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Ecology

Appraising forest diversity in the seasonally dry tropical region of the Gulf of Mexico

Valorando la diversidad forestal de la región tropical estacionalmente seca del golfo de México

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Abstract

Seasonally dry tropical regions in the Neotropics are remarkably biodiverse and provide valuable ecosystem services. Thus, it is crucial to increase and update our information on the biodiversity still preserved within them, particularly in poorly studied areas such as the central coastal plain of the Gulf of Mexico, our study area. A total of 6,007 individuals belonging to 156 species, 113 genera, and 43 families were recorded in 29 forest patches (total sampling area = 8.7 ha). From the floristic composition of these patches, 6 vegetation types were identified: Tropical Dry Oak Forest, Tropical Deciduous Forest, Semi-deciduous Forest, Late Secondary Forest, Intermediate Secondary Forest and Early Secondary Forest. Spatial variation in composition was strongly related to edaphic variables (pH, organic matter, carbon content). Some patches had high local (α) diversity, but even more noteworthy was the distinctively high regional (β) diversity of all the patches together. In spite of the high degree of forest fragmentation in central Veracruz, our results show that it is essential to acknowledge the value of this region to biodiversity and the urgency of developing and implementing protection and management policies that ensure the ecological functions of the landscape and the sustainable development of human activities.

Keywords: Forest management; Landscape ecology; Plant diversity; Seasonally Dry Tropical Forest; Secondary Forest

Resumen

Las regiones tropicales estacionalmente secas del Neotrópico son notablemente biodiversas y proveen valiosos servicios ecosistémicos. Es crucial aumentar y actualizar la información de la biodiversidad aún contenida en ellas, particularmente en áreas pobremente estudiadas como la zona central del golfo de México, nuestra zona de estudio. Un total de 6,007 individuos, de 156 especies, 113 géneros y 43 familias fueron registrados en 29 parches forestales (área total muestreada = 8.7 ha). A partir de la composición florística de estos parches, se identificaron 6 tipos de

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vegetación: encinar tropical seco, selva baja caducifolia, selva mediana sub-caducifolia, acahual tardío, acahual intermedio y acahual joven. La variación espacial de la composición estuvo relacionada con variables edáficas (pH, materia orgánica, contenido de carbono). Algunos parches tuvieron una alta diversidad local (α), pero aún más notable fue la distintivamente alta diversidad regional (β) de todos los parches en conjunto. A pesar de la intensa fragmentación forestal en la zona central del estado de Veracruz, nuestros resultados muestran que es necesario reconocer el valor de esta región para la biodiversidad y la urgencia de desarrollar e implementar políticas de protección y manejo que aseguren las funciones ecológicas del paisaje y el desarrollo sustentable de actividades humanas.

Palabras clave: Manejo forestal; Ecología del paisaje; Diversidad de plantas; Selva estacionalmente seca; Vegetación secundaria

Introduction

Seasonally dry tropical regions are characterized by a marked dry season that lasts from 3 to 8 months, a mean monthly precipitation of less than 100 mm and predominantly deciduous forest vegetation with a canopy that is 5 to 20 m in height (Castillo-Campos, 2006). Foliage is dense and green during the rainy season, contrasting with the open canopy and bare branches of the dry season (Banda et al., 2016; Dirzo, 2011). In the Neotropics, seasonally dry tropical regions are distributed from Mexico to northern Argentina, including parts of the Caribbean (Banda et al., 2016; Pennington et al., 2000). These regions have different types of vegetation in addition to tropical dry forest, such as mangroves, semi-deciduous tropical forest, tropical dry oak forest and others, that together harbor a degree of diversity comparable to that of the wettest tropical regions (Banda et al., 2016; Castillo-Campos et al., 2008; Portillo-Quintero & Sánchez-Azofeifa, 2010; Powers et al., 2009). Seasonally dry tropical regions are characterized by relatively fertile soils, leading to both increased agricultural activities and human settlement. This has caused a decrease in the original forest cover, of which only 10% remains (Banda et al., 2016; Laurance et al., 2012). This has led several authors to classify the vegetation of these regions as among the most threatened in the world (Banda et al., 2016; Sánchez-Azofeifa et al., 2005).

