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High Richness of Vascular Plants in the Tropical Los Tuxtlas Region, Mexico

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Abstract

We present an assessment of the recorded vascular plants in the Los Tuxtlas region, in the state of Veracruz, Mexico, an important portion of the humid tropical forest at the northern edge of its distribution. A literature review and the information contained in the two most important databases in Mexico with digitized information for the region report 2,548 species, of which 2,391 are native and 157 naturalized (exotic). The families with the highest number of species are Fabaceae, Orchidaceae, Asteraeae, and Rubiaceae. The composition of the flora is analyzed, and its similarity is compared with other tropical regions of Mexico. The humid tropical forest in Los Tuxtlas stands out as the site with the third highest number of tropical species in Mexico, and in particular for its high number of endemisms. A quarter of the species occurring in the region are threatened; despite this, the biosphere reserve within its limits plays an important role in the conservation of this type of vegetation.

Keywords

floristic richness, endemism, tropical rain forest, conservation, Veracruz

Introduction

The humid tropical forest (HTF; Villaseñor & Ortiz, 2014) is a biome that has attracted attention for several decades. Among the different causes of such attention are its high floristic richness (Myers, 1988), its anthropogenic importance since the dawn of civilization (Schmitter-Soto, Mariaca-Méndez, & Soto-Pinto, 2016), the ecosystem services it provides (Naidoo et al., 2008), its ability to cushion the impacts of climate change (Bonan, 2008), as well as the imminent threat of its disappearance due to continuous deforestation and land use change where it is established (Achard et al., 2002; Betts, Mahli, & Roberts, 2008; Dirzo & García, 1992; Flores-Villela & Gerez, 1994).

As a biome (Gurevitch, Scheiner, & Fox, 2002), the HTF encompasses a set of plant communities dominated by trees found in the lowlands of the Mexican tropics, where annual rainfall exceeds 1,500 mm and the temperature almost never drops to freezing (Villaseñor & Ortiz, 2014). The communities or vegetation types associated with this biome are mainly tropical rainforest, evergreen tropical forest, subperennifolian tropical forest, and tropical subdeciduous forests (sensu Rzedowski, 1978). Its presence has been documented in 18 of the 32 states into which the country is politically divided (Table 1). On the Pacific Ocean slope, HTF is of the subdeciduous or subperennifolian tropical forest type in the north of the state of Sinaloa (municipalities of Cosalá and Culiacán; Vega-Aviña & Villaseñor-Ríos, 2008) and on the Gulf slope of Mexico, in the south of the state of Tamaulipas (municipalities of Gómez Farías and Llera). In particular, Dirzo and Miranda (1991) evaluated the northern boundary distribution of the tropical humid forest, placing it in the Huasteca Potosina, in the southeast of the state of San Luis Potosí; however, they emphasize that at present, due to land use change, this boundary is located in the Los Tuxtlas region in the state of Veracruz, where relatively large fragments of this type of vegetation still persist.

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Table 1. Number of Species in Each Mexican State With Humid Tropical Forest Recorded in its Territory and Surface Occupied (Villaseñor, 2016).

State	Potential surface of humid tropical forest (km^2)	% state	Native species
Campeche	51,381.7	83.3	1,862
Chiapas	42,047.4	50.6	5,030
Colima	1,190.3	18.6	1,874
Guerrero	4,940.6	6.9	2,607
Hidalgo	2,663.7	11.7	1,558
Jalisco	4,432.2	5.2	2,277
Michoacán	2,891.9	4.5	1,999
Nayarit	11,560.7	38.4	1,685
Oaxaca	30,728.6	29.2	4,459
Puebla	3,069.4	8.1	2,100
Querétaro	47.7	0.4	1,455
Quintana Roo	40,401.3	84.5	1,788
San Luis Potosí	7,760.4	11.9	1,744
Sinaloa	2,190.0	3.8	1,391
Tabasco	21,104.3	77.9	2,413
Tamaulipas	505.4	0.6	1,403
Veracruz	57,548.1	73.7	4,385
Yucatán	36,610.2	85.2	1,443
Total	321,473.5	15.5	5,902

An account of the HTF's floristic richness in Mexico reports the existence of 6,187 species (Villaseñor, unpublished data). Of these, at least 3,941 are characteristic (shared with one or two neighboring biomes) and 1,185 are practically endemic to the biome (Villaseñor, 2016; Villaseñor & Ortiz, 2014). Table 1 presents a summary of the floristic richness documented in each of the states where the biome is present; the states of Chiapas (5,030), Oaxaca (4,459), and Veracruz (4,385) stand out for their number of species. It is important to emphasize that although the figures for these three states are similar, the area in which the species are settled varies from 29.2% of Oaxaca's state territory to 73.7% of the territory of Veracruz. Unfortunately most of the potential surface for this vegetation is currently covered by cultivated land and grazing, as well as by secondary vegetation; in particular in Veracruz, only 8.6% of the natural vegetation remains (Ellis, Martínez-Bello, & Monroy-Ibarra, 2011).

