Plant community attributes of a tropical dry forest physiognomically dominated by _Heteroflorum sclerocarpum_ (Fabaceae)

Atributos de la comunidad de plantas de un bosque tropical seco fisonómicamente dominado por _Heteroflorum sclerocarpum_ (Fabaceae)

Guillermo Ibarra-Manríquez[1*], Lina Adonay Urrea-Galeano[1,2], Jorge Cortés-Flores[1,3], Karen Beatriz Hernández-Esquivel[1,4], Armando Navarrete-Segueda[1,5] and Iván Leonardo Ek-Rodríguez[1]

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

[2] Instituto de Ecología, Universidad Nacional Autónoma de México, Ciudad de México, México.

[3] Jardín Botánico, Instituto de Biología, Sede Tlaxcala, Universidad Nacional Autónoma de México, Santa Cruz Tlaxcala, Tlaxcala, México.

[4] Jardín Etnobiológico de las Selvas del Soconusco, El Colegio de la Frontera Sur, Unidad Tapachula, Tuzantán, Chiapas, México.

[5] Escuela Nacional de Estudios Superiores, Unidad Morelia. Universidad Nacional Autónoma de México, Morelia, Michoacán, México.

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

Abstract

Background: _Heteroflorum_ (Fabaceae) is a monospecific genus endemic to western Mexico. Community attributes of the forest where _H. sclerocarpum_ is found are scarcely known, as well as its similarity with other tropical seasonal forests.

Question: What is the composition, structure, and diversity of the tropical deciduous forest where _H. sclerocarpum_ is physiognomically dominant?

Study site and date: The buffer area of the Zicuirán-Infiernillo Biosphere Reserve, in the Churumuco municipality of Michoacán, Mexico, in 2014.

Methods: In three 0.1-ha sites, we sampled trees with a diameter at breast height $\geq$ 1 cm and lianas whose rooted stem had a diameter of $\geq$ 1 cm. We calculated the density, biomass, rank-abundance, rank-basal area curves, as well as alpha and beta diversity measures for each site.

Results: We recorded 64 species from 21 families in 0.3 ha. Fabaceae had the highest number of genera, species, individuals, and biomass in all sites sampled. The sites varied in richness (33-41 species), density (176-247 individuals), basal area (2-2.9 m^2), and maximum height of trees (12-16 m). Rank-abundance curves differed significantly among sites. Rarefaction curves showed that $^0D\alpha$ and $^1D\alpha$ did not differ among sites, while $^2D\alpha$ separated one of the sites, which also showed a different diversity profile. Beta diversity did not show a strong species turnover among sites ($^0D_\beta$, 1.38-1.45; $^2D_\beta$, 1.35-1.56).

Conclusions: The composition of the forest sampled was similar to other seasonal forests, while the density and diversity were among the lowest values.

Keywords. Basal area, composition, Leguminosae, trees, tropical dry forest, true diversity.

Resumen

Antecedentes: _Heteroflorum_ (Fabaceae) es un género monoespecífico, endémico del occidente de México y los atributos comunitarios del bosque donde habita _H. sclerocarpum_ son apenas conocidos, al igual que el grado de similitud que presentan con otros bosques tropicales estacionalmente secos.

Preguntas: ¿Cuál es la composición, estructura y diversidad del bosque tropical caducifolio en el que _H. sclerocarpum_ es fisonómicamente dominante?

Sitio y años de estudio: Reserva de la Biosfera Zicuirán-Infiernillo, en el municipio de Churumuco, Michoacán, México, en 2014.

Métodos: En tres sitios, cada uno de 0.1 ha, se censaron los árboles y lianas con DAP $\geq$ 1 cm. Se calculó la densidad, biomasa, curvas de rango-abundancia y de rango-biomasa, así como la diversidad alfa y beta para cada sitio.

Resultados: Se registraron 64 especies y 21 familias. Independientemente del sitio, la familia Fabaceae presentó el mayor número de géneros, especies, individuos y biomasa. Los sitios variaron en riqueza (33-41 especies), densidad (176-247 individuos), área basal (2-2.9 m^2) y altura máxima (12-16 m). Las curvas de rango-abundancia difirieron significativamente entre los sitios. Las curvas de rarefacción con la diversidad $^0D\alpha$ y $^1D\alpha$ no difirieron entre los sitios, mientras que $^2D\alpha$ separo uno de éstos, el cual también presentó un perfil de diversidad distinto. La diversidad beta indica un bajo recambio de especies entre los sitios ($^0D_\beta$, 1.38-1.45; $^2D_\beta$, 1.35-1.56).

Conclusiones: La composición del bosque muestreado fue similar a lo documentado en otros bosques estacionales, en tanto que la densidad y diversidad los ubican entre los valores más bajos.

Palabras claves: árboles, área basal, bosque tropical caducifolio, composición, diversidad verdadera, Leguminosae.

Tropical dry forests constitute a set of communities in which plants are subjected to water restriction during the dry season (Murphy & Lugo 1985, Sánchez-Azofeifa *et al*. 2005, Trejo 2005, Lott & Atkinson, 2006). The variation in frequency and amounts of precipitation as well as the duration of the dry season are closely related to changes in species composition, structure, and functional strategies (Murphy & Lugo 1985, Poorter & Markesteijn 2008, Becknell *et al*. 2012, Dexter *et al*. 2018). Several studies have also highlighted the high richness, endemism, and diversity of neotropical dry forests (Gillespie *et al*. 2000, Linares-Palomino *et al*. 2010, Apgaua *et al.* 2014, Banda-R. *et al*. 2016).

Tropical dry forest is one of the most threatened biomes on the planet due to multiple pressures from human activities (Gillespie *et al*. 2000, Sánchez-Azofeifa *et al*. 2005, Trejo 2005, Miles *et al*. 2006). It has been proposed that only about 10 % of the original extent of Neotropical dry forest remains intact, and about 5 % of Mesoamerican dry forest is under official protection, the lowest protection area of all regions in the world (Miles *et al*. 2006). Trejo & Dirzo (2000) estimated that tropical deciduous forest (TDF) originally covered about 14 % (270,000 km^2) of Mexican territory. Based on Rzedowski (1978), these authors considered that, in 1990, only 27 % (72,850 km^2) of this area had a good state of conservation, while 50 % had an altered or degraded condition (74,825 and 61,500 km^2, respectively).

