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STRUCTURE AND TREE DIVERSITY PATTERNS AT THE LANDSCAPE LEVEL IN A MEXICAN TROPICAL DECIDUOUS FOREST

ELVIRA DURÁN^{1, 2, 6}, JORGE A. MEAVE³, EMILY J. LOTT⁴ AND GERARDO SEGURA⁵

¹ Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Unidad Oaxaca, Instituto Politécnico Nacional, Calle Hornos 1003, Sta. Cruz Xoxocotlán 71230, Oaxaca, Mexico.

² Unidad Académica de Geografía, Instituto de Geografía, Universidad Nacional Autónoma de México, Aquiles Serdán 382, Morelia 58000, Michoacán, Mexico.

³ Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, México 04510, D.F., Mexico.

⁴ Plant Resources Center, University of Texas at Austin, Austin, TX, 78712, USA

⁵ The World Bank, 1818 H Street NW, Washington, DC 20433, USA

⁶ Author for correspondence: CIIDIR-Oaxaca, IPN. Phone: +52 (951) 517-06-10 Ext. 82748; e-mail: eduran3@hotmail.com

Abstract: Landscape level variability of structure and tree species diversity was analyzed in a tropical deciduous forest at Chamela, Mexico. Trees with DBH ≥ 5 cm were sampled in 21 0.24 ha plots (5.04 ha in total) distributed among six different morpho-pedological land units. Average density was 1,385 individuals ha⁻¹, basal area 15.9 m² ha⁻¹, and canopy height 6.8 m. Trunks with DBH ≤ 14 cm accounted for 90% of the entire set. A total of 148 species, 102 genera, and 43 families were recorded. Seventy percent of all species were poorly represented (< 10 individuals ha⁻¹). A Principal Component Analysis (PCA) based on structure and diversity variables showed that plots from the same morpho-pedological land unit were not always located close to each other along the two first axes, but a further PCA based on dominant species clearly divided two groups of plots. Although canopy structure and tree species diversity varied continuously across the landscape, β -diversity (evaluated through species similarity between plot pairs) and the identities of dominant species exhibited the clearest distinction. The dichotomy between granitic vs. non-granitic lithology was the condition most clearly related with a lower similarity in species composition and the strongest contrast in the dominant species group.

Key words: Chamela, lithology, mesoscale, Mexico, morpho-pedological land units, species composition, tree community.

Resumen: La variabilidad a nivel de paisaje de la estructura y la composición de especies fue analizada en el bosque tropical caducifolio de Chamela, México. Se registraron todos los árboles con DAP ≥ 5 cm presentes en 21 parcelas de 0.24 ha (5.04 ha en total) distribuidas en seis unidades morfopedológicas diferentes. En promedio, la densidad fue de 1,385 individuos ha⁻¹, el área basal de 15.9 m² ha⁻¹ y la altura promedio del dosel fue 6.8 m. La mayoría (90%) de los troncos tuvieron un DAP ≤ 14 cm. En total se registraron 148 especies, 102 géneros y 43 familias de árboles. Más de 70% de las especies estuvieron pobremente representadas (< 10 árboles ha⁻¹). Un análisis de componentes principales basado en atributos estructurales y de diversidad mostró una pobre relación entre las parcelas de una misma unidad morfopedológica, pero el mismo tipo de análisis, basado en las especies dominantes, segregó a las parcelas en dos grupos. Aunque la estructura y la diversidad de especies cambiaron de forma continua en el paisaje, la diversidad beta (evaluada a través de la similitud de especies entre pares de parcelas) y el grupo de especies dominantes mostraron los mayores contrastes. Tales diferencias estuvieron claramente asociadas a diferencias en la litología (granito vs. no-granito).

Palabras clave: Chamela, composición de especies, comunidad de árboles, litología, mesoescala, México, unidades morfopedológicas.

Characterization of the structure and species composition of tree communities is the first step in understanding forest ecology and dynamics. For example, such information has been useful for comparing and understanding historical and ecological relationships among forests (Ashton *et al.*, 2004). Data on tree species distribution also allow to unravel complex concepts and develop models on

plant communities and their spatial patterns (Connell, 1978; Hubbell, 2001; Wright, 2002; Chase, 2005). The analysis of tree community structure and diversity is still challenging for researchers in tropical ecology (Bawa *et al.*, 2004; Losos *et al.*, 2004).

Traditionally, studies focused on tree communities had placed more emphasis on tropical humid forests (Richards,

1996), whereas tropical deciduous forests (TDFs) have received much less attention, despite their widespread occurrence in the inter-tropical belt (Murphy and Lugo, 1986; Bullock *et al.*, 1995). Nowadays, TDFs are becoming better studied, but basic knowledge about their structure and tree diversity patterns at the landscape level is still lacking. Moreover, detailed analyses on tree community structure and diversity in tropical forests have been commonly conducted at local scales (a few hectares or less), including the notorious efforts in “large” plots (≥ 16 -50 ha; Campbell, 1994; Losos *et al.*, 2004). In contrast, relatively few analyses are available at the mesoscale (hundreds of hectares to dozens of squared kilometers, *sensu* Delcourt and Delcourt, 1988).

At the mesoscale or landscape level, either through direct observation or by remote sensing tools, undisturbed tropical forests appear to exhibit homogeneous canopies (Campbell, 1994; Richards, 1996; Kalacska *et al.*, 2004). However, vegetation and plant community ecologists agree in that tree canopies regularly comprise a mixture of different structural and compositional patches (Cleef *et al.*, 1982; Rzedowski, 1986; Gentry and Ortiz, 1993; Condit, 1996; Ricklefs, 2000). Therefore, the analysis of the degree of structural and compositional heterogeneity in tropical landscapes is of paramount importance. Landscape level studies in tropical forests have documented spatial patterns in plant communities and explored their ecological relationships with physical factors, including geomorphology, soils, landforms, elevation and lithology. However, the heterogeneity of these factors is sometimes difficult to examine at smaller spatial scales (Duijvenvoorden and Lips, 1994; Clark *et al.*, 1995; Condit, 1996; Tuomisto *et al.*, 1995; Vázquez-G. and Givnish, 1999; Villers *et al.*, 2003; Pérez-García and Meave, 2004). These studies indicate that an initial survey of the physical environmental mosaic may suggest differences between habitats, allowing to put forward preliminary hypotheses on the relationships between vegetation patterns and the physical environment (Campbell, 1994; Wright, 2002). Knowledge of a landscape’s physical environment may also help locate vegetation samples and orient the discussion of results (Chazdon, 1996; Ricklefs, 2000).

Among Mexican TDFs, the ecosystem of Chamela (Jalisco State, Mexico), is one of the best known, because numerous patterns and processes have been studied there during more than three decades (Maass *et al.*, 2005). Particularly, tree community patterns have been described through rapid assessment procedures (Lott *et al.*, 1987), by detailed analyses in small-watersheds (Galicía *et al.*, 1999; Balvanera *et al.*, 2002; Segura *et al.*, 2003), and through meticulous review of data from different studies (Durán *et al.*, 2002). However, until now an examination of structure, species composition and diversity patterns at the landscape level is lacking. Thus, based on previous studies of the dif-

ferent morpho-pedological land units (Cotler *et al.*, 2002; Durán, 2004), here we aimed at describing and analyzing tree community patterns in the TDF of Chamela. We addressed two questions: How much does structure in the tree community vary across the landscape? How is tree species diversity organized within a mosaic of different morpho-pedological land units?

Materials and methods

Study Site. The study site was the Chamela Biological Field Station, which belongs to the Universidad Nacional Autónoma de México. It is located near the Pacific coast of Jalisco State, western Mexico. The climate, according to García’s (1988) modification of Köppen’s system, is the driest among tropical humid climates (A_{w0}). Mean annual temperature and precipitation are 24.9°C and 748 mm, respectively. A strong seasonality is observed, with 88% of annual precipitation falling between June and October (Bullock, 1986). In the 1,600 ha study area, 14 morpho-pedological land units were identified (figure 1; Cotler *et al.*, 2002; Durán, 2004). Tropical deciduous forest (TDF) dominates the landscape and is present in 11 out of the 14 land units, with the vegetation cover in the remaining units being tropical subdeciduous forest (Durán *et al.*, 2002).

