) Bernardi	Tree	3/6	61.44	7.0
<i>Ocotea rubriflora</i> Mez	Tree	1/0	7.49	4.1

Families/Species	Growth form	Density (ha ⁻¹)	Basal area (cm ² ha ⁻¹)	Maximum height (m)
LOGANIACEAE (1)				
<i>Strychnos panamensis</i> Seem.	Liana	2/0	66.06	NA
MALPIGHIACEAE (4)				
<i>Bunchosia lindeniana</i> A. Juss.	Tree	21/24	347.35	6.5
<i>Mascagnia vacciniifolia</i> Nied.	Liana	3/0	26.16	NA
<i>Stigmaphyllon lindenianum</i> A. Juss.	Liana	8/0	101.78	NA
<i>Tetrapterys glabrifolia</i> (Griseb.) Small	Liana	1/0	28.73	NA
MALVACEAE (8)				
<i>Hampea nutricia</i> Fryxell	Tree	1/0	72.58	10.0
<i>Heliocarpus appendiculatus</i> Turcz.	Tree	2/0	267.03	13.0
<i>Mortoniendron guatemalense</i> Standl. & Steyererm.	Tree	1/0	88.77	20.0
<i>Ochroma pyramidale</i> (Cav. ex Lam.) Urb.	Tree	2/0	2,254.51	23.0
<i>Quararibea funebris</i> (La Llave) Vischer	Tree	40/46	10,959.77	24.0
<i>Quararibea yunckeri</i> Standl. subsp. <i>sessiliflora</i> Miranda ex W.S. Alverson	Tree	42/45	8,411.48	25.0
<i>Robinsonella mirandae</i> Gómez Pompa	Tree	2/0	231.57	24.0
<i>Trichospermum galeottii</i> (Turcz.) Kosterm.	Tree	5/0	3,983.48	26.0
MELIACEAE (5)				
<i>Guarea glabra</i> Vahl	Tree	45/54	39,767.67	25.0
<i>Guarea guidonia</i> (L.) Sleumer	Tree	5/0	3,042.08	30.0
<i>Trichilia martiana</i> C. DC.	Tree	3/4	655.29	12.0
<i>Trichilia moschata</i> Sw.	Tree	4/5	127.34	5.5
<i>Trichilia pallida</i> Sw.	Tree	59/84	1,988.70	16.2
MENISPERMACEAE (4)				
<i>Abuta panamensis</i> (Standl.) Krukoff & Barneby	Liana	4/0	140.79	NA
<i>Disciphania calocarpa</i> Standl.	Liana	2/0	21.86	NA
<i>Hyperbaena mexicana</i> Miers	Tree	1/0	29.34	6.0
<i>Odontocarya mexicana</i> Barneby	Liana	16/18	68.10	NA
METTENIUSACEAE (1)				
<i>Calatola uxpanapensis</i> P. Vera & T. Wendt	Tree	72/84	25,665.31	23.0