Throughout the distribution of Mexican tropical dry forest there are important differences in vegetation abundance, biomass, composition, and height of species (Lott *et al*. 1987, Arriaga & León 1989, González-Iturbe *et al*. 2002, Trejo & Dirzo 2002, Lebrija-Trejos *et al*. 2008, Gallardo-Cruz *et al*. 2009, León de la Luz *et al*. 2012, Méndez-Toribio *et al*. 2014, Rojas-Martínez & Flores-Olvera 2019, Ibarra-Manríquez *et al*. 2021). It has been estimated that ca. 2,500 Angiosperms species are found exclusively in the TDF of Mexico, with endemism close to 40 % (Rzedowski 1991, Rzedowski & Calderón de Rzedowski 2013). The Balsas River Basin is one of the Mexican Floristic Provinces recognized by Rzedowski (1978), in which TDF is the most widely distributed vegetation type. Fernández-Nava *et al*. (1998) listed 4,442 species in this province, of which 7.6 % are endemic (Rodríguez-Jiménez *et al*. 2005). Due to its endemism and the threats to its preservation in the long term, the TDF of the Balsas Basin presents a high conservation priority (Olson & Dinerstein 2002, Bezaury-Creel 2010).

From several censuses of 0.1 ha of woody plants with DBH ≥ 1 cm (Trejo & Dirzo 2002, Pineda-García *et al*. 2007, Méndez-Toribio *et al*. 2014), it has been shown that different TDF in the Balsas River Basin vary in attributes including: i) richness (29-123 species), ii) number of individuals (285-419), and iii) basal area (1.92-3.47 m^2). Also, in the case of the alpha diversity (Fisher index), the lowest value has been recorded in the locality El Tarimo, in the state of Guerrero (12.4; Pineda-García *et al*. 2007) while the highest was in Tziritzícuaro, in Michoacán state (18.3; Méndez-Toribio *et al*. 2014). Regarding beta diversity, five localities sampled by Trejo & Dirzo (2002) showed low similarity values on the Sorensen index, between 6 (Caleta, Michoacán and Cerro Zopilote, Guerrero) and 27 % (Cerro Zopilote and Cerro Tuxpan, Guerrero).

In the Ejido Llano de Ojo de Agua, located in the municipality of Churumuco, Michoacán, within the Balsas Basin Province, Urrea-Galeano *et al*. (2018) reported areas physiognomically dominated by trees of *Heteroflorum sclerocarpum* M. Sousa (Fabaceae), which is the only known species of the genus *Heteroflorum* M. Sousa, whose distribution is limited to the TDF of western Mexico (Sousa 2010). The main objective of the present study is to describe the composition, structure, and diversity of the sites mentioned by Urrea-Galeano *et al*. (2018). Knowing these state variables could be the first approach (Pérez-García *et al*. 2021) to estimate the community characteristics where *H. sclerocarpum* is found today; achieving this objective could be an important reference frame to design: i) strategies that promote the conservation of *H. sclerocarpum*, classified as an Endangered species (B2ab(iii); Machuca-Machuca *et al*. 2021), ii) management programs at regional scale since it is considered as an important forage species (Luna-Nieves *et al*. 2017), and iii) contribute to the characterization of emerging community attributes of the tropical deciduous forest in one of the conservation priority areas of this vegetation type at a global scale (Olson & Dinerstein 2002, Bezaury-Creel 2010). Therefore, the present study has as particular objectives to characterize the taxonomic richness and abundance of the most relevant families in these sites, and to quantify the composition, structure, and diversity of each site, to compare these community attributes with other TDFs worldwide.

Materials and methods

Study area. This research was carried out in September 2014 in the community conservation areas of the Ejido Llano de Ojo de Agua, in the municipality of Churumuco, Michoacán, within the buffer area of the Zicuirán-Infiernillo Biosphere Reserve ([Figure 1](#)). This area belongs to the morphotectonic province of the Sierra Madre del Sur, in the Balsas Basin subprovince (Ferrusquía-Villafranca 1993). The geology is dominated by rocks from the Mesozoic (*e.g.*, andesite) and Cenozoic (*e.g.*, acid tuff), and the most abundant soil type is Leptosol (51.7 %) followed by Phaeozem (32.4 %) (CONANP 2014). The prevailing climate is dry, tropical, with summer rains (BS_0); during period from 1981 to 2010 the mean values of minimum and maximum temperature were 17.7 and 46 °C, respectively, with a mean annual rainfall of 564 mm (June-October), and a long dry season between November and May (Luna-Nieves *et al.* 2017, Ibarra-Manríquez *et al.* 2021). Two types of vegetation have been described in the area - TDF and tropical subdeciduous forest - in which 466 species were recorded from 84 families (Ibarra-Manríquez *et al.* 2021). Fabaceae, Euphorbiaceae, and Asteraceae families were the richest, with 83, 43, and 32 species, respectively. Detailed information about the reproductive phenology for some of the species in this forest and *H. sclerocarpum* can be found in Luna-Nieves *et al.* (2017) and Cortés-Flores *et al.* (2017, 2019). The ejido is a land tenure regime, where people take collective decisions on the land managements; Churumuco county people live in extreme poverty, with few basic services and the opportunities of jobs are scarce (INEGI 2010), and poorly paid. The main economic activities are the crop fields and land pastures, mainly for cattle raising (Ibarra-Manríquez *et al.* 2021).

Vegetation sampling. We sampled vegetation in three sites where *H. sclerocarpum* (hereafter, *Heteroflorum*) was physiognomically dominant. The sites were located between 370 and 550 m elevation at the following locations: El Guaricho (18° 42' 20.83'' N, 101° 40' 20.74'' W), La Joya de la Niña (18° 41' 59.67'' N, 101° 39' 48.44'' W), and El Zipimo (18° 42' 21.22'' N, 101° 39' 3.13'' W; [Figure 1](#)). We followed the sampling method proposed by Gentry (1982), establishing ten 50×2 m (0.1 ha) transects at each site, aligned in parallel and separated from each other by 20 m. Trees that were rooted within each transect and had a diameter at breast height (DBH) ≥ 1 cm were identified in the field, and their height was estimated visually (only by GI-M). Lianas that measured ≥ 1 cm at the base of the rooted trunk were also recorded and identified.

Data analysis. For the structural analysis of the vegetation, we obtained the relative values of density, frequency, and dominance (basal areas) of each species per site following Mueller-Dombois & Ellenberg (1974) to calculate the relative importance value (*i. e.*, sum of the relative values of all three variables: RIV). In the case of multi-stemmed plants (trees or lianas), the basal area calculation included all stems ≥ 1 cm DBH. Rank curves based on abundance and basal area were constructed to assess changes in dominant species among sites (pooling the data from all ten transects per site). The curves were constructed following Magurran (2004). We fit linear models for rank abundance and basal area curves and tested for differences among sites using an analysis of covariance (ANCOVA), considering as explanatory variables the rank (Rank; as numeric), the site (site; as categorical) and their interaction (Rank: site). Differences among slopes were evaluated between sites (Izsák 2006).