Tree community characterization. The tree community (DBH ≥ 5 cm) was studied in 21 plots of 0.24 ha each (30 \times 80 m). Plots were distributed among the six largest and most contrasting morpho-pedological land units with TDF (figure 1): (1) SAG: Summit areas on granite, (2) SAT: Summit areas on tuffs, (3) LSG: Low rectilinear slopes on granite, (4) ISG: Intermediate rectilinear slopes on granite, (5) HSG: High rectilinear slopes on granite, and (6) SACG: Summit areas with conglomerates cover on granite. In each land unit, the plots were established in similar slope and soil depth conditions.

Individual trunks were counted and their DBH measured. Canopy height was measured in each plot along two 80 m parallel transects, with 42 point readings taken at 2 m intervals with an optical range finder. Species level taxonomic identities were recorded *in situ*; in case of doubt identification was confirmed by comparison of tree samples with herbarium specimens.

Data analysis. Structure and diversity descriptive parameters were compared between the six morpho-pedological land units with non-parametric Kruskal-Wallis tests (Siegel and Castellan, 1995). Diversity was assessed through species richness and Shannon (base e) and Simpson indices (Magurran, 1990). Comparisons of shared species between pairs of plots (β -diversity), were made by calculating the quantitative version of Sørensen similarity index, which is less sensitive to very abundant species (Magurran, 1990;

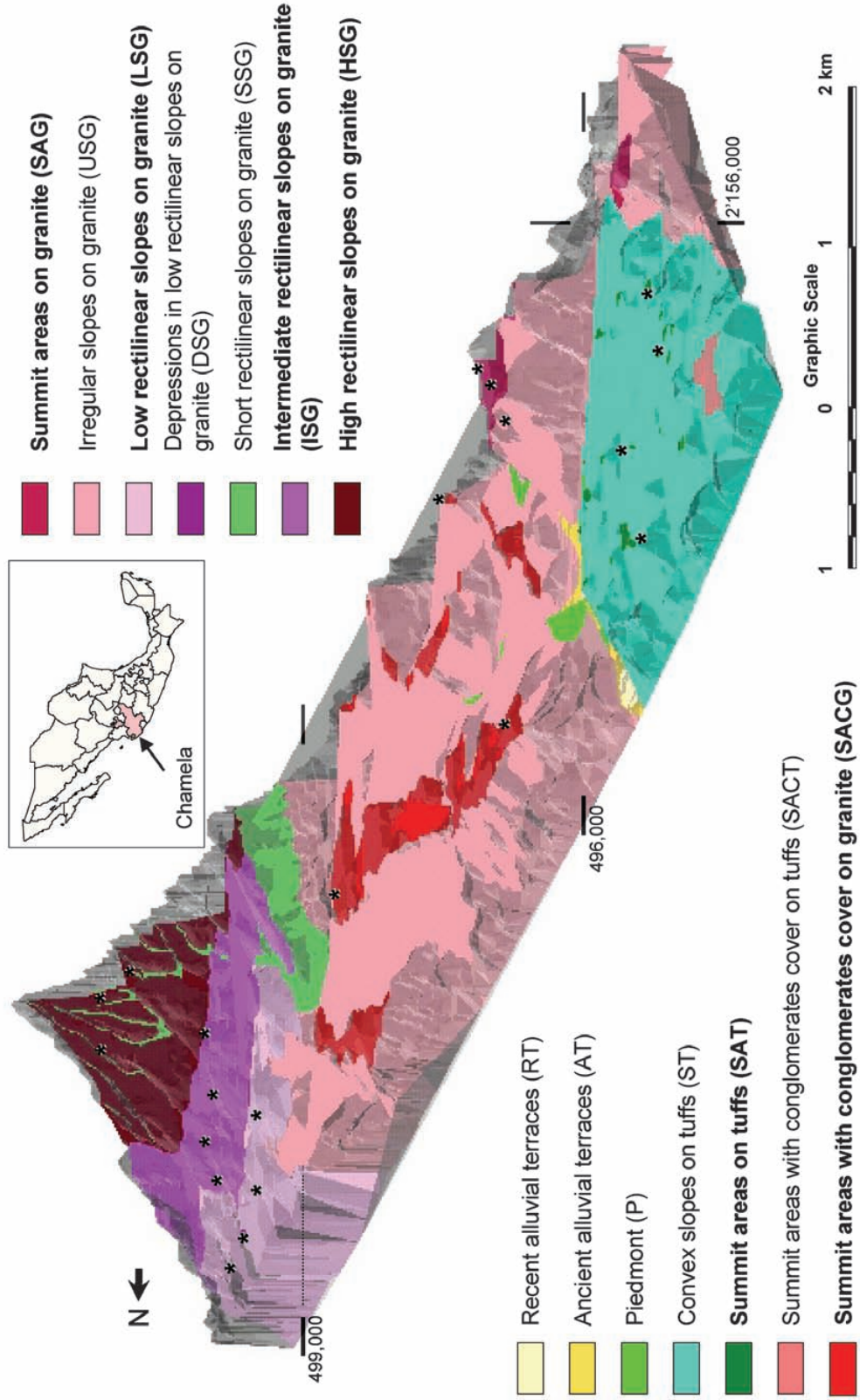


Figure 1. Three dimensional morpho-pedological map of the Chamela Biological Station in Jalisco, Mexico. Asterisks indicate the plot location on the morpho-pedological land units analyzed in this study (in bold). The vertical exaggeration factor was 3, and the grey color in borders is product of a technical deformation (UTM projection, Zone 14, Datum Nad 27, Spheroid Clarke 1886, Grid 1,000 m).

Moreno, 2001). Species abundances were used, according to the following formula:

$$\text{Sørensen index} = \frac{2 jN}{(aN + bN)}$$

where jN = sum of the lowest abundance values of each pair of species shared by the two plots, aN = total number of individuals in plot A, and bN = total number of individuals in plot B. Four similarity categories were defined based on this index: low (≤ 0.25), moderate ($> 0.25 - 0.50$), high ($> 0.50 - 0.75$), and very high (> 0.75). Frequency distributions in these categories were compared through Kruskal-Wallis tests (Siegel and Castellan, 1995); the number of species shared in plot pairs and similarity values for plot pairs located in the same and in different lithologies were compared by t -tests.

Species and family dominance was determined by plot, by morpho-pedological land unit, and for all plots combined. Percent dominance was estimated by using the equation:

$$\% \text{ dominance} = \frac{\text{relative density (\%)} + \text{relative basal area (\%)}}{2}$$

Completeness of the tree richness representation in the landscape was assessed by drawing cumulative species-area curves derived from the non-parametric Chao 1 model (Colwell, 2000), which uses species abundances for making the prediction (Moreno, 2001). Cumulative frequency was the mean value of 50 iterations for each morpho-pedological land unit (three or four increments) and for the entire study (21 increments). Observed and estimated species richness were compared through χ^2 tests (Siegel and Castellan, 1995).

Principal Component Analysis (PCA) was used to analyze the variation in structure and species composition among morpho-pedological land units (Jongman *et al.*, 1994). One PCA used a matrix with 15 structural variables per plot (number of trees, number of stems, mean DBH, standard deviation of DBH, total basal area, mean height, standard deviation of height, number of multi-stemmed trees, percent proportion of multi-stemmed trees, sum of importance values of the five most dominant species, Shannon index, Simpson index, number of species, number of genera, and number of families). A second PCA was performed based on a matrix containing percent dominance values of the ten most dominant species in each plot (63 species in total). Differences between plot scores on the first two Principal Components, when plots were grouped by morpho-pedological land units and by lithology (granite vs. non-granite) were compared through Mann-Whitney tests.