Topography-related variation of rainforest attributes

Families/Species	Growth form	Density (ha ⁻¹)	Basal area (cm ² ha ⁻¹)	Maximum height (m)
MONIMIACEAE (1)				
<i>Mollinedia viridiflora</i> Tul.	Tree	4/7	31.52	4.0
MORACEAE (8)				
<i>Brosimum alicastrum</i> Sw.	Tree	18/0	11,519.37	28.0
<i>Clarisia biflora</i> Ruiz & Pav.	Tree	22/23	19,573.73	28.0
<i>Ficus apollinaris</i> Dugand	Tree	3/0	3,510.17	30.0
<i>Ficus isophlebia</i> Standl.	Tree	4/19	1,194.55	29.0
<i>Ficus yoponensis</i> Desv.	Tree	5/8	1,740.23	40.0
<i>Poulsenia armata</i> (Miq.) Standl.	Tree	62/70	3,804.30	30.0
<i>Pseudolmedia glabrata</i> (Liebm.) C.C. Berg	Tree	200/219	21,716.10	28.0
<i>Trophis mexicana</i> (Liebm.) Bureau	Tree	220/282	5,494.13	15.0
MYRISTICACEAE (1)				
<i>Virola guatemalensis</i> (Hemsl.) Warb.	Tree	24/28	5,698.28	35.0
MYRTACEAE (5)				
<i>Eugenia aeruginea</i> DC.	Tree	3/0	952.29	15.0
<i>Eugenia colipensis</i> O. Berg	Tree	6/0	273.22	13.0
<i>Eugenia karwinskyana</i> O. Berg	Tree	2/4	33.54	5.0
<i>Eugenia macrocarpa</i> Roxb.	Tree	13/15	196.16	12.0
<i>Myrcia neopallens</i> A.R. Lourenço & E. Lucas	Tree	3/4	274.23	8.0
NYCTAGINACEAE (1)				
<i>Pisonia aculeata</i> L.	Liana	4/5	410.60	NA
OCHNACEAE (1)				
<i>Ouratea theophrasta</i> (Planch.) Baill.	Tree	2/0	3.14	2.5
PIPERACEAE (10)				
<i>Piper aduncum</i> L.	Shrub	6/21	69.56	5.8
<i>Piper aequale</i> Vahl	Shrub	111/461	915.94	3.8
<i>Piper auritum</i> Kunth	Tree	2/3	14.09	2.3
<i>Piper berlandieri</i> C. DC.	Tree	16/39	2,233.25	10.0
<i>Piper chamissonis</i> (Miq.) Steud. ex C. DC.	Tree	1/2	3.74	1.8
<i>Piper fraguanum</i> Trel.	Shrub	4/14	59.96	4.2

Families/Species	Growth form	Density (ha ⁻¹)	Basal area (cm ² ha ⁻¹)	Maximum height (m)
<i>Piper hispidum</i> Sw.	Shrub	15/60	77.63	3.5
<i>Piper lapathifolium</i> (Kunth) Steud.	Shrub	1/2	3.78	2.1
<i>Piper papantlense</i> C. DC.	Tree	5/17	337.68	8.0
<i>Piper yzabalanum</i> C. DC. ex Donn. Sm.	Shrub	1/0	1.54	2.5
POLYGONACEAE (2)				
<i>Coccoloba carnevalii</i> J.J. Ancona, P. Hern.-Led. & J.J. Ortiz-Díaz	Tree	3/6	350.74	8.0
<i>Coccoloba hondurensis</i> Lundell	Tree	1/0	3.46	1.5
PRIMULACEAE (3)				
<i>Ardisia compressa</i> Kunth	Tree	1/0	1.54	1.7
<i>Ardisia tuerckheimii</i> Donn. Sm.	Shrub	1/0	2.86	2.7
<i>Parathesis calzadae</i> Lundell	Tree	1/0	23.54	6.4
RHAMNACEAE (1)				
<i>Gouania lupuloides</i> (L.) Urb.	Liana	1/0	11.27	NA
RUBIACEAE (9)				
<i>Faramea occidentalis</i> (L.) A. Rich.	Tree	64/76	3,410.61	15.0
<i>Hamelia longipes</i> Standl.	Tree	19/35	801.82	7.0
<i>Palicourea faxlucens</i> (Lorence & Dwyer) Lorence	Tree	1/0	486.63	7.5
<i>Palicourea simiarum</i> (Standl.) Borhidi	Tree	18/20	1,287.90	13.0
<i>Palicourea tetragona</i> (Donn. Sm.) C.M. Taylor & Lorence	Tree	42/51	2,663.10	14.0
<i>Psychotria flava</i> Oerst. ex Standl.	Tree	5/0	114.44	6.0
<i>Psychotria sarapiquensis</i> Standl.	Tree	1/0	2.15	2.4
<i>Randia pterocarpa</i> Lorence & Dwyer	Tree	2/0	18.32	2.7
<i>Randia retroflexa</i> Lorence & M. Nee	Tree	1/0	1.40	NA
RUTACEAE (1)				
<i>Zanthoxylum acuminatum</i> (Sw.) Sw.	Tree	1/0	145.77	12.0
SALICACEAE (3)				
<i>Casearia sylvestris</i> Sw.	Tree	2/3	218.66	14.0
<i>Lunania mexicana</i> Brandegee	Tree	13/14	1,593.99	17.0
<i>Pleuranthodendron lindenii</i> (Turcz.) Sleumer	Tree	17/20	2,751.47	15.0