To analyze local diversity and species turnover, we used the multiplicative partitioning of diversity into its independent components ($\gamma = \alpha \times \beta$) or true diversity measures, which depends on the parameter "q" (diversity order), which is sensitive to species abundance (Jost 2006). As q increases, the most abundant species are increasingly favored. Local diversity (α) was analyzed by calculating the effective number of species ($qN = (\sum pqi)^{1/(1-q)}$) using three values of the diversity order (Jost 2006, Moreno *et al.* 2011, Cultid-Medina & Escobar 2019): i) 0 ($^0D\alpha$), in which the abundances of the species do not influence the diversity value and is equivalent to the species richness, ii) 1 ($^1D\alpha$), in which the abundance of all species in the community community has proportional importance, indicating the number of common or frequent species, and iii) 2 ($^2D\alpha$), which unequally favours the most dominant species and give us their number.
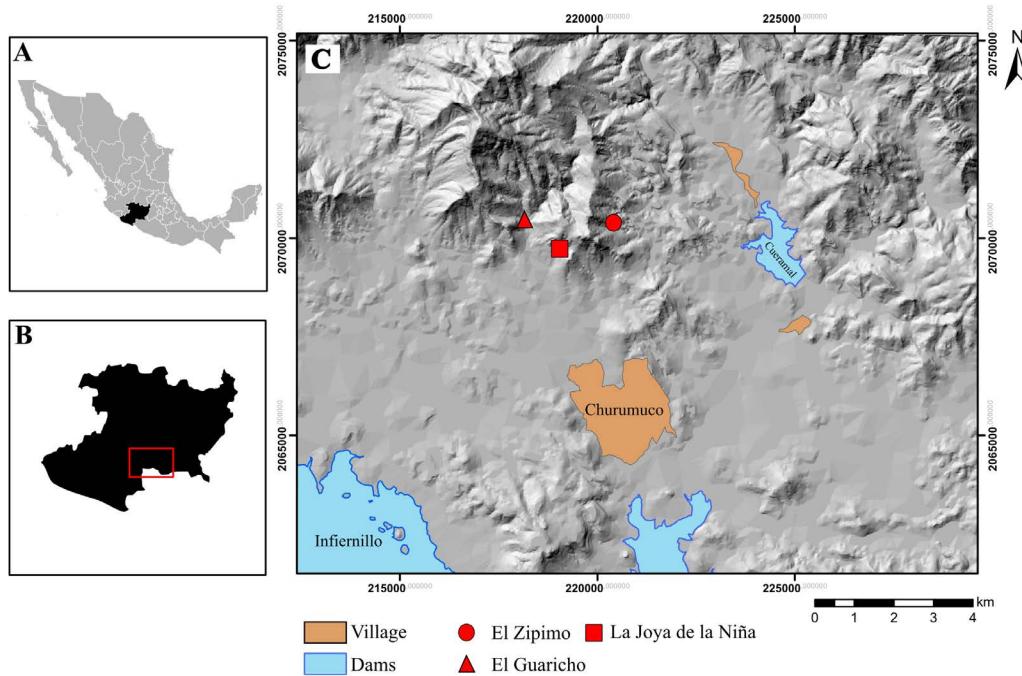
Figure 1. Location of the study sites. A) Michoacán state (black area), Mexico. (B) Localization of the Churumuco municipality. (C) Location of plots within the Ejido Llano de Ojo de Agua. The digital elevation model was created based on contour lines of the vector data set of topographic information E14A62 and E14A61 (INEGI 2015).

To compare diversity between sites, rarefaction curves and diversity profiles were obtained for each one with the confidence intervals estimated for $^0D\alpha$, $^1D\alpha$, and $^2D\alpha$. Confidence intervals were constructed at 100 and 10 simulations for rarefaction curves and diversity profiles, respectively, and a risk level of alpha = 0.05 for both. In diversity profiles, the effective number of species decreases as the value of q increases because species with greater abundance are increasingly favored; thus, a larger decrease in the value of $^qD\alpha$ from q = 0 to q = 2 indicates greater dominance and, therefore, lower diversity. This phenomenon is quantified by dividing $^2D\alpha$ by $^0D\alpha$, which is known as the evenness factor (EF). The closer this value is to 1, the greater the community evenness; the closer to 0, the lower the evenness (Jost 2010). Rarefaction curves were performed with iNEXT function in the iNEXT package v. 2.0-20 (Hsieh *et al.* 2016, Hsieh *et al.* 2020) and diversity profiles were performed with DivProfile function in the entropart package v. 1.6-8 (Marcon & Hérault 2015, 2021).

Species turnover (β) was analyzed by calculating true beta diversity ($^qD_\beta$) for order 0 and 2, as they reflect all species and dominant species turnover, respectively. The calculation of $^qD_\beta$ was performed with DivPart function in entropart package v. 1.6-8 (Marcon & Hérault 2015, 2021), using 100 simulations and alpha = 0.05 to estimate confidence intervals. True beta diversity values vary between 1 (all communities are identical) and the number of plots compared (all communities are different). We computed a paired distance matrix between plots, so the maximum value for $^qD_\beta$ is two. All diversity analyses were performed in R version 3.6.1 (R Core Team 2020).

Results

Composition. We recorded 64 species belonging to 47 genera, and 21 families of Magnoliophyta, of which six species were lianas (Table 1). The number of species and families was similar among all sites, although it was slightly higher in El Zipimo (Table 2). The highest richness of tree species (41) was also recorded at El Zipimo, and the lowest was at El Guaricho (33). There were fewer species of lianas (2-4 species) than trees in all sites. Six families accounted for 67.6 % of the total genera and 78.6 % of the species (Table 3). Fabaceae had the highest number of

genera and species in all sites. Burseraceae, even though it was represented only by the genus *Bursera*, was the family with the second highest species richness when considering all three sites, although at El Guaricho, Burseraceae tied for second most species rich family with Cactaceae and Euphorbiaceae.

Structure. A total of 636 individuals were counted, of which only 20 were lianas. Thus, this growth form accounted for less than 5 % of individuals and 0.4 to 1.7 % of the basal area; the site with the highest tree density was El Zipimo, while El Guaricho had larger biomass (Table 2). The six families that were most important in terms of their contribution to the richness of genera and species also contributed the most in terms of individual density (75.1-83.7 %) and basal area (86.2-94.6 %). Fabaceae had the highest contribution to these structural attributes at the three sites studied (Table 3) and had three of the five most important species based on RIV (Table 1). The five species with the highest RIV values represented between 40.1 to 47.4 % of the total RIV obtained for each site. The most important species differed among sites; *Heteroflorum* had the highest RIV value only at La Joya de la Niña, whereas in the other sites it was in the fourth place (Tables 1, 4).

Table 1. Relative importance value (RIV) and mean height (MH) of species recorded in three 0.1 ha sites in the Ejido Llano de Ojo de Agua. The position of the first five species with the highest RIV for each site is indicated in a format superscript and bold. NA: indicates that the height was not recorded, because it is a species of liana.