Results

Structure, diversity and species composition. Tree community structure was highly variable within and among morpho-pedological land units (table 1a). Mean density for the 21 plots was 1,385 individual trees ha^{-1} (range: 804 — 2,117 trees ha^{-1}). SAG plots had the largest tree density; however, basal area in them was lower than in other land units where densities were lower (SAT, SACG, and LSG). These differences are related to the frequencies in DBH classes. Trunks with ≤ 14 cm DBH accounted for 90% of the total (figure 2a). SAT, SACG, and LSG land units showed similar relative frequencies in the $\geq 5-14$ ($\pm 85\%$) and $\geq 15-24$ ($\pm 10\%$) DBH classes; in contrast, SAG and ISG land units had the most slender trunks. Overall, trunks with ≥ 25 cm DBH were infrequent (2.5%). Although some trees reached heights of 17 m, more than 61% of the 1,722 canopy height readings ranged between 5 and 9 m, and 4% of them were ≤ 2 m (figure 2c). Mean canopy height for the 21 plots was 6.82 m (± 1.99 , S.D.). Only for SAG mean height was shorter (5.9 m) than the overall mean, but it displayed a larger coefficient of variation (36.6%) than the other land units. In addition, the proportion of multi-stemmed trees was similar on granite land units (SAG, LSG, ISG, HSG), where it was around 15%, but in plots on non-granite lithology (tuffs and conglomerates) this condition was observed in about 20% of trees (table 1a). Significant differences in the proportion of multi-stemmed trees were found between plots on granite and non-granite lithology ($U = 21$, $P < 0.05$).

In total, 42 families, 102 genera and 148 species were recorded (table 1b). Maximum and minimum values showed that richness at family, genera and species level, as well as diversity indices, were highly variable among plots. There were no significant differences in tree diversity between morpho-pedological land units ($U = 5$, $P = 0.05$), even though extreme diversity values were found in SACG and HSG. Families with the largest genera and species richness were Leguminosae, Euphorbiaceae and Rubiaceae (figure 3a, b; appendix 1). The three most speciose genera were *Lonchocarpus*, *Bursera*, and *Caesalpinia*, which together accounted for 28% of total species richness (figure 3c). The families/genera (1:2.4), families/species (1:3.5), and genera/species (1:1.4) ratios indicate that genera richness is relatively large in the canopy of Chamela's TDF. Most families, genera and species were poorly represented, despite their important contributions to richness. Species composition and abundance were variable among plots and morpho-pedological land units, and no single species occurred or was dominant in all land units (table 2; appendix 1). When data for all plots were combined, *Caesalpinia eriostachys* emerged as the most dominant species (importance value of 12.5%).

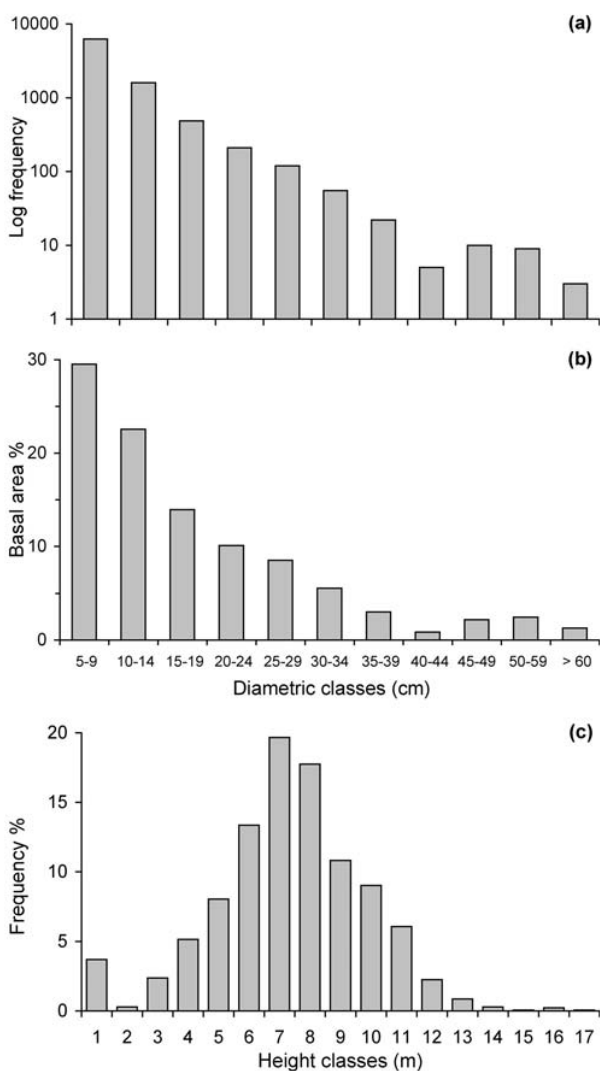


Figure 2. Structure of the tree component of Chamela's TDF. (a) Frequency distribution in diameter classes. (b) Percent distribution of basal area among diameter classes. (c) Frequency distribution of canopy height readings.

Spatial organization. Species-area curves suggested that a large proportion of the tree species richness of Chamela's TDF was represented in the five hectares covered by this study (figure 4a, b). However, it is likely that there are more tree species, given the significant differences between the observed and estimated species richness from the curves based on all 21 plots ($\chi^2 = 35.75$, $P < 0.05$). Particularly, the number of species may be larger in the four land units for which significant differences ($P < 0.05$) between observed and estimated species richness were obtained (SAT, $\chi^2 = 7.98$; SACG, $\chi^2 = 11.08$; LSG, $\chi^2 = 18.31$; HSG, $\chi^2 =$

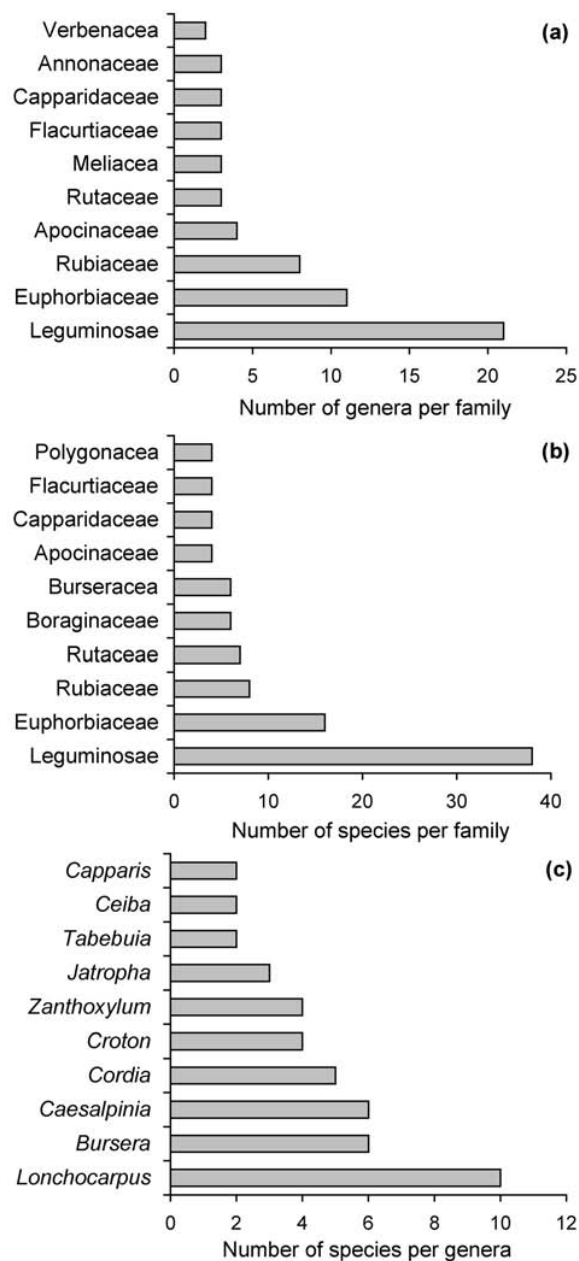


Figure 3. (a) Distribution of genera among the most important families. (b) Distribution of species among families. (c) Distribution of species among genera.

Table 1. Synthesis of tree community structure and diversity variables for the total sample (5.04 ha) and for the six analyzed morpho-pedological land units. Mean values include standard deviations, in parenthesis. Abbreviations: SAG = Summit areas on granite; SAT = Summit areas on tuffs; SACG = Summit areas with conglomerates cover on granite; LSG = Low slopes on granite; ISG = Intermediate slopes on granite; HSG = High slopes on granite.