As Dirzo and Miranda (1991) point out, the Los Tuxtlas region, in the state of Veracruz, constitutes the largest fragment of HTF within its boreal distribution boundary. Unfortunately, much of its original vegetation has also disappeared, giving way to secondary vegetation (pastures), dwellings, and agricultural areas (Castillo-Campos & Laborde, 2004; Guevara, Laborde, & Sánchez-Ríos, 2004). The region has attracted the attention of many investigators; there are several floristic studies that address part of this territory, several of them focused on the existing protected natural regions. Of special attention are the inventories made at the Los Tuxtlas Tropical Biology Station of the Universidad Nacional Autónoma de México (Bongers, Popma, Meave, & Carabias, 1988; Ibarra-Manríquez & Sinaca, 1987; Ibarra-Manríquez & Sinaca-Colín, 1995, 1996a, 1996b; Lira-Noriega, Guevara, Laborde, & Sánchez-Ríos, 2007), in the Sierra de Santa Marta (Ramírez, 1999), or in the Los Tuxtlas Biosphere Reserve (Acebey, Krömer, Vázquez-Torres, & Tejero-Díez, 2015; Arroyo-Rodríguez, Dunn, Benítez-Malvido, & Mandujano, 2009). However, there is no work documenting the total floristic richness of this important tropical rainforest remnant. The work presented here is the first effort to document the floristic richness of the entire region. The evaluation of the vascular plant richness of the Los Tuxtlas region will allow the determination of the most characteristic floristic elements, so the questions to answer are how representative this flora is of the tropical humid biome of Mexico and how distinct it is from other sites in the country with this biome.

Methods

Study Area

For the delimitation of the study area, the polygon proposed by Guevara et al. (2004) was employed. They circumscribed the Los Tuxtlas region in terms of its volcanic origin, which makes it different, edaphically, geomorphologically, and climatically, from the coastal plain of the lower basin of the Papaloapan and Coatzacoalcos rivers. Based on these criteria, they demarcated a region subject to the influence of the volcanoes, separated from the area of the coastal plain subject to sedimentation processes (Guevara et al., 2004). The polygon has an area of approximately 3,300 km^2.

The Los Tuxtlas region includes plains and a northwest-southeast oriented volcanic chain, located on the coast of the Gulf of Mexico. It is located between 18° 6′ and 18° 42′ N and 94° 36′ and 95° 24′ W (Figure 1). The region constitutes the eastern boundary of the Transverse Volcanic Belt, here surrounded by the coastal plain of the Gulf of Mexico. It is relatively isolated from other mountainous areas; the closest one is the Sierra de Juárez in Oaxaca, 150 km away (Dirzo, González, & Vogt, 1997).

In general, the Sierra de Los Tuxtlas presents three types of biomes: HTF (74% of the surface), temperate forest (16%), and humid mountain forest (10%; Villaseñor & Ortiz, 2014). The first one is distributed practically throughout the region, while the other two

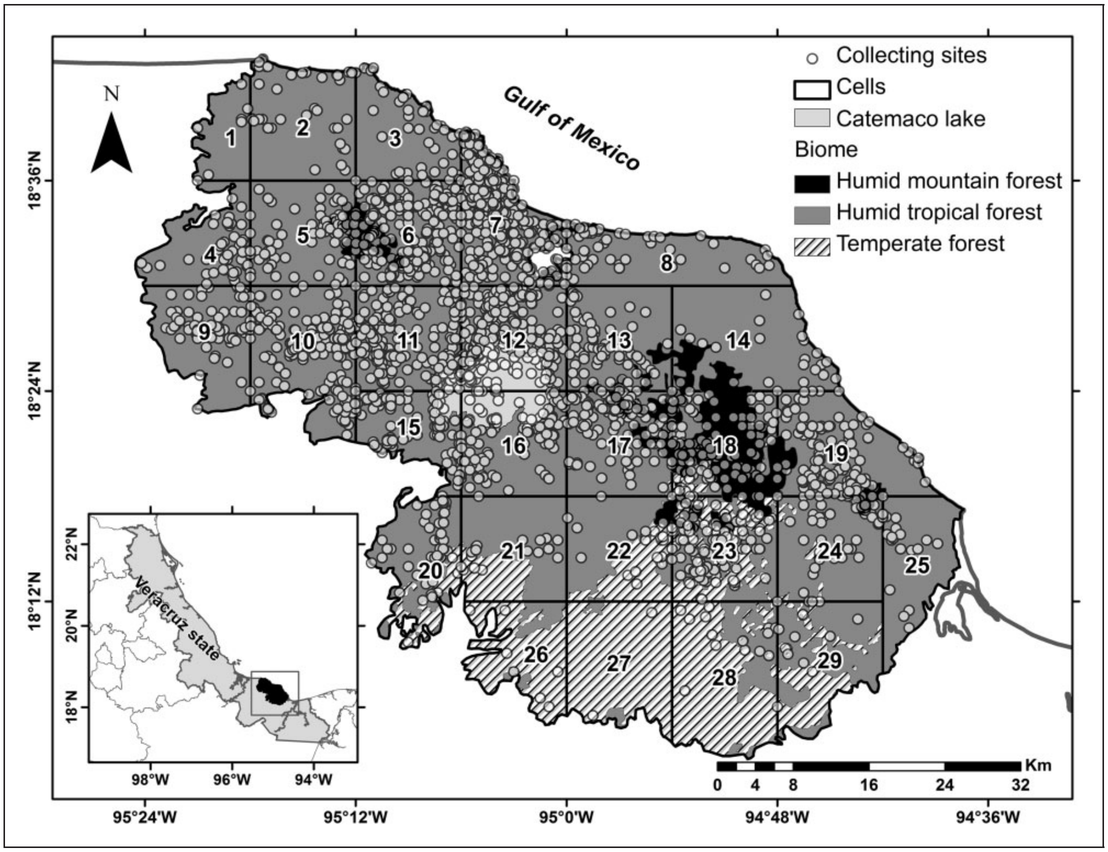

Figure 1. The region of Los Tuxtlas, Veracruz, divided into 29 6′ × 6′ squares showing the potential distribution of the biomes present in the region. At this scale, a grid-square measures approximately 116 km^2. The points indicate the collection sites.

are in the southern portions of the area, mainly in high parts of the Sierra de Santa Marta and on the San Martín Pajapan and San Martín Tuxtla volcanoes (Figure 1). Under the denomination of biome (Gurevitch et al., 2002), different communities or types of vegetation documented in the zone by Guevara et al. (2004) were grouped within the HTF, such as high evergreen tropical forest, medium evergreen tropical forest, savanna, mangrove coastal dunes, and inundated low tropical forest. The humid mountain forest biome includes the humid montane forest and the tropical montane cloud forest. Finally, within the temperate forest biome, vegetation types such as the pine forest and oak forest are included.