Family/Species	El Guaricho		La Joya de la Niña		El Zipimo	
	MH (m)	RIV	MH (m)	RIV	MH (m)	RIV
ANACARDIACEAE						
Cyrtocarpa procera Kunth	11	6.81	4.8	4.79	12	8.15
Amphipterygium adstringens (Schltdl.) Standl.			4.2	5.5	3.8	13.45
Spondias purpurea L.	8	4.91			5.2	4.64
APOCYNACEAE						
Apocynaceae	NA	1.42				
Plumeria rubra L.			4.2	4.41	5.7	5.06
ASTERACEAE						
Otopappus epaleaceus Hemsl.	NA	1.43				
BIGNONIACEAE						
Handroanthus impetiginosus (Mart. ex DC.) Mattos	4.7	12.93	3.3	3.49	6.4	8.63
BIXACEAE						
Cochlospermum vitifolium (Willd.) Spreng.					11	2.53
BURSERACEAE						
Bursera copallifera (DC.) Bullock	5	1.64	5.7	6.46	4.5	10.34
Bursera crenata Paul G. Wilson					3.2	5.62
Bursera coyucensis Bullock			6	1.84	6.9	7.98
Bursera grandifolia (Schltdl.) Engl.	5	1.72	7.9	5.5	6.7	8.29
Bursera infernidialis Guevara & Rzed.			6.2	5.09	5.5	**26.58**[2]

Family/Species	El Guaricho		La Joya de la Niña		El Zipimo	
	MH (m)	RIV	MH (m)	RIV	MH (m)	RIV
Bursera trimera Bullock			8.4	2.73	4.7	**23.81[3]**
Bursera sp. nov.	6.2	1.48	8.2	5.17	4	1.32
CACTACEAE						
Backebergia militaris (Audot) Bravo ex Sánchez-Mej.	4.8	10.71	3.8	11.39		
Opuntia bensonii Sánchez-Mej.					6.5	2.13
Pachycereus tepamo Gama & S. Arias					6	2.03
Pilosocereus purpusii (Britton et Rose) Byles et G.D. Rowley			2.3	2.7		
Stenocereus chrysocarpus Sánchez-Mej.	6	2.13			3	2.04
Stenocereus queretaroensis (F.A.C. Weber) Buxb.	6.3	13.29	2.2	3.12		
Stenocereus quevedonis (González Ortega, Jesús) Buxb.			7	4.91	3.4	12.49
COMBRETACEAE						
Combretum farinosum Kunth	NA	1.41				
CORDIACEAE						
Cordia elaeagnoides DC.	5.3	6.43	7.6	2.84		
Cordia morelosana Standl.	3.4	3.78	3.8	8.52	3.2	1.2
CUCURBITACEAE						
Dieterlea fusiformis E.J. Lott	NA	4.67			NA	6.48
EUPHORBIACEAE						
Adelia oaxacana (Muell. Arg.) Hemsl.	3.5	2.11				
Croton alamosanus Rose	3.3	**20.75[5]**			3.3	1.69
Croton sp.	4.3	6.57			3	1.18
Dalembertia populifolia Baill.			NA	5.32		
Euphorbia schlechtendalii Boiss.	3.5	8.1			4.9	3.55
Jatropha jaimejimenezii V.W. Steinm.					4.1	6.82
Jatropha stephani J. Jiménez Ram. & M. Martínez	6.5	2.63				
Manihot crassisepala Pax & K. Hoffm.					2.8	1.26
Pouzolzia guatemalana (Blume) Wedd.					2.1	1.66
FABACEAE						
Apoplanesia paniculata C. Presl	7	1.54	5.8	5.55	6.3	2.92

Family/Species	El Guaricho		La Joya de la Niña		El Zipimo	
	MH (m)	RIV	MH (m)	RIV	MH (m)	RIV
Coulteria platyloba (S. Watson) N. Zamora					4.4	5.07
Coursetia glandulosa A. Gray	7	1.76				
Erythrina oliviae Krukoff	11	**29.91[3]**	12.5	10.4	6.4	**19.46[5]**
Erythrostemon macvaughii (J.L. Contr. & G.P. Lewis) E. Gagnon & G.P. Lewis	8.7	5.85	6.7	13.94	6.9	10.49
Gliricidia sepium (Jacq.) Kunth ex Walp.	8.2	5.51				
Heteroflorum sclerocarpum M. Sousa	7.3	**23.33[4]**	3.9	**37.87[1]**	5.5	**20.24[4]**
Lonchocarpus balsensis M. Sousa & J. C. Soto			5	1.68	10.1	3.31
Lonchocarpus huetamoensis M. Sousa & J. C. Soto			6.5	10.07	6.2	9.69
Mariosousa acatlensis (Benth.) Seigler & Ebinger	8.4	6.68	8.3	**14.98[5]**		
Mimosa rosei B.L. Rob.	5	8.95	5	**21.36[3]**		
Mimosa sp.	6	1.44			5	1.19
Piptadenia flava (Spreng. ex DC.) Benth.	4.9	19.73	5.4	5.19	5.2	7.66
Poincianella eriostachys (Benth.) Britton & Rose	5.4	**31.75[2]**	4.4	1.7	4.6	**31.59[1]**
Senegalia macilenta (Rose) Britton & Rose	6	1.89	4.5	3.42		
Senegalia picachensis (Brandegee) Britton & Rose	7	1.55				
Senna wislizeni (A. Gray) H.S. Irwin & Barneby			4	2.13		
Vachellia campechiana (Mill.) Seigler & Ebinger	7.5	3.07	2.1	5.44		
MALPIGHIACEAE						
Malpighia mexicana A. Juss.	4.4	5.05	3.9	14.09	3.4	1.25
MALVACEAE						
Ceiba aesculifolia (Kunth) Britten & Baker f.	9.5	1.97				
Gossypium lobatum Gentry	6	5.9			5.9	12.91
POLYGONACEAE						
Ruprechtia fusca Fernald			10	2.26		
RESEDACEAE						
Forchhammeria pallida Liebm.					8	1.83
RHAMNACEAE						
Colubrina triflora Brongn. ex G. Don			4.1	**25.09[2]**		

Family/Species	El Guaricho		La Joya de la Niña		El Zipimo	
	MH (m)	RIV	MH (m)	RIV	MH (m)	RIV
RUBIACEAE						
Randia thurberi S. Watson	3.4	**36.45**[1]	3.8	**20.73**[4]	5	1.42
Guettarda elliptica Sw.	3	2.91			3	1.23
Randia laevigata Standl.			3.7	2.09	4.5	1.32
SAPOTACEAE						
Sideroxylum obtusifolium (Humb. ex Roem. & Schult.) T.D. Penn.					5	1.27
VITACEAE						
Cissus verticillata (L.) Nicolson & C.E. Jarvis			NA	4.65	NA	1.57

Table 2. Taxonomic richness and structure attributes according to growth form in the three sites sampled within the tropical dry forest of the Ejido Llano de Ojo de Agua, Churumuco municipality, Michoacán, Mexico.