	All Plots			Morpho-pedological land units					
	Total	Mean (S.D.)	Range	SAG	SAT	SACG	LSG	ISG	HSG
(a) Structure									
Density (trees ha ⁻¹)		1,386 (347)	804-2,117	1,772 (92)	1,163 (250)	1,307 (111)	1,297 (512)	1,347 (204)	1,543 (499)
DBH (cm)		9.4 (1.3)	5-72	8.5 (3.6)	10.1 (6.6)	9.9 (5.3)	10.3 (6.5)	8.2 (3.6)	9.3 (4.6)
Basal area (m ² ha ⁻¹)		15.9 (5.3)	6.7-27.6	14.8 (4.2)	17.6 (3.5)	17.1 (3.8)	18.8 (8.9)	10.7 (4.4)	16.4 (2.6)
Canopy height (m)		6.8 (2.0)	2-17	5.7 (1.8)	6.6 (2.3)	7.6 (2.3)	7.4 (1.8)	6.0 (1.8)	7.9 (1.9)
Multiple-stemmed trees (%)		17.2 (6.7)	9.7-38	14.7 (0.4)	22.4 (10.8)	21.6 (7.9)	14.9 (5.7)	13.8 (0.7)	15.8 (6.3)
(b) Diversity									
Number of species	148	44 (9)	30-58	45 (2)	46 (11)	38 (11)	45 (12)	43 (9)	48 (3)
Number of genera	102	36 (7)	22-51	37 (0)	36 (9)	30 (11)	34 (5)	40 (10)	40 (2)
Number of families	42	22 (4)	16-28	20 (2)	24 (5)	20 (6)	21 (4)	23 (4)	25 (2)
Shannon Index		3.08 (0.33)	2.30-3.47	3.17 (0.11)	3.08 (0.28)	2.69 (0.52)	2.99 (0.34)	3.19 (0.27)	3.33 (0.16)
Simpson Index		14.80 (5.12)	5.2-24.3	16.3 (2.9)	13.8 (4.1)	9.7 (6.5)	12.49 (4.2)	17.0 (3.8)	20.0 (4.9)

Table 2. Percent dominance values for the ten dominant tree canopy species in the entire sample and in the different morpho-pedological units where they occur. Dominant species in the entire community account for a large proportion of the total value for all species, but they are not always the most important in the different units, and in some cases, that they are not even present. Abbreviations: SAG = Summit areas on granite; SAT = Summit areas on tuffs; SACG = Summit areas with conglomerates cover on granite; LSG = Low slopes on granite; ISG = Intermediate slopes on granite; HSG = High slopes on granite.

Species	All Plots	Morpho-pedological units					
		SAG	SAT	SACG	LSG	ISG	HSG
<i>Caesalpinia eriostachys</i>	12.5	7.9	22.6	18.2	15.1	-	8.5
<i>Gliricidia sepium</i>	4.3	8.1	-	0.7	4.6	7.3	6.1
<i>Plumeria rubra</i>	4.2	10.2	0.2	0.6	3.9	9.9	1.3
<i>Exostema caribaeum</i>	4.1	1.7	0.1	-	5.6	7.4	8.5
<i>Lonchocarpus constrictus</i>	4.1	0.4	8.8	13.1	2.3	0.5	1.8
<i>Caesalpinia coriaria</i>	3.9	-	3.5	12.0	6.7	-	-
<i>Cordia alliodora</i>	3.5	1.0	4.3	0.8	5.8	2.9	5.0
<i>Apoplanesia paniculata</i>	2.7	1.7	7.9	7.9	0.4	-	-
<i>Cordia elaeagnoides</i>	2.7	-	2.4	7.9	5.0	-	-
<i>Psidium sartorianum</i>	2.7	0.8	0.3	0.1	6.4	4.2	3.0
Sum	44.9	31.7	49.9	61.3	55.8	32.1	34.2
Total for all species	148	69	74	68	92	78	85

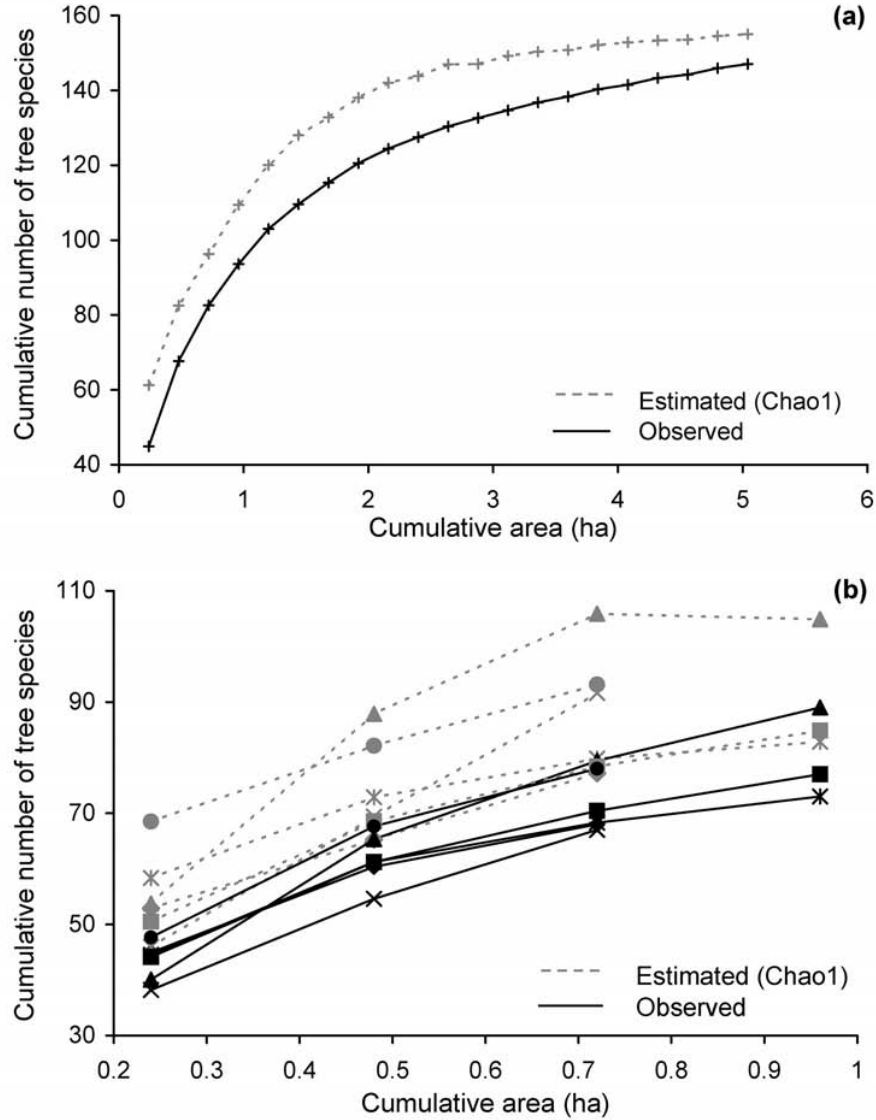


Figure 4. Observed and estimated species-area curves with Chao 1 model. (a) Cumulative species-area curve for 21 plots (total area = 5.04 ha). (b) Cumulative species-area curve for each morpho-pedological land unit (3 or 4 plots). Symbols and abbreviations: diamond = SAG (Summit areas on granite); asterisk = SAT (Summit areas on tuffs); cross = SACG (Summit areas with conglomerates cover on granite); triangle = LSG (Low slopes on granite); square = ISG (intermediate slopes on granite); circle = HSG (high slopes on granite).

11.45). In contrast, observed and estimated values did not differ significantly in SAG and ISG, suggesting that a surface < 1 ha is sufficient to represent species richness in them. Different slopes in species-area curves by morpho-pedological land unit suggested differences, albeit moderate, in the total diversity of each one (figure 4b). SACG was consistently the poorest land unit regarding species richness, while HSG and LSG appeared as the most diverse.