Seasonally dry tropical forests are often classified as fragile and several authors have stated that they have a very low recovery capacity in the face of anthropic disturbance (Derroire et al., 2016; Janzen, 1988). In fact, forest regeneration in these regions can be strongly limited by both low seed arrival (i.e., dispersal limitation) and also by unfavorable conditions for plant establishment, growth and survival (i.e., niche limitation; Norden et al., 2009). In sites disturbed by humans, these limitations result in patches of vegetation in which secondary succession can be arrested, resulting in impoverished patches composed of just a handful of secondary species of shrubs or trees. In these degraded patches, neither the recovery of a taxonomic composition similar to that of a conserved forest, nor functional recovery —zoochorous and nitrogen-fixing species— of the original forest can occur. Thus, for some time, there was a consensus that patches of secondary forest would not be always useful for recovering the original native diversity or the ecological value of a region (Janzen, 1988; Laurance et al., 2012). However, in the last decade, several studies have shown that patches of secondary seasonally dry tropical forests have a high potential for harboring diversity and providing ecosystem services (e.g., carbon sequestration) from the early stages of succession (Chazdon, 2014; Chazdon et al., 2016; Mesa-Sierra & Laborde, 2017). Given the current fragmented distribution of tropical forests, it is of great importance to identify those landscape elements —small forest patches, live fences— that still preserve native species and thus could be valuable for the conservation of biodiversity. This would allow us to plan for the long-term sustainable use of these landscapes.

Keeping in mind that for many of the landscapes modified by anthropogenic disturbances it is not feasible to establish large areas of natural habitat or relatively well preserved areas as natural reserves, it is necessary to protect all of the elements that, together, maintain their diversity and ecosystem functions at the landscape level (Halffter, 2007; Melo et al., 2013), as well as to identify those environmental factors (e.g., climate, topography, edaphic properties) that shape plant communities. In particular, transformed landscapes with forest fragments and other arboreal elements that still harbor native species that have a restricted geographic distribution or unique functional traits are essential for maintaining the ecological processes that favor the regeneration of the original woody vegetation (Arroyo-Rodríguez et al., 2009; Castillo-Campos et al., 2008).

In Mexico, which has the largest area of seasonally dry regions in tropical America, there are 3 large regions: the Pacific coast, including the Balsas Basin, the northwestern part of the Yucatán Peninsula, and central Veracruz on the Gulf of Mexico (Castillo-Campos et al., 2008; Lott

& Atkinson, 2006). These regions differ from each other mainly in their topography, edaphology and biogeographic processes, as well as in their physiognomy and floristic composition (Lott & Atkinson, 2006; Sosa et al., 2018). Historically, research efforts have mainly focused on the Pacific Coast (Chamela in Jalisco, and Nizanda in Oaxaca), and more recently on the Yucatán Peninsula, with central Veracruz receiving much less attention. The Pacific Coast has elevations from 0 to 500 m asl, a highly diverse flora (more than 651 vascular plant species), a high proportion of endemisms and it is subject to strong human (tourist attraction development) and natural (hurricanes) pressure (Lott & Atkinson, 2006; Pérez-García et al., 2001). The karst plain of the Yucatán Peninsula (elevation: 0-190 m asl) has more than 200 woody species, all of which have been recorded in the seasonally dry forest of the state of Yucatán. This is a region that has been characterized by a high density of settlements since the pre-Hispanic times of the Maya, a factor that has shaped diversity in this region (Ibarra-Manríquez et al., 1995; López-Martínez et al., 2013).