The Los Tuxtlas region includes seven main volcanoes, the highest reaching an altitude of 1,680 m. There are several peaks of lower altitude and many volcanic cones and hills. A central basin contains Lake Catemaco, the third largest lake in Mexico. The lowlands drain into the systems of the Coatzacoalcos and Papaloapan rivers (Andrle, 1964; Guevara et al., 2004). Although known altogether as the Los Tuxtlas region, its physiognomy is better defined by two mountainous massifs (Sierra de Los Tuxtlas): one to the northwest, that includes the San Martín Volcano as its nucleus and another located to the southeast, known as Sierra de Santa Marta (Dirzo et al., 1997).

The Sierra de Los Tuxtlas is a result of volcanic and erosion processes, which after its marine emergence in the Tertiary has gradually transformed the earth's surface up to the present time into a landscape of elevated craters, steep cones, valleys, and undulating plateaus. Most soils in the region are derived from basic volcanic materials and some from sedimentary rocks. The depth and variable composition of the soil is reflected in a complex surface configuration and causes a marked variability in the structure of the vegetation (Andrle, 1964). For a long period of its geological history, the region maintained a forest aspect, typical of a tropical region, but in the last two millennia of human occupation, the vegetation has been destroyed and modified in more than half of its territory.

In most of the region, the climate is warm and semiwarm, although there are patches of temperate climate at the highest elevations of the three main volcanoes. The average annual temperature is 24 to 26 °C, and precipitation varies from 1,200 to 7,000 mm (Gutiérrez-García & Ricker, 2011). Los Tuxtlas is one of the wettest regions along the coast of the Gulf of Mexico, from Florida to

Campeche. The driest month is usually May, and the rainiest period occurs from July to November. The climate of the sierra is influenced by its accentuated altitudinal gradient and complex topography, as well as its proximity to the sea and location to the south of the Gulf of Mexico. The Sierra de Los Tuxtlas is a climatic barrier between the sea and the interior of the continent (Soto, 2004; Soto & Gama, 1997); it generates climatic differences between the northeast slope facing the Gulf of Mexico and the southwest slope oriented toward the interior of the continent (Soto, 2004; Soto & Gama, 1997).

Background

The botanical history in the Los Tuxtlas region began at the end of the 18th century, with the passage of the Royal Botanic Expedition to New Spain, when the first botanical specimens of the region are collected. Although study and general collection have been relatively continuous, several works have been in specific botanical groups or taxonomic families or in areas of particular interest (e.g., trees: Vázquez-Torres, Armenta, Campos, & Carvajal, 2010; vascular epiphytes: Hietz-Seifert, Hietz, & Guevara, 1996; Araceae: Acebey & Krömer, 2008; plant diversity patterns: Krömer, Acebey, Kluge, & Kessler, 2013). Since the middle of the last century, several national and foreign institutions have maintained their interest in the region, so that projects emerged in such diverse subjects as ecology, floristics, and ethnobotany, among others. In particular, with the founding of projects such as Flora de Veracruz and Flora of the Los Tuxtlas region, constant botanical exploration and specimen collection is maintained. Along with the explorations and collecting by other national and foreign institutions, the region has more than 50,000 unique collection numbers.

Floristic List

The list of species was obtained from a bibliographic search, and the information included in two digital collections. One is the National Biotic Information System (SNIB-REMIB) at the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), and the other is the digital repository of the National Herbarium of Mexico (MEXU-UNIBIO), at the Instituto de Biología, Universidad Nacional Autónoma de México (UNAM). Most of the specimens studied are available online on the CONABIO and UNIBIO (UNAM) websites. Based on the information obtained, the collection sites were georeferenced, which allowed the generation of a database of species with their geographical distribution, whose sites of occurrence are shown in Figure 1.

After evaluating the scientific names documented in each record, reviewing them in the catalogs of http://www.tropicos.org and http://www.ipni.org/ and eliminating the names considered synonyms, this article reports the number of vascular plant species (subspecific taxa were not included) of the HTFs (and to a lesser extent of the humid mountain forest) in Los Tuxtlas that have at least one specimen deposited in 1 of the 61 herbaria that recorded specimens in the data bases reviewed. Finally, the information obtained from the databases was synthesized in a matrix of presences-absences of the species in each grid-square into which the study area was divided.