The number of species shared in plot pairs was very

variable (range: 4 - 40 species). However, an overall large species turnover (β -diversity) was observed in Chamela's TDF, because 50% of 210 comparisons performed between pairs of plots produced low similarities (Sørensen index ≤ 0.25), whereas not a single one had a value > 0.75 (figure 5). Frequencies in three similarity categories (low, moderate, high) differed significantly from each other ($\chi^2 = 159.2$; $P < 0.05$). In addition, the mean number of shared species between two plots from different lithologies was signifi-

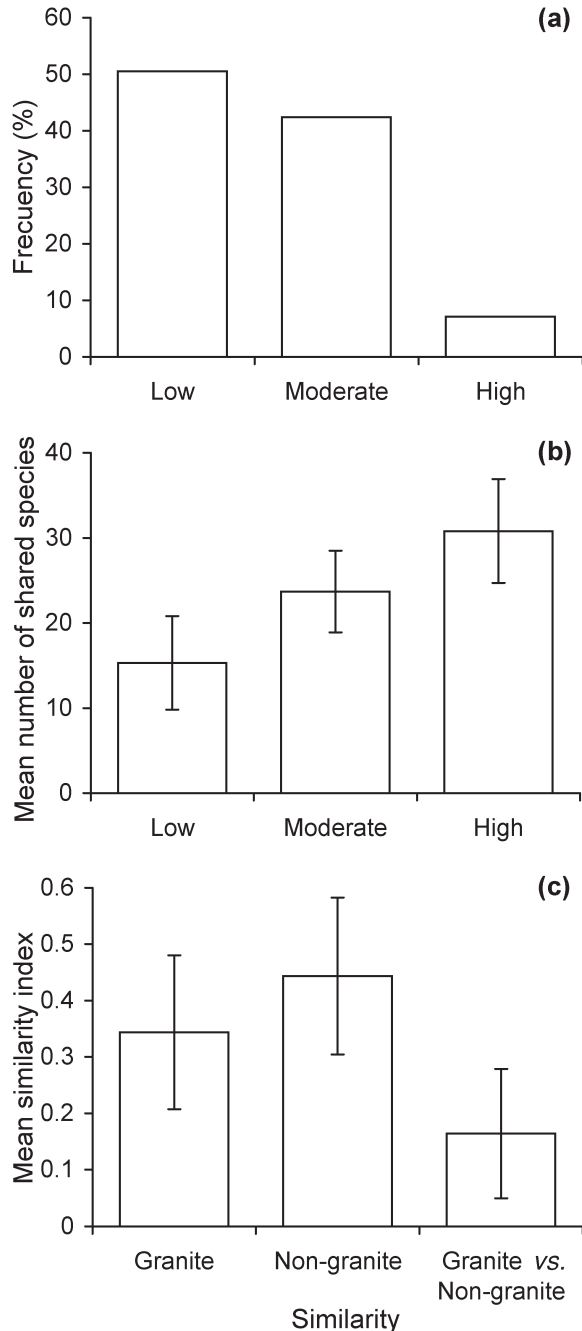


Figure 5. (a) Frequency of the Sørensen index values in three different similarity categories. (b) Mean (± 1 S.D.) number of species shared in different similarity categories. (c) Mean (± 1 S.D.) similarity values within and between lithologies.

cantly smaller than the mean number of shared species by plots from the same lithology, either granite or non-granite ($t = 7.80$; $P < 0.05$). The comparison of similarity index values for plot pairs from mixed lithologies and from a single lithology was also significant ($t = 10.73$; $P < 0.05$).

PCA ordination showed that plots from the same morpho-pedological land unit were not in close proximity to each other (figures 6a, b). However, significant differences in the scores of plots from granite and non-granite lithology were obtained for the second Principal Component (PC2) based on structural attributes ($U = 14$; $P < 0.05$), and for the first two axes (PC1 and PC2) based on dominant species ($U = 96$, and $U = 75$; $P < 0.05$). In the structure-based PCA, PC1 and PC2 explained together 69% of total variance (figure 6a). Plots located on the right (positive) side of PC1 had larger DBH and height means, while those located on the upper (positive) part of PC2 had large dominance values for the five most important species, and they were the least dense and diverse. In contrast, in the PCA based on dominant species, the first two principal components accounted for 32% of variance. *Bourreria purpusii*, *Comocladia engleriana*, *Gliricidia sepium*, and *Plumeria rubra* made a major contribution in defining PC1, whereas *Bahuinia unglata*, *Erythroxylum mexicanum*, *Cordia alliodora* and *Croton pseudoniveus* took the lead in defining PC2.

Discussion

Structure and species diversity. Chamela’s TDF canopy is essentially dominated by trees, contrasting with other Mexican TDFs, where arborescent columnar cacti stand out among the physiognomic elements (Rzedowski, 1986; Búrquez *et al.*, 1999; Pérez-García *et al.*, 2001). Based on the analysis of trees with DBH ≥ 5 cm, Chamela’s TDF may be described as having a moderate to high density ($> 1,000$ individuals ha^{-1}), with a prevailing DBH of < 10 cm and a typical inverse J-shaped distribution, a canopy mean height ≤ 10 m, and a minor presence of multi-stemmed trees ($< 20\%$). In total, 148 tree species were identified, and apparently species diversity was high everywhere (average per plot = 40 species). Both structural attributes and species diversity estimators displayed spatial differences, and even the dominant species group was variable among sites. Such variability does not seem to be an exclusive character of Chamela, as it has been found in other tropical forest landscape studies (Vázquez-G. and Givnish, 1998; Duivenvoorden and Lips, 1995; Kalacska *et al.*, 2004; Pérez-García *et al.*, 2005).

The spatial variation in tree canopy structure and composition calls out for caution when attempting to extrapolate local particularities to landscape or regional levels. When comparisons between tree communities are performed, the use of unique or mean values for structural and

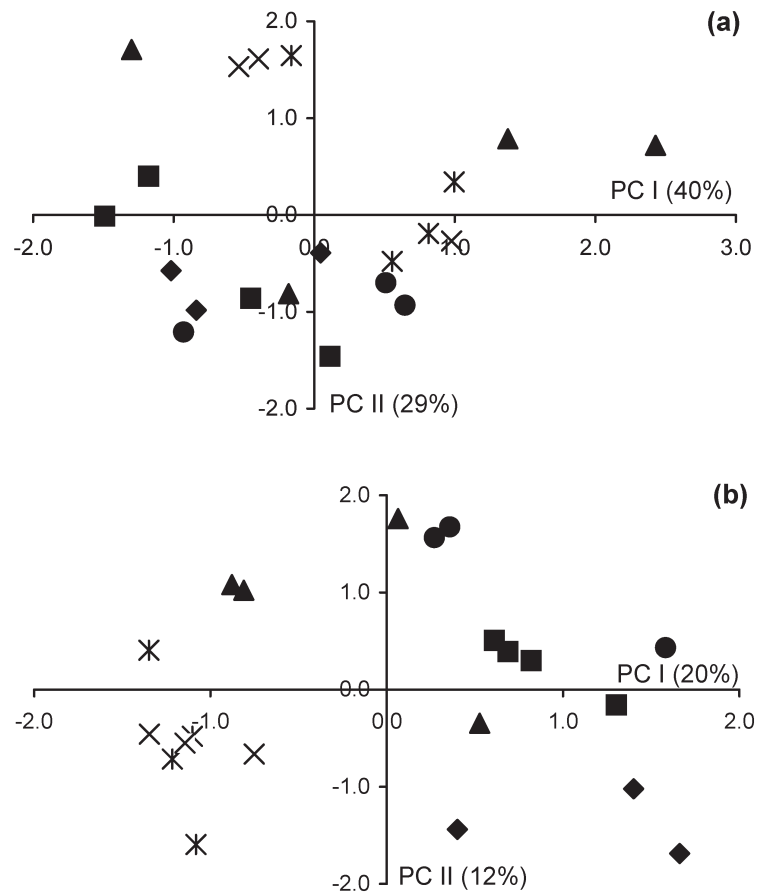


Figure 6. Ordination of plots along two first principal components. (a) PCA based on 15 structural attributes. (b) PCA based on ten dominant species in each plot (63 species). Black symbols correspond to plots on granite, open symbols to plots on non-granite lithology. Symbols and abbreviations: diamond = SAG (Summit areas on granite); asterisk = SAT (Summit areas on tuffs); cross = SACG (Summit areas with conglomerates cover on granite); triangle = LSG (Low slopes on granite); square = ISG (intermediate slopes on granite); circle = HSG (high slopes on granite).