Sites	Trees (%)	Lianas (%)	Total
El Guaricho			
Families	12 (75.0)	4 (25.0)	16
Species	33 (89.2)	4 (10.8)	37
Individuals	208 (97.7)	5 (2.3)	213
Basal area (m²)	2.84 (99.3)	0.05 (1.7)	2.9
Height range (m)	1.4-16		
Height mean	5.1 (S.D. ± 2.2)		
La Joya de la Niña			
Families	12 (85.7)	2 (14.3)	14
Species	36 (94.9)	2 (5.1)	38
Individuals	168 (95.5)	8 (4.5)	176
Basal area (m²)	1.95 (97.5)	0.03 (2.5)	2.0
Height range (m)	1.3-13		
Height mean	5 (S.D. ± 2.5)		
El Zipimo			
Families	15 (88.2)	2 (11.8)	17
Species	41 (95.3)	2 (4.7)	43
Individuals	240 (97.2)	7 (2.8)	247
Basal area (m²)	2.36 (99.6)	0.01 (0.4)	2.37
Height range (m)	1.3-12		
Height mean	5.2 (S.D. ± 2.3)		

Table 3. Number of genera and species, density, and basal area (m²) of the six dominant families recorded for each site (0.1 ha) sampled in the tropical dry forest of the Ejido Llano de Ojo de Agua, Churumuco municipality, Michoacán.

Sites/Family	Genera (%)	Species (%)	Density (%)	Basal area (%)
El Guaricho				
Anacardiaceae	2 (6.6)	2 (5.4)	3 (1.4)	0.22 (7.5)
Burseraceae	1 (3.3)	3 (8.1)	3 (1.4)	0.02 (0.7)
Cactaceae	2 (6.6)	3 (8.1)	8 (3.7)	0.46 (15.9)
Euphorbiaceae	2 (6.6)	3 (8.1)	31 (14.6)	0.12 (4.3)
Fabaceae	13 (43.3)	14 (37.8)	84 (39.4)	1.73 (60)
Rubiaceae	2 (6.6)	2 (5.4)	47 (22.1)	0.18 (6.2)
La Joya de la Niña				
Anacardiaceae	2 (6.6)	2 (5.2)	4 (2.3)	0.15 (7.7)
Burseraceae	1 (3.3)	6 (15.6)	14 (7.9)	0.17 (8.7)
Cactaceae	3 (10.0)	4 (10.5)	7 (4.0)	0.25 (12.6)
Euphorbiaceae	3 (10.0)	3 (7.9)	11 (6.3)	0.05 (2.9)
Fabaceae	12 (40.0)	13 (34.2)	79 (44.9)	0.95 (48.5)
Rubiaceae	2 (6.6)	2 (5.2)	17 (9.7)	0.12 (5.8)
El Zipimo				
Anacardiaceae	3 (8.8)	3 (6.9)	21 (8.5)	0.14 (6)
Burseraceae	1 (2.9)	7 (16.3)	71 (28.7)	0.69 (29.5)
Cactaceae	3 (8.8)	4 (9.3)	8 (3.2)	0.26 (11)
Euphorbiaceae	4 (11.8)	5 (11.6)	14 (5.7)	0.03 (1.5)
Fabaceae	9 (26.5)	10 (23.3)	90 (36.4)	0.99 (42.1)
Rubiaceae	3 (8.8)	3 (6.9)	3 (1.2)	0.01 (0.6)

Table 4. Structural data of *Heteroflorum sclerocarpum* for the three sites sampled (0.1 ha) in the tropical dry forest in the Ejido Llano de Ojo de Agua, Churumuco municipality, Michoacán. Abbreviations: DBH (Diameter breast height).

Structure data	El Guaricho	La Joya de la Niña	El Zipimo
Individuals number	9	18	13
Log-density rank	Sixth	Second	Seventh
DBH range (cm)	3.5-29	2.3-26.1	1.6-18.4
Log-basal area rank	Second	First	Fourth
Height range [mean] (m)	2.3-10 [7.3]	1.3-13 [3.9]	1.3-11.2 [5.5]
Relative Importance Value rank	Fourth	First	Fourth

The rank-abundance curves indicated that the five most important species in the sampling sites were different, especially those that occupied the first three positions (Figure 2). *Heteroflorum* was recorded at the first three positions only at La Joya de la Niña. The rank abundance curve at El Guaricho differed significantly from the curves at El Zipimo ($F_1 = 67$, $P < 0.000$) and La Joya de la Niña ($F_1 = 62$, $P < 0.006$), whereas the curves of the last two sites showed no difference from each other ($F_1 = 71$, $P = 0.362$). When considering the rank-basal area curves, there was stronger similarity between the first five dominant species, especially for *Heteroflorum* and *Erythrina oliviae*, exchanging the first and second position at El Guaricho and La Joya de la Niña (Figure 2). The rank basal area curve from El Guaricho differed significantly from the other two sites (El Zipimo, $F_1 = 67$, $P < 0.000$; La Joya de la Niña, $F_1 = 62$, $P < 0.0001$), which also differed from each other ($F_1 = 71$, $P < 0.0001$).
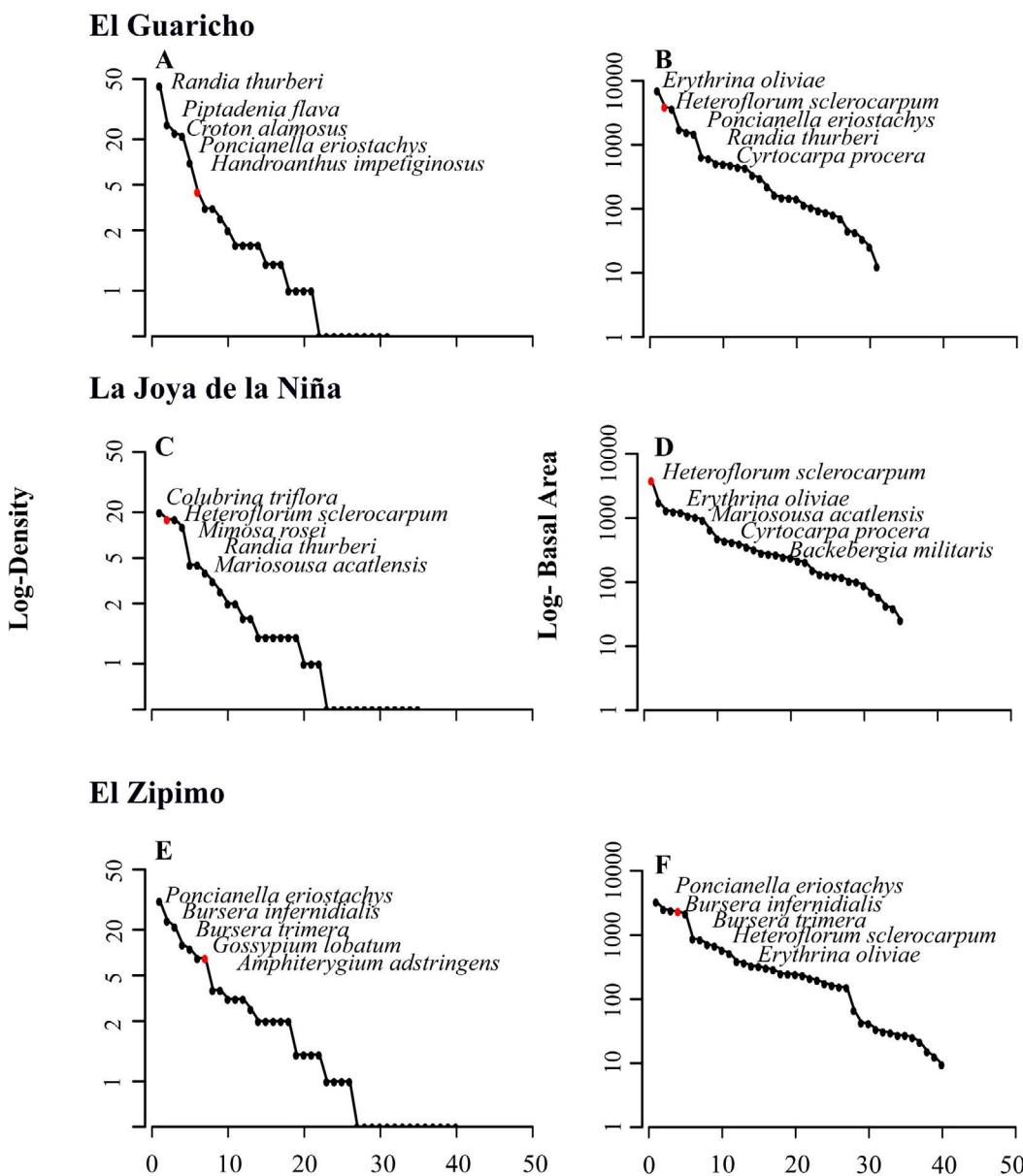
Figure 2. Species-rank curves based on species density (left) and basal area (right) for species assemblages in the Ejido Llano de Ojo de Agua, Churumuco municipality. Curves correspond to each of the three studied sites. The top five species are shown in each case; the rank of *Heteroflorum sclerocarpum* is indicated with a red ellipse. Log data were obtained using the logarithm of abundance/basal area using the logarithm base 10.