Regional Richness Patterns

The polygon of the Los Tuxtlas region was divided into 32 grid-squares of 6 min latitude and longitude, approximately 116 km^2 (Figure 1). To discard species that were not tropical or from humid mountain forests, the species from temperate forests in the south and southwest of the region (Grids 26, 27, 28, and 29) were eliminated. The territory was thus divided into 29 operational geographical units (OGUs). Some grid-squares are larger because neighboring cells containing less than 50% of the surface within the polygon of the study region were fused. The grid size used represented the best compromise between the distribution of collecting effort and the gaps in such effort; if a finer scale is used, the majority of grids have no records. The side of each grid cell is approximately 10% of the distance between the two extreme points of the study area; this distance could be used to estimate the areas where the species of the region are located and to evaluate them as their areas of occupation (International Union for Conservation of Nature [IUCN], 2001), to be used as a risk parameter in local conservation strategies. The databases analyzed (CONABIO and MEXU-UNIBIO) allowed the combination of 52,197 records, from 61 different herbaria. Once grouped by scientific name (i.e., species), date, collector, and geographical coordinates of the localities, the number of records was reduced to 29,373. Finally, these records were documented as present or absent in each of the 29 6′ by 6′ grids. In summary, the number of unique records of each species per cell resulted in a presence or absence matrix with 12,078 presence records.

An evaluation of the floristic similarities between our study site and the main regions in Mexico with recorded areas with remaining HTF was carried out using the Sorensen-Dice similarity coefficient. The selected areas were Chimalapa-Uxpanapa (Márquez, Gómez-Pompa, & Vázquez-Torres, 1981), Chinantla, Oaxacan Coast (Salas-Morales, Saynes-Vásquez, & Schibli, 2003; Salas-Morales, Schibli, Nava-Zafra, & Saynes-Vásquez, 2007), Lacandona region (Durán-Fernández, Aguirre-Rivera, García-Pérez, Levy-Tacher, & de Nova-Vázquez, 2016; Levy-Tacher, Aguirre-Rivera, García-Perez, & Martínez-Romero, 2006; Martínez, Ramos-Alvarez, & Chiang, 1994; Meave et al., 2008), and Soconusco (Long & Heath, 1991; López-Cruz, Alemán, Pérez-Farrera, & Farrera-Sarmiento, 2010; Martínez-Camilo, Pérez-Farrera, & Martínez-Meléndez, 2012; Martínez-Meléndez, Pérez-Farrera, & Farrera-Sarmiento, 2008; Matuda, 1950). The Jalisco Coast, in western Mexico (Lott, 1993; Ramírez & Cupul, 1999) and the portion of the Yucatan peninsula (Gutiérrez, 2001; Martínez, Sousa-Sánchez, & Ramos Alvarez, 2001; Zamora, 1999) with HTF were also included. The list of species of these areas was obtained from the references cited, the review of floristic works, new reports of species, as well as the CONABIO and UNIBIO databases already described. The Oaxacan Coast, Jalisco Coast, and Yucatan peninsula regions have, in addition to HTF, large extensions of tropical dry forest; thus, in the comparisons, only the species with recorded occurrence in HTF was used for comparison.

The surfaces of these areas (Table 6) were obtained from the description of the area given by the authors and calculated using a geographic information system. It should be noted that there are other areas of HTF (mostly much reduced) in Mexico, such as the Tabasco lowlands and neighboring lower slopes of the mountains of northern Chiapas, some smaller areas in central and northern Veracruz, and many scattered small areas along

Table 2. Vascular Plant Species Richness and Collecting Effort Recorded in the 29 Grid-Squares Into Which the Los Tuxtlas Region Was Divided.

Grid-square	Families	Genera	Species	Endemic	Exotic	Records
1	26	33	38	3	2	44
2	56	96	108 (2)	9	3 (2)	122
3	91	218	284 (4)	26 (1)	7	390
4	67	143	167 (3)	8	6 (1)	197
5	124	328	505 (22)	54 (8)	5	994
6	132	439	762 (43)	97 (6)	11 (1)	1,564
7	174	703	1,379 (181)	114 (33)	68 (25)	10,634
8	78	152	182 (8)	14 (2)	6	229
9	93	227	292 (1)	21	6	380
10	134	494	759 (27)	42 (4)	36 (1)	1,483
11	154	572	963 (43)	74 (5)	62 (8)	2,072
12	150	609	1,112 (38)	93 (3)	59 (4)	2,697
13	111	275	415 (9)	45 (3)	11	711
14	66	134	160 (8)	10 (1)	9	161
15	94	254	327 (6)	23 (1)	20	373
16	115	339	484 (14)	27	24 (2)	787
17	125	310	501 (18)	61 (2)	5	865
18	150	383	666 (48)	77 (13)	11	1,293
19	138	436	719 (35)	61 (3)	23 (3)	1,422
20	70	149	192 (6)	9 (1)	11 (1)	297
21	63	139	163 (7)	28 (2)	2	186
22	73	129	162 (8)	11 (1)	13 (1)	176
23	155	504	830 (64)	56 (9)	48 (8)	1,723
24	97	234	307 (12)	30 (2)	13	345
25	39	58	62 (5)	1	3	71
26	10	15	15 (1)			23
27	5	5	5	1		5
28	25	37	43 (2)	2	2	45
29	38	67	71 (2)		4	84
	208	1,018	2,548 (617)	307 (100)	157 (57)	29,373

The number of species endemic to Mexico (Endemic) and the number of introduced species (Exotic) per cell are also indicated. The number of exclusive species (recorded only in that grid-square) is indicated in parenthesis.

the Pacific coast that would add additional species to the HTF flora.

Results

In the Los Tuxtlas region, a total of 2,548 vascular plant species were recorded (subspecific taxa were not included), distributed among 1,018 genera and 208 families. Angiosperms dominate the flora with 91% of species, ferns and lycophytes constitute 8.8% and gymnosperms 0.2%. Most species occur in the HTF, and only 358 of them restrict their distribution to the patches with humid mountain forests found in the higher altitudes of the region. A total of 2,391 species are native and 157 naturalized (Table 2). Among the native species, 307 are endemic to Mexico, 51 of them endemic to the state of Veracruz, and 34 apparently only known from the LosTuxtlas region (Table 3).