diversity variables, as well as generalizations on species composition, should be avoided. Measures of variability, such as standard deviations and ranks, may be much more useful in describing and comparing forest communities (Jongman *et al.*, 1995; Greig-Smith, 1996). Species lists, together with dominance and distributional data, may also provide a better insight of existing patterns of species composition. For example, from the compositional information obtained in this study we have learned about the exclusivity of species such as *Apoplanesia paniculata*, *Caesalpinia coriaria* and *Lonchocarpus minor* on non-granite lithologies, or the presence of *Comocladia engleriana*, *Exostema caribaeum*, *Gliricidia sepium*, and *Piptadenia constricta* restricted to granite. These results illustrate how more detailed descriptions of vegetation mosaics in tropical forest regions may help identify basic landscape patterns of

species distributions (Hubbell and Foster, 1992), and expose fundamental structural and diversity information for tree communities that, undoubtedly, is still incomplete (Chazdon, 1996; Ricklefs, 2000).

Tree canopy landscape pattern. Chamela has been pointed out as one of the most species rich sites among Neotropical TDFs (Gentry, 1988; Trejo-Vázquez, 1998). In less diverse TDFs in Puerto Rico (Murphy and Lugo, 1986), India (Parthasarathy and Karthikeyan, 1997), and Bolivia (Killeen *et al.*, 1998), species-area curves exhibited stability in areas smaller than, or similar to, those we used in this study. In contrast, species-area curves for Chamela did not achieve stability, although they appear to provide a good depiction of total species richness by land unit. Nevertheless, the generalized agreement on the large het-

erogeneity in the physical conditions of Chamela's landscape warrants the expectation that more species may be added by increasing sampling effort (Galicia *et al.*, 1999; Balvanera *et al.*, 2002; Cotler *et al.*, 2002; Durán *et al.*, 2002).

Landscape-level mosaics in the physical environmental of tropical forests are widely recognized as promoters of habitat heterogeneity, thus enhancing structural and compositional variation in plant communities (Cleef *et al.*, 1982; Campbell, 1994; Condit, 1996; Richards, 1996; Hubbell and Foster, 1992; Gentry and Ortíz-S., 1993; Clark *et al.*, 1995; Búrquez *et al.*, 1999; Wright, 2002). In this study, examination of tree patterns showed that Chamela's TDF canopy was made-up by different assemblages with variable structure and species composition, but above all in dominant species. Structural attributes or species diversity in the plots did not show any obvious relationship with their corresponding morpho-pedological land unit. However, differences in the dominant species group and species turnover (β -diversity) were clearly related to lithology (granite *vs.* non-granite). Lithology has been repeatedly pointed out as influencing vegetation heterogeneity across tropical landscapes (Killeen *et al.*, 1998; Lieberman *et al.*, 1996; Tuomisto *et al.*, 1995; Vázquez-G. and Givnish, 1998; Villers *et al.*, 2003; Pérez-García and Meave, 2004, 2006). The ecological role of lithology may reside in its potential to influence soil nutrients, physical and chemical properties, and landforms (Gerrard, 1992). Thus, in addition to the recognition of riparian *vs.* non-riparian habitats (Lott *et al.*, 1987), and the insolation and elevation gradients within small watersheds (Galicia *et al.*, 1999; Balvanera *et al.*, 2002; Segura *et al.*, 2003) as key factors explaining structural and compositional contrasts in Chamela's TDF, we have shown here the importance of lithology at the landscape level.

TDFs thrive on multiple lithologies (Rzedowski, 1986; Trejo-Vázquez, 1998; Gillespie *et al.*, 2000), and in Mexico continuous TDF canopies are common across mosaics comprising different lithologies (Vázquez-G. and Givnish, 1999; Búrquez *et al.*, 1999; van Devender *et al.*, 2000; Villers *et al.*, 2003; Pérez-García *et al.*, 2005). Therefore, in the absence of intense or chronic anthropogenic disturbances, lithology should be focused on as a key factor in analyzing dominant species of these forests, as well as α - and β -diversity patterns in tree community studies at landscape and regional levels.

Floristic spatial patterns. Focusing on the floristic patterns at the landscape level, this study showed that Chamela's TDF was diverse not only in species, but also in genera and families. However, no one tree species occurred in all sampled sites and, in contrast to the relative high species richness, only a few species were widely distributed and prevalent in the canopy (appendix 1). The ten dominant species

represented a cumulative importance value of 44.9%, with the extreme case being *Caesalpinia eriostachys* (12.7%). However, these species were unimportant or even absent from some land units. This pattern was clearly reflected as a high β -diversity, with the prevalence of low species similarities in the comparisons between plot pairs.

Distribution and abundance patterns of species of Chamela's TDF seems to be influenced by internal and external floristic variation, as many species are shared with other TDF sites. *Caesalpinia eriostachys* is one example of species found in other Mexican TDFs, *e.g.* Caleta, Michoacán, and Copalita, Oaxaca (Trejo-Vázquez, 1998), but it was absent from one land unit in Chamela and from another TDF close to Chamela (Vázquez-G. and Givnish, 1992). Other species, such as *Ceiba aesculifolia*, *Lysiloma microphyllum* (now *L. divaricatum*), *Hintonia latiflora*, and *Erythroxylum mexicanum*, all of which have been reported as being relatively abundant and widely distributed in Mexican TDFs (Trejo-Vázquez, 1998; Van Devender *et al.*, 2000), were encountered in Chamela, but poorly represented and concentrated in some sites.

Very few genera had many species (*Lonchocarpus*, *Bursera*, and *Croton*). *Caesalpinia*, a genus with a broad range and important in the structure of other TDFs (Lott and Atkinson, 2002), was noticeable for its abundance and wide distribution across the landscape. In contrast, *Tabebuia*, *Casearia*, and *Trichilia*, all of them widely distributed genera in Neotropical TDFs (Gentry, 1995), were not dominant, nor did they occur in all morpho-pedological land units. According to the number of families, Chamela was comparable to TDFs located elsewhere in Mexico (Trejo-Vázquez, 1998), Costa Rica (Gillespie *et al.*, 2000), and Brazil, Colombia and Venezuela (Sampaio, 1995). Over 40% of species and genera in Chamela belong in the Leguminosae, Euphorbiaceae and Rubiaceae families; these families are also dominant in other TDFs. Dominance of Leguminosae and Euphorbiaceae is consistent among different Neotropical TDFs (Gentry, 1995; Killeen *et al.*, 1998; Sampaio, 1995; Trejo-Vázquez, 1998; Gillespie *et al.*, 2000; Kalacksa *et al.*, 2004), but not in those from the Paleotropics (Parthasarathy and Karthikeyan, 1997), and Rubiaceae prevailed in a Caribbean island (González and Zak, 1996). Other families, such as Rutaceae and Boraginaceae, are also important in other Mexican (Trejo-Vázquez, 1998) and Indian TDFs (Parthasarathy and Karthikeyan, 1997).

Common families that are well represented in Chamela and other Neotropical TDFs suggest the existence of a same phytogeographic pattern (Gentry, 1995). Although the presence of common genera and species in Neotropical TDFs was less evident, many such taxa are shared among Mexican TDFs (Vázquez-G. and Givnish, 1992; Trejo-Vázquez, 1998; Búrquez *et al.*, 1999; van Devender *et al.*, 2000; Lott and Atkinson, 2002; Pérez-García, 2002), sug-

gesting that Chamela forms an integral part of a large regional flora. In contrast, local patterns of species distributions and abundances may be more closely related to ecological processes, mediated by biotic and abiotic factors and recent history (natural and anthropogenic disturbances).