The top five species of each site were distinct between the two types of species rank curves, although this dissimilarity was stronger at El Guaricho since it only shared *Poincianella eriostachys* ([Figure 2](#)). In this last site, *Heteroflorum* presented the higher number of individuals in the category with the highest DBH (20-24.9 cm); in contrast, the other two sites had the highest frequencies towards the classes with the lowest DBH values ([Figure 3](#)). The other species included in this figure showed all (*Randia thurberi*) or an important number of individuals grouped in the two firsts DBH categories, and often lacked of individuals in the category with bigger individuals (*e.g.*, *Colubrina triflora* or *Mimosa rosei*).

Trees had similar average height (5 m) and similar height ranges in all three sites ([Table 2](#)). The tallest species at El Guaricho were *Gliricidia sepium* (12 m) and *E. oliviae* (16 m); at La Joya de la Niña they were *Cyrtocarpa procera* (12 m), *E. oliviae* (12 m), and *Heteroflorum* (13 m); and at El Zipimo they were *Lonchocarpus balsensis*, and *E. oliviae* (both 12 m). All those species belonged to Fabaceae, except *C. procera* (Anacardiaceae). Additional structural information on *Heteroflorum* is provided in [Table 4](#).
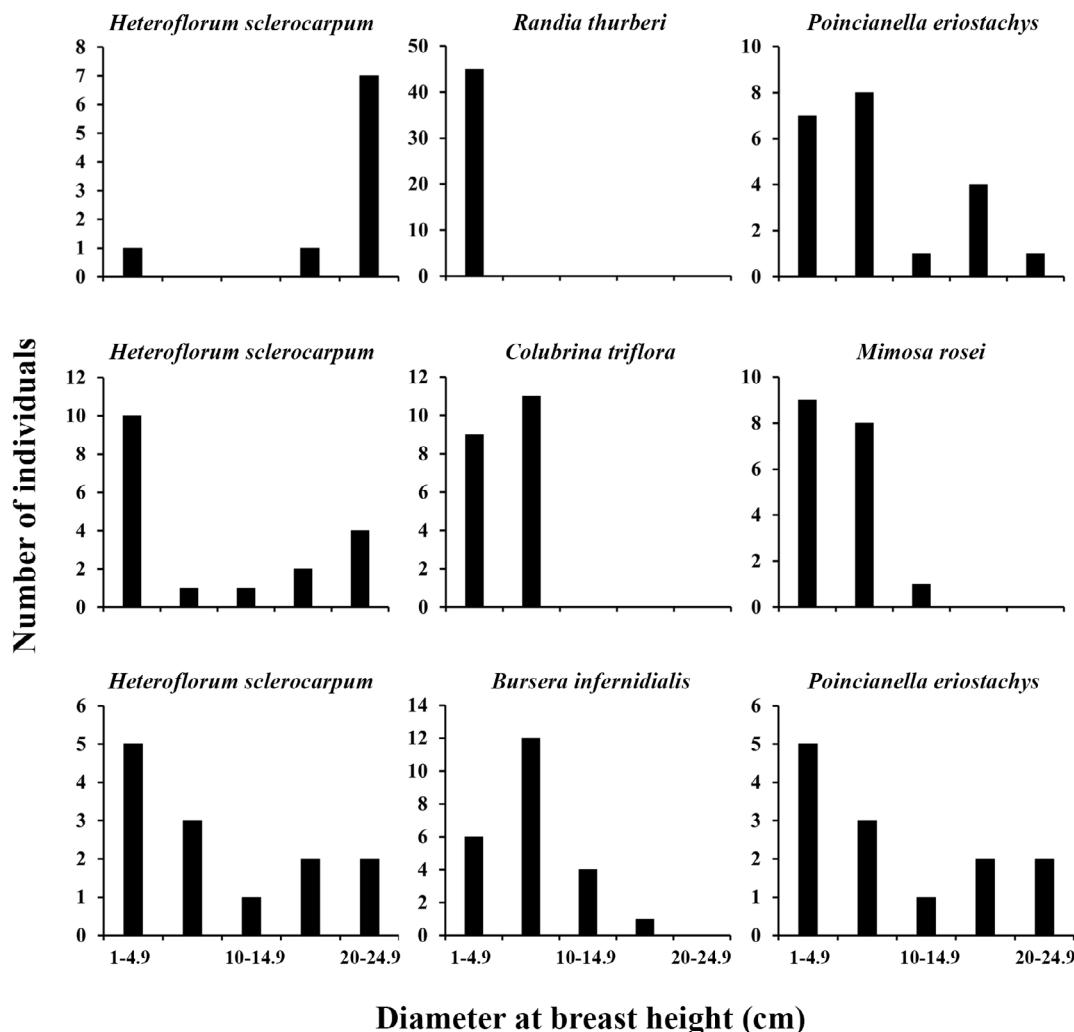
Figure 3. Diameter class-wise distribution of *Heteroflorum* and the two co-dominant species in El Guaricho (top row), La Joya de la Niña (middle row), and El Zipimo (bottom row) in the tropical dry forest of the Ejido Llano de Ojo de Agua.