Topography-related variation of rainforest attributes

Families/Species	Growth form	Density (ha ⁻¹)	Basal area (cm ² ha ⁻¹)	Maximum height (m)
SAPINDACEAE (5)				
<i>Allophylus camptostachys</i> Radlk.	Tree	3/0	1,063.09	12.5
<i>Cupania glabra</i> Sw.	Tree	1/0	5.35	6.0
<i>Paullinia clavigera</i> Schltldl.	Liana	13/16	96.55	NA
<i>Paullinia venosa</i> Radlk.	Liana	1/0	21.24	NA
<i>Talisia macrophylla</i> (Mart.) Radlk.	Tree	2/0	45.33	6.0
SAPOTACEAE (6)				
<i>Chrysophyllum venezuelanense</i> (Pierre) T.D. Penn.	Tree	1/0	118.57	12.0
<i>Lucuma campechiana</i> Kunth	Tree	1/0	2.50	2.2
<i>Peteniodendron durlandii</i> (Standl.) Lundell	Tree	14/17	2,291.58	19.0
<i>Pouteria reticulata</i> (Engl.) Eyma	Tree	1/0	11.27	4.1
<i>Pouteria rhynchocarpa</i> T.D. Penn.	Tree	18/24	810.49	11.0
<i>Sideroxylon portoricense</i> Urb. subsp. <i>minutiflorum</i> (Pittier) T.D. Penn.	Tree	20	15,578.03	25.5
SIPARUNACEAE (1)				
<i>Siparuna thecaphora</i> (Poepp. & Endl.) A. DC.	Tree	13/16	59.99	4.9
SMILACACEAE (2)				
<i>Smilax aristolochiifolia</i> Mill.	Liana	3/4	20.03	NA
<i>Smilax domingensis</i> Willd.	Liana	1/2	13.33	NA
SOLANACEAE (3)				
<i>Cestrum racemosum</i> Ruiz & Pav.	Tree	3/0	114.20	7.1
<i>Cestrum</i> sp.	Tree	1/0	20.12	6.0
<i>Solanum schlechtendalianum</i> Walp.	Tree	2/4	34.82	5.0
STAPHYLEACEAE (1)				
<i>Turpinia occidentalis</i> (Sw.) G. Don	Tree	1/0	39.57	2.2
ULMACEAE (1)				
<i>Ampelocera hottlei</i> (Standl.) Standl.	Tree	3/0	4,808.67	26.9
URTICACEAE (4)				
<i>Cecropia obtusifolia</i> Bertol.	Tree	63	7,557.02	28.0
<i>Myriocarpa longipes</i> Liebm.	Tree	228/484	11,008.57	12.2

Families/Species	Growth form	Density (ha ⁻¹)	Basal area (cm ² ha ⁻¹)	Maximum height (m)
<i>Urera glabriuscula</i> V.W. Steinmann	Tree	5/24	263.06	5.3
<i>Urera simplex</i> Wedd.	Tree	6/16	153.08	5.0
VERBENACEAE (1)				
<i>Citharexylum affine</i> D. Don	Tree	1/0	165.47	14.0
VIOLACEAE (2)				
<i>Orthion veracruzense</i> Lundell	Tree	2/0	253.48	11.0
<i>Rinorea guatemalensis</i> (S. Watson) Bartlett	Tree	11/12	1,051.52	15.0
VITACEAE (3)				
<i>Cissus gossypifolia</i> Standl.	Liana	21/24	405.50	NA
<i>Cissus microcarpa</i> Vahl	Liana	2/0	29.17	NA
<i>Vitis tiliifolia</i> Humb. & Bonpl. ex Schult.	Liana	2/0	18.32	NA
VOCHYSIACEAE (1)				
<i>Vochysia guatemalensis</i> Donn. Sm.	Tree	1/0	751.83	21.0