Our results support the idea of the large heterogeneity of tree communities and species assemblages making up the term tropical deciduous forest in Chamela. Also, they show fundamental phytogeographical and environmental determinants in the characteristics of these tree communities. The complexity of the spatial patterns in these tree communities needs to be better documented with quantitative data on structural attributes, diversity and species dominance, because this information together provides valuable information and helps develop a more realistic understanding of, and sensible comparisons between, seasonally dry tropical forests. Empirical data derived from landscape studies on species composition and abundance patterns are needed in order to test more complex concepts related to tropical plant communities, of which the metacommunity theory is an example (Chase, 2005).

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Appendix 1. Frequencies of species and morpho-species in the plots of the different morpho-pedological land units. Abbreviations: SAG = Summit areas on granite; SAT = Summit areas on tuffs; SACG = Summit areas with conglomerates cover on granite; LSG = Low slopes on granite; ISG = Intermediate slopes on granite; HSG = High slopes on granite.

Species	Total plots	Morpho-pedological land units					
		SAG	SAT	SACG	LSG	ISG	HSG
ACHATOCARPACEAE							
<i>Achatocarpus gracilis</i> H.Walter	6	-	2	3	1	-	-
AMARANTHACEAE							
<i>Lagrezia monosperma</i> (Rose) Standl.	3	-	3	-	-	-	-
ANACARDIACEAE							
<i>Comocladia engleriana</i> Loes.	10	2	-	-	2	3	3
<i>Spondias purpurea</i> L.	7	1	4	2	-	-	-
ANNONACEAE							
<i>Annona palmeri</i> Saff.	2	-	-	1	1	-	-
<i>Oxandra lanceolata</i> (Swartz) Baill.	1	-	-	-	-	-	1
<i>Sapranthus violaceus</i> (Dunal) Saff.	1	-	-	-	-	-	1
APOCYNACEAE							
<i>Alstonia longifolia</i> (A.DC.) Pichon	12	2	-	2	3	3	2
<i>Plumeria rubra</i> L.	13	3	1	2	2	4	1
<i>Stemmadenia</i> cf. <i>grandiflora</i> (Jacq.) Miers	1	-	-	-	-	1	-
<i>Thevetia ovata</i> (Cav.) A.DC.	4	1	-	-	-	3	-
ARALIACEAE							
<i>Sciadodendron excelsum</i> Griseb.	1	-	1	-	-	-	-
BIGNONIACEAE							
<i>Crescentia alata</i> Kunth	1	-	1	-	-	-	-
<i>Swietenia humilis</i> Zucc.	1	-	-	-	1	-	-
<i>Tabebuia chrysantha</i> (Jacq.) G.Nicholson	8	1	-	-	2	2	3
<i>T. impetiginosa</i> (Mart. ex DC.) Standl.	3	1	-	-	-	-	2
BOMBACACEAE							
<i>Ceiba aesculifolia</i> (Kunth) Britten et Baker f.	2	-	-	1	1	-	-
<i>C. grandifolia</i> Rose	8	2	4	1	-	-	1
BORAGINACEAE							
<i>Bouyeria</i> cf. <i>purpusii</i> Brandegee	14	3	3	-	3	4	1
<i>Cordia alliodora</i> (Ruiz et Pav.) Oken	15	2	3	1	3	3	3
<i>C. dentata</i> Poir.	2	-	-	1	1	-	-
<i>C. elaeagnoides</i> DC.	7	-	2	3	2	-	-
<i>C. seleriana</i> Fernald	2	-	1	-	1	-	-
<i>Cordia</i> sp.	2	-	-	2	-	-	-
BURSERACEAE							
<i>Bursera arborea</i> (Rose) L.Riley	18	3	3	2	3	4	3
<i>B. excelsa</i> (Kunth) Engl.	5	2	-	-	1	2	-
<i>B. fagaroides</i> (Kunth) Engl.	7	2	-	1	1	2	1
<i>B. heteresthes</i> Bullock	7	3	-	1	1	2	-
<i>B. instabilis</i> McVaugh et Rzed.	10	2	3	-	2	2	1
<i>Bursera</i> sp.	2	-	2	-	-	-	-

TREE COMMUNITY STRUCTURE AND DIVERSITY IN A TROPICAL DECIDUOUS FOREST LANDSCAPE

Species	Total plots	Morpho-pedological land units					
		SAG	SAT	SACG	LSG	ISG	HSG
CAPPARACEAE							
<i>Capparis indica</i> (L.) Druce	6	-	2	-	2	-	2
<i>C. verrucosa</i> Jacq.	1	-	-	-	1	-	-
<i>Forchhammeria pallida</i> Liebm.	8	-	3	1	3	-	1
<i>Morisonia americana</i> L.	1	-	-	-	-	-	1
CARICACEAE							
<i>Jacaratia mexicana</i> A.DC.	7	-	3	2	-	1	1
COCHLOSPERMACEAE							
<i>Cochlospermum vitifolium</i> (Willd.) Spreng.	9	3	-	1	-	4	1
CONVOLVULACEAE							
<i>Ipomoea wolcottiana</i> Rose	18	3	4	2	3	4	2
EBENACEAE							
<i>Diospyros aequoris</i> Standl.	11	3	1	-	2	4	1
ERYTHROXYLACEAE							
<i>Erythroxylum mexicanum</i> Kunth	13	1	1	3	3	3	2
<i>E. rotundifolium</i> Lunan <i>sensu lato</i>	15	2	3	1	3	4	2
EUPHORBIACEAE							
<i>Adelia oaxacana</i> (Muell.Arg.) Hemsl.	7	3	-	1	1	1	1
<i>Bernardia mexicana</i> (Hook. et Arn.) Muell.Arg.	1	-	-	-	-	-	1
<i>B. spongiosa</i> McVaugh	1	-	-	-	-	-	1
<i>Cnidosculus spinosus</i> Lundell	4	1	2	-	-	1	-
<i>Croton alamosanus</i> Rose	6	-	-	-	2	3	1
<i>C. niveus</i> Jacq.	2	-	-	-	1	1	-
<i>C. pseudoniveus</i> Lundell	11	-	3	1	3	2	2
<i>Croton</i> sp.	2	1	-	-	-	-	1
<i>Jatropha chamelensis</i> Pérez-Jim.	3	1	-	1	1	-	-
<i>J. malacophylla</i> Standl.	8	-	3	3	1	1	-
<i>J. sympetala</i> S.F. Blake et Stand	3	-	3	-	-	-	-
<i>Margaritaria nobilis</i> L.f.	1	-	-	-	-	-	1
<i>Matayba spondioides</i> Standl.	1	-	-	-	-	-	1
<i>Ophellantha spinosa</i> Standl.	1	-	-	-	-	-	1
<i>Pedilanthus calcaratus</i> Schldtl.	2	-	-	-	-	2	-
<i>Phyllanthus botryanthus</i> Müll.Arg.	3	-	1	-	1	1	-
<i>Sapium pedicellatum</i> Huber	1	-	1	-	-	-	-
FLACOURTIACEAE							
<i>Casearia corymbosa</i> Kunth	7	-	2	3	2	-	-
<i>C. tremula</i> (Griseb.) Griseb. ex C.Wright	14	2	4	3	3	2	-
<i>Prockia crucis</i> P.Browne ex L.	1	-	-	1	-	-	-
<i>Samyda mexicana</i> Rose	16	3	3	1	3	4	2
HERNANDIACEAE							
<i>Gyrocarpus jatrohifolius</i> Domin	4	1	3	-	-	-	-
JULIANACEAE							
<i>Amphipterygium adstringens</i> (Schldtl.) Standl.	9	2	3	2	-	2	-