Diversity. Regardless of the diversity q value, El Zipimo was the site with the highest values, followed by La Joya de la Niña and El Guaricho, ([Table 5](#)). The rarefaction curves of $^0D\alpha$ and $^1D\alpha$ did not differ among sites ([Figure 4](#)). The $^2D\alpha$ rarefaction curve showed that El Guaricho differed from the other two sites in the effective number of dominant species, and this tendency was reflected in the diversity profiles ([Figure 4](#)). Of the 64 species recorded, 14 (21.9 %) were present in the three sites studied (including *Heteroflorum*), while 22 (34.4 %) were present at only one site ([Table 1](#)). The beta diversity analysis showed that El Guaricho has an $^0D_\beta$ estimate value more similar to La Joya de la Niña, and El Zipimo, whereas the comparison between both last sites had a minor value ([Figure 5A](#)). All comparisons among couples of sites showed different estimates values to $^2D_\beta$ and again La Joya de la Niña, and El Zipimo has the higher value ([Figure 5B](#)).

Table 5. Alpha diversity for the three sites sampled in the tropical dry forest in the Ejido Llano de Ojo de Agua.

Diversity index	El Guaricho	La Joya de la Niña	El Zipimo
$^0D\alpha$	37	38	43
$^1D\alpha$	17.8	23.6	25.3
$^2D\alpha$	10.9	17.0	18.2
Evenness Factor	0.30	0.45	0.42
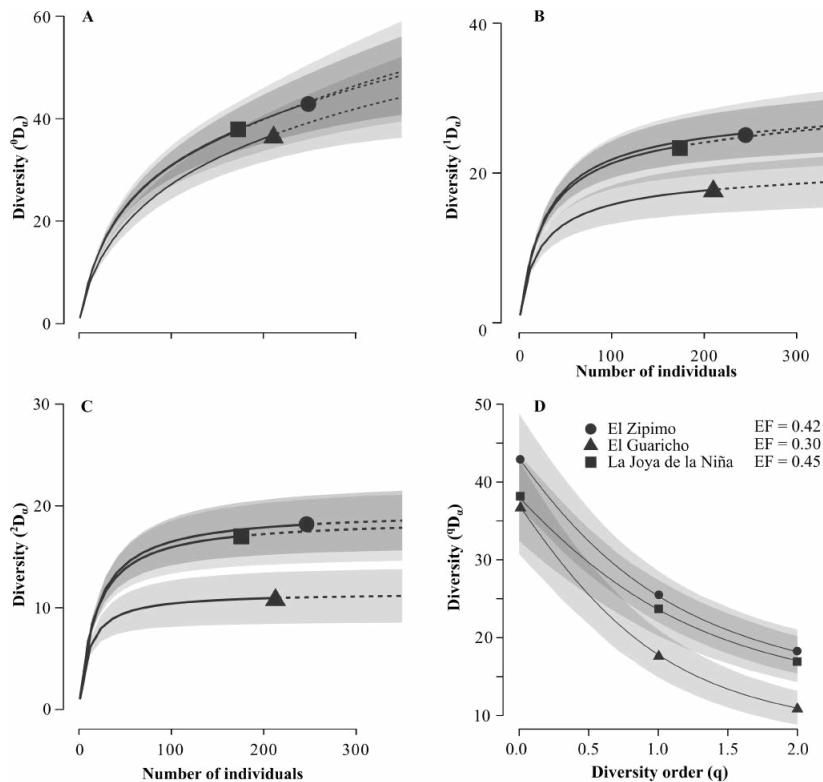
Figure 4. Diversity estimated with different sample sizes (number of individuals; A-C) for different q values. Symbols represent observed diversity values in each site sampled in tropical dry forest of the Ejido Llano de Ojo de Agua, while solid and dotted lines represent interpolated and extrapolated diversity values, respectively. D) Diversity profiles for each site with confidence intervals estimated for q = 0, 1, and 2. Number of simulations: A-C = 100 and D = 10; *Alpha* = 0.05.
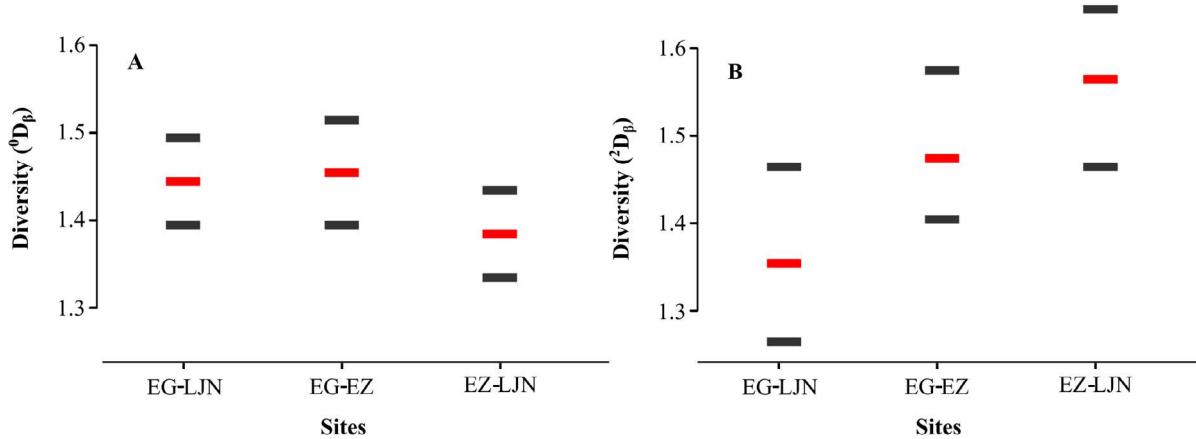
Figure 5. True beta diversity between pairs of sites for orders 0 (A) and 2 (B). The red bars indicate the average estimate, while the black bars designate the confidence interval given by the maximum and minimum estimates (Number of simulations = 100; *Alpha* = 0.05). EG, El Guaricho; LJN, La Joya de la Niña; EZ, El Zipimo.