The review of floristic information by grid-squares (Table 2, Figure 1) reveals the existence of at least 12,078 unique records documenting the presence of the species at least once among the OGUs into which the region was divided. Table 2 shows the distribution of the richness (alpha diversity) per OGU. It can be observed that there are cells with extremely low richness, such as Cell 27 (5 recorded species), to cells with more than 1,000 species, such as Grids 7 (1,379 species) or 12 (1,122). The median richness per cell is 219 species. Table 2 also indicates the collecting effort, which shows that grid cells with high number of specimens also contain a higher number of species.

Among the recorded species, 617 are known only from one grid-square, constituting the rare species of the flora of Los Tuxtlas. Among them are 100 species endemic to Mexico (out of a total of 307 recorded for the entire region). Of the 34 species mentioned earlier as being restricted to the Los Tuxtlas region, 20 are known only from one plot (with an area of occupation of no more than 116 km^2), and 6 are apparently restricted to the Los Tuxtlas Tropical Biology Station, UNAM (*Capparidastrum tuxtlense, Diospyros tuxtlensis, Guadua tuxtlensis, Hoffmannia altipetens, Justicia tuxtlensis*, and *Styrax tuxtlensis*).

The family with the highest number of species in the Los Tuxtlas region is Fabaceae (212), followed by Orchidaceae (171), Asteraceae (150), and Rubiaceae (143). Table 4 includes the 15 families with the highest species richness in the region; in total, these families

Table 3. Species Endemic to the Los Tuxtlas Region.

Annona longipes Saff. (Annonaceae)
Arachnothryx tenuisepala Borh. (Rubiaceae)
Arachnothryx tuxtlensis (Lorence & Cast. Campos) Borh.(Rubiaceae)
Archibaccharis tuxtlensis G.L. Nesom (Asteraceae)
Ardisia bastonalensis Ricketson & Pipoly (Primulaceae)
Aristolochia veracruzana J.F. Ortega (Aristolochiaceae)
Bourreria veracruzana Campos-Ríos & F. Chiang (Boraginaceae)
Capparidastrum tuxtlense X. Cornejo & H.H. Iltis (Capparaceae)
Croton sousae Martínez-Gordillo & Cruz-Durán (Euphorbiaceae)
Chamaedorea hooperiana Hodel (Arecaceae)
Dichapetalum mexicanum Prance (Dichapetalaceae)
Diospyros tuxtlensis Provance & A.C. Sanders (Ebenaceae)
Epidendrum dressleri Hágsater (Orchidaceae)
Eupatoriastrum johnbeamanii B.L. Turner (Asteraceae)
Gentlea cuneifolia Lundell (Primulaceae)
Guadua tuxtlensis Londoño & Ruiz-Sánchez (Poaceae)
Goniopteris tuxtlensis (T. Krömer, Acebey & A.R. Sm.) Salino & T.E. Almeida (Thelypteridaceae)
Hoffmannia altipetens Dwyer ex A. Torres-Montúfar & H. Ochoterena (Rubiaceae)
Inga lacustris M. Sousa (Fabaceae)
Justicia tuxtlensis T.F. Daniel (Acanthaceae)
Magnolia lopezobradorii A. Vázquez (Magnoliaceae)
Magnolia sinacacolinii A. Vázquez (Magnoliaceae)
Magnolia zoquepopolucae A. Vázquez (Magnoliaceae)
Malpighia latifolia F.K. Mey. (Malpighiaceae)
Miconia ibarrae Almeda (Melastomataceae)
Mikania neei W.C. Holmes (Asteraceae)
Parathesis pajapanensis Lundell (Primulaceae)
Parathesis tuxtlensis Lundell (Primulaceae)
Randia manglaris Borh. & E. Martínez (Rubiaceae)
Randia veracruzana Borh. & E. Martínez (Rubiaceae)
Salvia tuxtlensis Ramamoorthy (Lamiaceae)
Stromanthe popolucana Cast.-Campos, Vovides & Vázq. Torres (Marantaceae)
Styphnolobium parviflorum M. Sousa & Rudd (Fabaceae)
Styrax tuxtlensis P.W. Fritsch (Styracaceae)

Table 4. The 15 Families and Genera With the Highest Number of Native Species in the Los Tuxtlas Region.

Family	Species	Genus (Family)	Species
Fabaceae	212	*Piper* (Piperaceae)	29
Orchidaceae	171	*Solanum* (Solanaceae)	29
Asteraceae	150	*Tillandsia* (Bromeliaceae)	25
Rubiaceae	143	*Peperomia* (Piperaceae)	25
Poaceae	82	*Epidendrum* (Orchidaceae)	24
Malvaceae	68	*Psychotria* (Rubiaceae)	21
Euphorbiaceae	67	*Ipomoea* (Convolvulaceae)	21
Solanaceae	64	*Asplenium* (Aspleniaceae)	20
Apocynaceae	58	*Cyperus* (Cyperaceae)	19
Piperaceae	54	*Palicourea* (Rubiaceae)	19
Bromeliaceae	52	*Ficus* (Moraceae)	17
Cyperaceae	47	*Miconia* (Melastomataceae)	17
Melastomataceae	41	*Croton* (Euphorbiaceae)	16
Lauraceae	40	*Ocotea* (Lauraceae)	16
Araceae	40	*Randia* (Rubiaceae)	15

account for 50.8% of the total recorded native flora. The genera with the highest number of species are (Table 4) *Piper* and *Solanum* (both with 29), followed in importance by *Tillandsia* (25), *Peperomia* (25), and *Epidendrum* (24).