Central Veracruz, located on the Gulf of Mexico, is the subject of this study and has different types of tropical forest dominated by different deciduous tree species that coexist under the same seasonally dry climate regime. The most conspicuous vegetation types in this landscape are similar to those described by several authors in other seasonally dry regions within the Neotropics (Powers et al., 2009; Banda et al., 2016), including: semi-deciduous and deciduous tropical forest, tropical dry oak forest, coastal dune scrub, mangroves, and patches of secondary vegetation in different stages of succession (Travieso-Bello & Campos, 2006). While the tropical dry oak forest is not usually regarded as a type of seasonally dry tropical forest in the Americas (sensu Pennington et al., 2000), it is important to note that *Quercus*-dominated forest is common in tropical Mexico. It often grows in close proximity to other types of tropical vegetation, such as mixed deciduous forest, and thus may contain several of the latter's tropical species (Banda et al., 2016; Powers et al., 2009). This region is subjected to recurrent strong winds from the north during winter known locally as "nortes". These winds bring relatively cold, humid weather, and as a result, while strongly seasonal in annual precipitation, the region is one of the most humid seasonally dry tropical regions of Mexico.

It has been estimated that the remaining forested area in the lowlands of Central Veracruz with a seasonally dry climate covers approximately 12% of its original area, and is now mainly secondary forest (Williams-Linera & Lorea, 2009). The current, low proportion of forest cover is explained by the long history of human occupation of this region since pre-Hispanic times (Sluyter, 1999), and particularly in recent decades as a result of the expansion of modern agriculture, which has markedly transformed the landscapes of the region with extensive cattle ranching and intensive agriculture (e.g., sugar cane). Deforestation in the region has also resulted from unplanned tourist development, and more recently the extraction of rocks for building projects, from quarries located on rocky sites that are not suitable for agriculture but precisely where there were remnants of the original forest.

Considering that forests growing in seasonally dry tropical regions are threatened by the high degree of anthropic transformation, it is essential to generate reliable, quantitative information on the current state of the diversity they support. In this study we provide a detailed description of the forest diversity for the central region of Veracruz, thereby increasing the floristic and ecological knowledge of these ecosystems. The objectives of this study were: *i*) to identify the different types of forest that grow in the seasonally dry tropics in this Gulf of Mexico region, *ii*) to compile an inventory of the species richness and composition associated with each of these forest types, and *iii*) to assess which environmental variables (climatic, edaphic and topographic) could explain the spatial variation in floristic composition of these forests. This will allow us to have a current, quantitative estimate of the conservation value of this region based on the plant species that grow in these types of seasonally dry tropical ecosystems in their northernmost coastal distribution on the Atlantic slope of the Americas.

Materials and methods

The seasonally dry tropical region of the Gulf of Mexico located in the central part of Veracruz (19°16'55.4" - 19°48'15.9" N, 96°19'12.9" - 96°48'47.9" W) is distributed from the piedmont of the Manuel Díaz mountain range that runs down to the Atlantic coast, extends southwards along the coastal plain and ends at Puente Nacional. The region's weather is classified as AW_2, characterized by seasonal rainfall with a mean annual precipitation of 1,200 to 1,500 mm/year, and annual temperatures of 22 to 26 °C (Travieso-Bello & Campos, 2006). For 5 (December - April) to 8 (October - May) months of the year, precipitation is very low in the region (< 60 mm/month) compared to the wetter, less seasonal areas to the west, north and south of the study area. The region's soils vary widely in their fertility, sand content and moisture retention capacity. Travieso-Bello and Campos (2006) identified 10 different types of soils (sensu FAO/UNESCO) within the region, the most common being fibrist histosol, cambid aridisol, lithic leptosol and mollic gleysol. A thorough bibliographic review of the region's flora by Castillo-Campos and Travieso-Bello (2006) reported a total of 837 species belonging to 465 genera and 118 families of vascular plants occurring in mangroves, wetlands, deciduous forest, riparian vegetation and coastal dune scrub. Currently, the most extensive types of land cover are man-made pastures for cattle ranching, followed by sugarcane fields.

SPOT5 satellite images (5m/pixel resolution) from April 2014 were processed to differentiate forest from non-forest cover using an unsupervised classification with ERDAS imagine 6 (Hexagon, 2017) software. This was done to obtain an updated, high resolution map of all the patches with forest or woody cover within the study area. Based on this processed map, a total of 10 sites with relatively large forest fragments or wooded patches separated by at least 1 km, were selected for sampling. Each of the 10 sites selected had an area of 36 ha (600 × 600 m), within which all forest fragments and wooded patches larger than 1 ha and a stand-age greater than or equal to 5 years (with owners, pers. com.) were selected. Based on these criteria, site accessibility and permission to enter granted by landowners, a total of 29 forested patches were selected for vegetation sampling (Fig. 1; Table 1).