Discussion

Composition and structure. The number of families was similar among the surveyed sites (12-15), and the same six families contributed most strongly to the composition and structure among all three sites (Table 2). In all cases, Fabaceae was the most important family in these community attributes. This finding is consistent with those reported in different regions of Mexico (Lott *et al.* 1987, Pineda-García *et al.* 2007, Pérez-García *et al.* 2010, Trejo & Dirzo 2002, Gallardo-Cruz *et al.* 2005, Trejo 2005, Almazán-Núñez *et al.* 2012, Martínez-Cruz *et al.* 2013, Méndez-Toribio *et al.* 2014, Cervantes-Gutiérrez *et al.* 2017, Steinmann 2021) and other Neotropical regions or countries of America (Gentry 1988, 1995, Gillespie *et al.* 2000, Gordon *et al.* 2004, Ruiz *et al.* 2005, Lott & Atkinson, 2006, Linares-Palomino *et al.* 2010, Banda-R. *et al.* 2016). Fabaceae had an important contribution in the RIV values, since three out of the five species with the highest RIV value belong to this family (Table 1). It is important to note that the other five families included in Table 3 are also cited as important to the TDF in America (Phillips & Miller 2002, Rzedowski *et al.* 2005, Trejo 2005, Lott & Atkinson 2006, Pérez-García *et al.* 2010, Rzedowski & Calderón de Rzedowski 2013, Villanueva *et al.* 2015, Banda-R. *et al.* 2016).

There was a larger number of species of trees than lianas in all three sites (Table 2). This asymmetry in the species richness is congruent with findings in other areas of the Balsas Basin and the Neotropics (Gentry 1995, Gillespie *et al.* 2000, Trejo & Dirzo 2002, Pineda-García *et al.* 2007, Martínez-Cruz *et al.* 2013). For lianas, the six families recorded at the study site only had 1-2 species, low density (2.3-4.5 %) and there were no species of Bignoniaceae or Fabaceae, which was unexpecting since for other TDF localities these families had the greatest species richness (Gentry 1995, Lott & Atkinson 2006, Pineda-García *et al.* 2007). The low representativeness of the lianas in the surveyed sites could be due to human intervention. Ibarra-Manríquez *et al.* (2015) pointed out that a frequent practice in managed forests is to cut lianas (especially those with large stem diameters) to facilitate the transit of livestock through the forest. This is a productive activity that has been recorded at the study site (Ibarra-Manríquez *et al.* 2021).

Considering its physiognomic dominance at the sites, we expected *Heteroflorum* to be the species with the highest density and basal area values. Nevertheless, it only had particularly high density in La Joya de La Niña, where it is the species with the second highest density (Figure 2, Table 1, 4). In contrast, the basal area of *Heteroflorum* was important in all sites and it occupied the first place at La Joya de La Niña (Figure 2, Table 1). Considering

the RIV values (Table 1), *Heteroflorum* ranks first at this last site and fourth in the other two sites. Consequently, the physiognomic dominance of this species is mainly reflected in its contribution to the biomass in each site. The population structure of *Heteroflorum* in El Guaricho shows a low regeneration, which contrasts with the other two locations sampled (Figure 3). If we compare these frequencies with those shown by the other species included in Figure 3, it is possible to suggest that La Joya de la Niña and El Zipimo have a better level of conservation than El Guaricho. A point that reinforces the above is that El Zipimo also registered the highest number of species and families, which can explain, in part, by being further away from human settlements, and consequently, presenting a lower probability and/or intensity of disturbance derived from its economic activities, for instance, cattle grazing.

Regarding the density, the values recorded at the Llano de Ojo de Agua Ejido (176-247 individuals) are lower than those found by Trejo (2005), which ranged from 203 to 770 individuals (mean 582). This tendency is maintained when we compare the values of censuses with ≥ 2.5 DBH. For the Balsas Basin, from 198 to 300 individuals have been reported (Pineda-García *et al.* 2007, Martínez-Cruz *et al.* 2013, Méndez-Toribio *et al.* 2014), whereas in other Neotropical sites there were between 135 and 520 individuals (Gentry 1995, Gillespie *et al.* 2000, Phillips & Miller 2002). Basal area values in all sites sampled (1.95-2.84 m²) were similar (2.67-3.47 m²) to those found in Pineda-García *et al.* (2007). For TDF in other parts of the Neotropics (Phillips & Miller 2002), there is a wider range in basal area, varying from 4.49 m² (Nuevo Mundo, Bolivia) to 1.19 m² (Estación Biológica de Los Llanos, Venezuela). Gentry (1995) emphasized that although species richness varies widely, density and basal area values are remarkably uniform in TDF, although he did not propose a specific explanation for this trend. Pérez-García *et al.* (2021) mentioned that biomass and density are community variables that could be predicted in a particular climatic region. Structural similarity is also reflected in the significant relationship between the height and basal area of trees. The average height of the sites is homogeneous (5-5.2 m), and is close to that reported for Tziritzícuaro, Michoacán (4.6 m) and Nizanda, Oaxaca (4.1 m) (Gallardo-Cruz *et al.* 2005, Méndez-Toribio *et al.* 2014). The height range (Table 1) also coincides with the values reported in Mexico overall, which is between 5 and 15 m (Rzedowski 1978).

Diversity. The richness of TDF plots of 0.1 ha (Gentry's method) for trees and lianas with DBH ≥ 1 cm in the Balsas Basin shows very wide variation; the lowest value is recorded in Calipam, Puebla (29 species), while 123 species were reported at Caleta, Michoacán (Trejo & Dirzo 2002, Pineda-García *et al.* 2007). The three surveyed sites are located towards the lower richness values (37-43 species), and they are surpassed by other localities in Michoacán, closely to Zináparo (48 species) but far to Caleta. This result requires more detailed studies, since near to the study area (ca. 58 km linear distance), in the locality of El Tarimo (Guerrero), a richness between 45 and 55 species was recorded (Pineda-García *et al.* 2007). These ranges of low richness contrast strongly with that documented by Phillips & Miller (2002) for 10 of the most relevant localities in richness for TDF in the world, whose richness reaches between 100 and 169 species with DBH ≥ 2.5 cm.

$^0D\alpha$ and $^1D\alpha$ rarefaction curves indicated that the sites do not differ in their diversity values (Figure 4). Furthermore, the $^2D\alpha$ rarefaction curve and the diversity profiles indicate that El Guaricho is a community with a significant minor number of dominant species and the lowest evenness factor in comparison with the other two sites sampled (Table 5). The analysis of β diversity among sites suggest that species turnover is relatively low, particularly for $^0D_\beta$ (Figure 5). However, $^2D_\beta$ was higher between El Zipimo and La Joya de la Niña which could be an indicator of the conservation state of these sites.

Comparison of diversity attributes with other tropical dry forests indicates that the localities studied differ mainly in terms of low values of species richness. Determining whether this is due to the dominance of *Heteroflorum* or to other factors (*e.g*., human disturbance or dispersal limitation) requires further studies. Finally, we hope to promote, in the short term, the development of research that allows a more comprehensive understanding of the ecological processes that regulate the community attributes of TDF in this region whose conservation status is a priority (Olson & Dinerstein 2002, Miles *et al.* 2006, Bezaury-Creel 2010).

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