How Distinct Is the HTF of the Los Tuxtlas Region?

At the national level, the most important family in the HTF is Fabaceae (see also Wendt, 1993), which dominates by its number of species in seven of the analyzed regions (Table 5); only in the Lacandona region, it is surpassed by the family Orchidaceae. In five regions, the Asteraceae family occupies the second place, being displaced in three of them by Fabaceae (Lacandona) and Orchidaceae (Soconusco and Los Tuxtlas). Other characteristic HTF families in Mexico with high numbers of species in all the regions are Euphorbiaceae, Malvaceae, Poaceae, and Rubiaceae. Some families stood out for being among the 10 most important in some regions but not others; for example, Bromeliaceae was relevant in two regions (Soconusco and Los Tuxtlas), as well as Piperaceae (Coast of Jalisco and Lacandona). Table 5 summarizes the 10 most important families for each region, highlighting the five with the highest number of species.

A total of 5,902 species was recorded on the eigth regions, Figure 2 and Table 6 report the values of alpha diversity (species richness) recorded in each of the seven regions with which Los Tuxtlas was compared. Only the Coast of Chiapas (Soconusco, 3,357 species), the Lacandona region (3,177), and the Chinantla region (2,555) surpassed Los Tuxtlas in their number of species (2,548). The regions with the lowest number of recorded species are the Yucatan peninsula (1,769) and the Jalisco Coast (1,910). The species/area ratio (Table 6) shows that the Los Tuxtlas region has the highest species/area ratio, while the lowest proportion is found in the Yucatan Peninsula.

Although the richness values among the eight regions are contrasting, all of them are characterized by having exclusive species (recorded only in their territory). The maximum number of these species was found in the Lacandona region (765), followed by Los Tuxtlas (617) and Soconusco (607), and the Coast of Oaxaca had the lowest value (427). An evaluation of the floristic similarities between the main regions in Mexico with HTF showed that the Los Tuxtlas and Lacandona region (Durán-Fernández et al., 2016; Levy-Tacher et al., 2006; Martínez et al., 1994; Meave et al., 2008) have the highest percentage of shared species (Figure 2). Using the Sorensen-Dice coefficient of similarity, these two regions share more than 60% of their flora and in turn are grouped together with four other regions of southern and southeastern Mexico (Figure 2): Chimalapa-Uxpanapa (Márquez et al., 1981), Chinantla, Oaxacan

Table 5. The 10 Families With the Highest Number of Species in the Eight Main Regions of Mexico With Remaining Humid Tropical Forest.

Family	CHIMA	CHINA	JALIS	LACAN	OAXAC	SOCON	TUXT	YUCAT
Acanthaceae	61			68	55		25	
Apocynaceae		56			62	80	58	54
Asteraceae	**154**	**166**	**142**	**147**	**190**	**227**	**150**	**110**
Bromeliaceae						77	52	
Convolvulaceae			46				32	
Cyperaceae							47	63
Euphorbiaceae	67	**88**	63	83	77	98	67	**92**
Fabaceae	**201**	**206**	**235**	**235**	**272**	**326**	**212**	**183**
Malvaceae	**75**	68	**64**	68	78	96	68	59
Melastomataceae	60	53		77			41	
Orchidaceae	**102**	**127**	**71**	**315**	**134**	**247**	**171**	**83**
Piperaceae			41	73			54	
Poaceae	72	82	**85**	**150**	**94**	**112**	**82**	**102**
Rubiaceae	**118**	**148**	64	**188**	**133**	**160**	**143**	64
Solanaceae	61	65	58		68	86	64	46

In bold are the five most important families by region. CHIMA = Chimalapa-Uxpanapa, Oaxaca-Veracruz (Márquez et al., 1981); CHINA = Chinantla, Oaxaca (Salas-Morales et al., 2003, 2007); JALIS = Coast of Jalisco (Lott, 1993; Ramírez & Cupul, 1999); LACAN = Lacandona, Chiapas (Durán-Fernández et al., 2016; Levy-Tacher et al., 2006; Martínez et al., 1994; Meave et al., 2008); OAXAC = Coast of Oaxaca (Salas-Morales et al., 2003, 2007); SOCON = Coast of Chiapas (Long & Heath, 1991; López-Cruz et al., 2010; Martínez-Camilo et al., 2012; Martínez-Meléndez et al., 2008; Matuda, 1950); TUXT = Tuxtlas, Veracruz (this work); and YUCAT = Peninsula of Yucatán, Campeche, Quintana Roo, Yucatán (Gutiérrez, 2001; Martínez et al., 2001; Zamora, 1999).