Species	Total plots	Morpho-pedological land units					
		SAG	SAT	SACG	LSG	ISG	HSG
LEGUMINOSAE							
<i>Acacia cochliacantha</i> Humb. et Bonpl. ex Willd.	4	-	-	2	2	-	-
<i>Acacia</i> sp.	2	-	1	-	-	1	-
<i>Albizia occidentalis</i> Brandegee	3	1	-	-	1	1	-
<i>Apoplanesia paniculata</i> C.Presl	10	1	4	3	2	-	-
<i>Bauhinia unguolata</i> L.	6	-	-	-	1	3	2
<i>Brongniartia</i> sp. nov. ined. O.Dorado	7	3	1	-	-	2	1
<i>Caesalpinia caladenia</i> Standl.	6	3	2	-	-	1	-
<i>C. coriaria</i> (Jacq.) Willd.	10	-	4	3	3	-	-
<i>C. eriostachys</i> Benth.	14	2	4	3	2	-	3
<i>C. platyloba</i> S.Watson	3	1	-	1	1	-	-
<i>C. pulcherrima</i> (L.) Sw.	4	-	3	1	-	-	-
<i>C. sclerocarpa</i> Standl.	11	-	3	3	3	-	2
<i>Calliandra emarginata</i> (Humb. et Bonpl. ex Willd.) Benth.	1	-	-	-	-	1	-
<i>Chloroleucon mangense</i> (Jacq.) Britton et Rose var. <i>leucospermum</i>	17	2	4	3	3	3	2
<i>Conzattia multiflora</i> (B.L.Rob.) Standl.	2	-	-	-	-	-	2
<i>Conzattia</i> sp.	2	-	-	-	-	2	-
<i>Dalbergia</i> sp.	13	2	2	1	1	4	3
<i>Diphysa occidentalis</i> Rose	6	-	-	1	2	3	-
<i>Erythrina lanata</i> Rose var. <i>occidentalis</i> Standl.	10	1	3	2	2	2	-
<i>Gliricidia sepium</i> (Jacq.) Kunth ex Walp.	15	3	-	1	4	4	3
<i>Haematoxylum brasiletto</i> H.Karst.	3	2	-	-	1	-	-
<i>Leucaena lanceolata</i> S.Watson	5	1	2	-	1	1	-
<i>Lonchocarpus cochleatus</i> Pittier	4	-	2	-	1	-	1
<i>L. constrictus</i> Pittier	18	3	4	3	4	1	3
<i>L. eriocarinalis</i> Micheli	12	3	3	1	1	2	2
<i>L. guatemalensis</i> Benth.	3	-	-	-	1	-	2
<i>L. magallanesii</i> M.Sousa	3	2	1	-	-	-	-
<i>L. minor</i> M.Sousa	5	-	4	1	-	-	-
<i>L. mutans</i> M.Sousa	15	3	3	-	3	3	3
<i>Lonchocarpus</i> sp. 1	3	2	-	-	-	-	1
<i>Lonchocarpus</i> sp. 2	2	1	-	-	-	-	1
<i>Lysiloma microphyllum</i> Benth.	11	2	1	1	3	3	1
<i>Pityrocarpa constricta</i> (Micheli et Rose ex Micheli) J.F.Macbr.	12	2	1	-	2	4	3
<i>Pithecellobium unguis-cati</i> (L.) Benth.	5	-	1	2	2	-	-
<i>Poeppegia procera</i> C.Presl	3	-	-	-	-	1	2
<i>Pterocarpus</i> sp.	1	-	-	-	-	1	-
<i>Senna atomaria</i> (L.) H.S.Irwin et Barneby	1	-	-	-	-	1	-
MALPHIGIACEAE							
<i>Malpighia ovata</i> Rose	13	1	1	2	3	3	3
MELIACEAE							
<i>Trichilia trifolia</i> L. subsp. <i>palmeri</i> (C.DC.) T.D.Penn.	5	-	2	1	2	-	-
<i>Trichilia</i> sp.	3	1	-	-	1	1	-

TREE COMMUNITY STRUCTURE AND DIVERSITY IN A TROPICAL DECIDUOUS FOREST LANDSCAPE

Species	Total plots	Morpho-pedological land units					
		SAG	SAT	SACG	LSG	ISG	HSG
MORACEAE							
<i>Chlorophora tinctoria</i> (L.) Gaudich. ex Benth.	6	-	3	2	1	-	-
<i>Ficus cotinifolia</i> Kunth	4	-	-	1	1	1	1
MYRTACEAE							
<i>Eugenia rekoii</i> Standl.	1	-	-	-	-	-	1
<i>Psidium sartorianum</i> (O.Berg) Nied.	15	1	3	1	4	3	3
NYCTAGINACEAE							
<i>Guapira cf. macrocarpa</i> (Miranda) Miranda	18	3	3	2	3	4	3
OCHNACEAE							
<i>Ouratea mexicana</i> (Humb. et Bonpl.) Engl.	2	-	-	-	-	-	2
OLACACEAE							
<i>Schoepfia</i> sp.	5	-	-	-	2	1	2
OLEACEAE							
<i>Forestiera cf. rhamnifolia</i> Griseb.	2	-	-	-	1	-	1
ONAGRACEAE							
<i>Hauya elegans</i> DC.	4	-	-	-	-	1	3
POLYGONACEAE							
<i>Coccoloba liebmannii</i> Lindau	7	-	4	2	1	-	-
<i>Coccoloba</i> sp.	8	1	-	-	-	4	3
<i>Ruprechtia fusca</i> Fernald	10	1	4	3	2	-	-
<i>R. pallida</i> Standl.	2	-	1	1	-	-	-
RHAMNACEAE							
<i>Colubrina heteroneura</i> (Griseb.) Standl.	8	1	-	-	1	3	3
<i>C. triflora</i> Brongn. ex Sweet	7	-	-	1	1	2	3
<i>Karwinskia latifolia</i> Standl.	4	-	-	-	1	1	2
RUBIACEAE							
<i>Allenanthus hondurensis</i> Standl. var. <i>parvifolia</i> L.Wms.	5	3	1	-	-	1	-
<i>Chiococca alba</i> (L.) Hitchc.	1	-	-	-	-	1	-
<i>Exostema caribaeum</i> (Jacq.) Roem. et Schult.	14	3	1	-	3	4	3
<i>Guettarda elliptica</i> Sw.	14	3	2	1	1	4	3
<i>Hintonia latiflora</i> (Sessé et Moc. ex DC.) Bullock	11	1	2	1	3	3	1
<i>Machaonia acuminata</i> Bonpl.	4	2	-	-	-	2	-
<i>Psychotria microdon</i> (DC.) Urb.	2	-	-	-	-	-	2
<i>Randia thurberi</i> S.Watson	14	3	2	3	4	2	-
RUTACEAE							
<i>Esenbeckia berlandieri</i> Baill. ex Hemsl. subsp. <i>acapulcensis</i> (Rose) Kaastra	5	-	2	-	1	-	2
<i>E. nesiotica</i> Standl.	9	3	-	-	2	2	2
<i>Helietta lottiae</i> F.H.Chiang	7	3	-	-	1	2	1

Species	Total plots	Morpho-pedological land units					
		SAG	SAT	SACG	LSG	ISG	HSG
<i>Zanthoxylum arborescens</i> Rose	1	-	-	-	1	-	-
<i>Z. caribaeum</i> Lam. vel aff.	5	2	-	-	-	2	1
<i>Z. fagara</i> (L.) Sarg.	2	-	-	-	-	-	2
SAPINDACEAE							
<i>Thouinia paucidentata</i> Radlk.	6	-	3	1	1	1	-
SAPOTACEAE							
<i>Sideroxylon stenospermum</i> (Standl.) T.D.Penn.	11	3	-	-	2	3	3
SIMAROUBACEAE							
<i>Recchia mexicana</i> Moc. et Sessé ex DC.	3	-	-	1	2	-	-
THYMELEACEAE							
<i>Daphnopsis</i> sp.	1	-	-	-	-	1	-
THEOPHRASTACEAE							
<i>Jacquinia pungens</i> A.Gray	11	-	3	3	3	1	1
TILIACEAE							
<i>Heliocarpus pallidus</i> Rose	6	1	4	1	-	-	-
<i>Luehea candida</i> (Moc. et Sessé ex DC.) Mart.	9	1	-	1	2	3	2
VERBENACEAE							
<i>Citharexylum hirtellum</i> Standl.	1	1	-	-	-	-	-
<i>Citharexylum standleyi</i> Moldenke var. <i>mexicanum</i> Moldenke	3	-	2	1	-	-	-
<i>Lippia mcvaughii</i> Moldenke	5	-	3	-	2	-	-
VIOLACEAE							
<i>Hybanthus mexicanus</i> Ging.	2	-	-	-	-	-	2