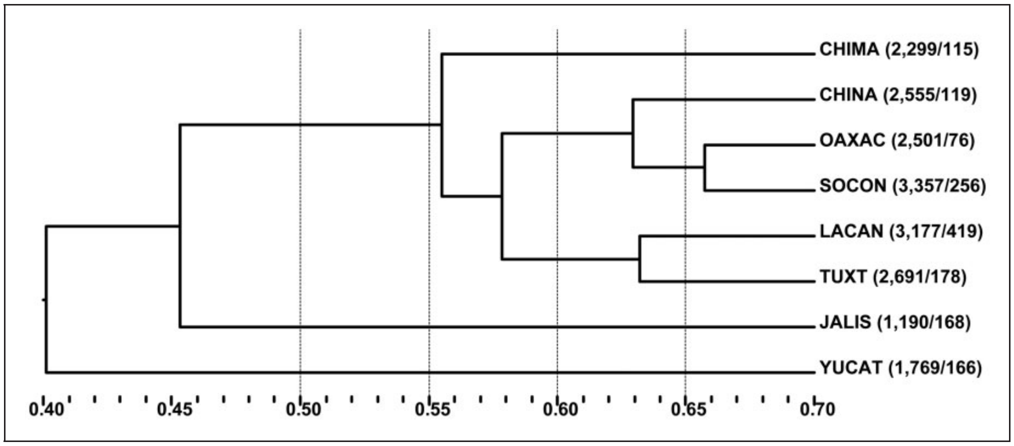

Figure 2. Floristic similarities between the main regions of Mexico with humid tropical forest. The total number of species is indicated in brackets, and the number of species restricted to the region is after the slash. CHIMA = Chimalapa-Uxpanapa, Oaxaca-Veracruz; CHINA = Chinantla, Oaxaca; JALIS = Coast of Jalisco; LACAN = Lacandona, Chiapas; OAXAC = Coast of Oaxaca; SOCON = Soconusco, Coast of Chiapas; TUXT = Tuxtlas, Veracruz; YUCAT = Peninsula of Yucatán (Campeche, Quintana Roo, Yucatán). Coefficient of similarity: Sorensen-Dice; Grouping method: UPGMA.

Table 6. Number of Species, Surface, and Species/Area Ratio in the Eight Main Regions in Mexico With Remaining Humid Tropical Forest.

Region	Number of species	Surface (km^2)	Species/area
Chimalapa-Uxpanapa	2,299	11,319	0.20
Chinantla	2,555	4,857	0.52
Jalisco coast	1,190	3,440	0.34
Lacandona	3,177	12,988	0.24
Oaxaca coast	2,501	8,302	0.30
Soconusco	3,357	5,050	0.66
Tuxtlas	2,548	3,300	0.77
Peninsula of Yucatán	1,769	49,727	0.03
Total in eight regions	5,902	98,983	0.06

Coast (Salas-Morales et al., 2003, 2007), and Soconusco (Long & Heath, 1991; López-Cruz et al., 2010; Martínez-Camilo et al., 2012; Martínez-Meléndez et al., 2008; Matuda, 1950). With similarity values of below 50%, the Jalisco Coast, in western Mexico (Lott, 1993; Ramírez & Cupul, 1999) and the Yucatan peninsula (Gutiérrez, 2001; Martínez et al., 2001;Zamora, 1999) are more isolated.

Discussion

The Los Tuxtlas region contains a substantial portion (41.1%) of all the floristic richness of the humid tropical biome recorded in Mexico (Figure 2). It occupies the fourth position by its species richness value, below only the Soconusco (54.2% of the known richness of the HTF), the Lacandona (51.3%), and the Chinantla (41.2%) regions. However, it is the region that contains the second largest number of exclusive species (known only from the region), as well as a significant number of species endemic to Mexico (313).

The dominance of families Fabaceae, Orchidaceae, and Rubiaceae seems to be a characteristic of the humid tropical biome. The Asteraceae family, although always occupying one of the first places, does not dominate by its number of species in the biome (Table 5), occupying second or third place. Similar results are reported in other parts of the world with HTF, where one of these families occupies the predominant position. For example, the Rubiaceae family occupies the first place by number of species in the West Indies (Acevedo-Rodríguez & Strong, 2008); Fabaceae in Brazil (BFG, 2015) and Colombia (Rangel, 2015); and Orchidaceae in Nicaragua (Stevens, Ulloa, Pool, & Montiel, 2001) and Panama (D'Arcy, 1987).

A significant number of species (617 native and 57 exotic) were recorded in only one grid-square; such species represent the rare element by its extent of occurrence in the region. However, the distribution of the other species is not as homogeneous as would be expected; the most widely distributed species are *Siparuna thecaphora* (22 grid-squares), *Dendropanax arboreus* (21), *Conostegia xalapensis* (21), *Guarea glabra* (20), and *Garcinia intermedia* (20). Another 52 species are recorded in 15 to 19 squares, and the other species occur in 2 to 14 squares (Appendix A, Supplementary Material).

It could be postulated that the entire region of Mexico with HTF (Villaseñor & Ortiz, 2014) constitutes a single biogeographic unit with high numbers of shared species (Figure 2), each one with particular features characterizing them. Although richness values show significant differences (minimum 1,769 in the Yucatan peninsula, maximum 3,357 in the Soconusco region), with a range of 1,588 species, at least six of the eight regions analyzed share an important floristic component (>55%; Figure 2). It is possible that the lesser number of species in the Yucatán Peninsula is due to abiotic factors; this region has the lowest precipitation values and the karstic substrate is not efficient for water retention. On the other hand, it is important to point out that each region has an important exclusive component (minimum 76 in the Coast of Oaxaca, maximum 419 in the Lacandona), with a range of 343. Apparently, such a geographically restricted element (exclusive to each region) is more important on the slope of the Gulf of Mexico than on the Pacific Ocean slope. Although outside the scope of the present study, it would be interesting to explore whether historical factors help to explain these important observed richness patterns, or whether the differences are due to the lack of exploratory work in some of the regions. Surely many of the species considered rare here have a wider distribution than is currently known (Wendt, 1993), and future collecting work in the HTF (hopefully before its imminent disappearance) will reduce the high values of rarity observed here; additional studies and a thorough examination of the specimens deposited in the herbaria will also contribute to a better knowledge of the flora of the region (Bebber et al., 2010).

It has been argued that biological richness (number of species) varies considerably from one region to another (Hutchinson, 1959), and very few species are found throughout the territory where they could survive. The flora of Mexico's humid tropical biome is a clear example; as shown in Figure 2, a relatively low percentage of species is widely distributed throughout the biome. For example, only 351 of 5,902 species (5.9%) are registered in the eight regions of Mexico with HTF, while 1,492 (25.2%) are only known from one of them. Examples of species widely distributed in the HTF of Mexico are *Roseodendron donnell-smithii* (Bignoniaceae), *Davilla kunthii* (Dilleniaceae), *Andira inermis* or *Pterocarpus rohrii* (Fabaceae), and *Guettarda macrosperma* (Rubiaceae).

Implications for Conservation

The database analyzed allowed us to answer two important questions for biogeography and macroecology (Soberón, Llorente, & Oñate, 2000) with conservation implications. The first one (which species are recorded in the Los Tuxtlas region?) resulted in the generation of the floristic list that includes a total of 2,548 species (Appendix 1, Supplementary Material). The second (how are these species distributed in the study area?) shows that richness is not evenly distributed throughout the studied region. Centers with an important concentration of species were identified, probably as a result of greater collection effort there, but also due to better conservation of the original vegetation. One of these centers is Grid 7 (Figure 1), located in the core area of the Los Tuxtlas Biosphere Reserve, including the UNAM Biological Station where intense collection effort has been carried out; this grid cell alone registers one third of all the collections in the region. At the other extreme is a grid cell (27) with only five species recorded from only five collections. However, the historical review of the collection effort throughout the region reveals important sites that once reported a greater species richness. Future restoration efforts could be better oriented, based on information collected for each of the sites in which the Los Tuxtlas region was divided. In general, from 0 to 600 m a.s.l., the original vegetation has disappeared, leaving only small islands of natural vegetation from 1 to 100 ha, greatly altered by agriculture, hunting, and livestock activities. These areas should have priority for restoration or creating corridors and conservation areas, taking advantage of being remaining islands of original vegetation. Before any seed collection, well-planned projects must be in place to ensure the success of restoration in degraded areas.

Within the Los Tuxtlas region lies the Los Tuxtlas Biosphere Reserve, with an area of 1,551 km^2; three core zones have been declared within the reserve, Volcán San Martín Tuxtla, Sierra Santa Marta, and San Martin Pajapan, with a combined area of 297 km^2. The core area of a reserve is composed of a protected ecosystem that contributes to the conservation of landscapes, ecosystems, species, and genetic variations; the surface of this core area is composed of humid mountain forest (58% of potential vegetation) and HTF (42%; contrasting with 10% and 74%, respectively, in the entire Los Tuxtlas region). Within this core area, research and other low-impact activities are allowed for the ecosystem. The core zones of the Los Tuxtlas Biosphere Reserve contain 1,575 species, 190 of them endemic to Mexico, and 25 endemic to the region. Together they protect 58% of the flora of the region and 60% of the local endemism, contributing significantly to the conservation efforts in the area (Acebey et al., 2015; Arroyo-Rodríguez et al., 2009; Arroyo-Rodríguez & Mandujano, 2006; Bongers et al., 1988; Ibarra-Manríquez & Sinaca, 1987; Ibarra-Manríquez & Sinaca-Colín, 1995, 1996a, 1996b; Lira-Noriega et al., 2007; Ramírez, 1999). Undoubtedly such areas can be important for collecting seeds or the placement of nurseries for seedlings useful for future reforestation of deforested sites, which constitute a large part of the region (Chazdon, 2008).

If the polygon of Figure 1 is considered an equivalent of the extent of occurrence of the regional criteria proposed by the IUCN (2012) and the cells into which it was divided similar to the area of occurrence, one could estimate the degree of threat of the species in the Los Tuxtlas region. Of the 2,548 native species of Los Tuxtlas, 617 of them occur in a single cell (6 min latitude and longitude, roughly equivalent to 116 km^2). Thus, applying only the criterion of area of occurrence (Criterion B2), these species could be considered endangered (EN) in the region, having an area smaller than 500 km^2. Under this threat assessment, it is alarming that a quarter of the flora of Los Tuxtlas is classified as EN and therefore facing a high risk of extinction in the wild; especially several of them endemic to this region (Table 2, Appendix 1, Supplementary Material). Similarly, a recent conservation assessment of *Peperomia* from Veracruz by Vergara-Rodríguez, Mathieu, Samain, Armenta-Montero, and Krömer (2017) revealed that eight species endemic to this state are EN, and another 11 species endemic to Mexico are in a risk category according to the IUCN criteria. However, it should be mentioned that many species classified here as EN for Los Tuxtlas could have a different conservation status or even be abundant in other regions or at other geographical scales.

The importance of the Los Tuxtlas region as a center of endemism or priority site for HTF conservation has been discussed earlier (Villaseñor, Meave, Ortíz, & Ibarra-Manríquez, 2003; Wendt, 1993). Its importance can be partly explained by its remarkable floristic richness and important number of Mexican endemic species and those known only from the region. The region, and in general the HTF in Mexico, requires a commitment to a more collecting effort throughout the region and to keeping up-to-date lists such as the one presented here, to keep up with constant taxonomic and nomenclatural changes, as well as the continuous discoveries that are made when carrying out more exploration work. Only in this way will it be possible to continue evaluating its priority role in the conservation of this important biome, facilitating more comprehensive studies by other scientists as well as decision-makers involved in the conservation of biodiversity.

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