Three 50 × 20 m plots (at least 20 m apart) were set up in each of the 29 selected patches (87 plots in total). Each plot was at least 20 m away from the nearest forest edge. All woody plants and palms with a DBH ≥ 5 cm and rooted within a plot were identified and their DBH measured (lianas rooted within the plot were measured at 1.3 m from the ground). Collected specimens were identified by Gonzalo Castillo-Campos, and Carlos Manuel Durán Espinosa. Taxonomic nomenclature follows Tropicos (2019) and Villaseñor (2016). Along the longest side and the central part of each plot, every 5 m, the maximum height of the canopy and the percentage of canopy cover was estimated with a canopy densiometer. We estimated the age of each patch sampled by interviewing the landowners and local people who had been using those patches and living in the area for several years. Secondary patches ranged in age from 7 up to 23 years of abandonment before sampling, while those patches not cleared during the last 30 years or more were labelled as old-growth forest.

A soil sample (300 gr) from the top 10 cm of mineral soil (i.e., excluding the litter layer) was collected at 3 evenly spaced sites along each plot. These samples were dried at room temperature and ground for analysis in the Soils Laboratory at Instituto de Ecología, A. C. (Xalapa, Mexico). Soil characteristics determined for each sample were: pH, organic matter (OM), and relative (%) sand, clay and silt content (Appendix 1). Additionally, the weight of the stones present in the sample was determined relative to the total weight of each sample to estimate the mean (n= 3 samples/plot) content of stones in the soil for each plot.

A cluster analysis was run, following Ward's method, in the statistical programming language R (R Development Core Team, 2015) to classify the 29 patches sampled into similar groups or vegetation types based on species composition and abundance. The resulting cluster classification was refined whenever the grouped patches had clearly distinct physiognomic attributes —canopy height, tree density, trunk diameters— or stand ages (time since abandonment or last disturbance).

Total species richness and abundance were estimated per patch and per vegetation type. Sampling completeness was evaluated with the $\hat{C}n$ parameter proposed by Chao and Jost (2012) for each vegetation type. Diversity profiles for each vegetation type were also estimated with the Hill numbers for observed richness (q0), for typical diversity (q1), and for the diversity of the most abundant species (q2) using the iNEXT package for R (Hsieh et al., 2016).

Table 1

Characteristics of the 10 sites (see Fig. 1) in which the 29 forested patches sampled were located (numbers in parenthesis are those used in Fig. 1). Vegetation types distinguished by the cluster analysis based on species abundances as well as physiognomic and stand age attributes (see Methods), were: Tropical Dry Oak Forest (TOF), Tropical Deciduous Forest (TDF), Semi-deciduous forest (SDF), Late Secondary Forest (LSF), Intermediate Secondary Forest (ISF) and Early Secondary Forest (ESF). Surrounding agricultural matrix: Pasture (P), Secondary Vegetation (SV). Forest cover (%) within the 36 ha (600 × 600 m) area defined for each sampling site (see Methods).

Site	Elevation (m asl)	Vegetation type	Surrounding matrix	Forest Cover (%)
A (4,5)	1,045	ESF	Shaded coffee	92
B (1,2,3)	767	ESF	P, Mango orchard	47
C (20,21,22)	198	SDF, LSF, ISF	Various crops	60
D (26,27)	702	LSF	P, Citrus orchard	95
E (23,24,25)	259	TDF	P	70
F (14,15,16)	436	TOF	P, SV	22
G (12,13)	93	ISF	P	92
H (29,28)	28	SDF	Various crops	53
I (6,7,8,9,10,11)	206	SDF, LSF, ISF	P, SV, Sugarcane	52
J (17,18,19)	80	SDF, ISF	P, Sugarcane	90

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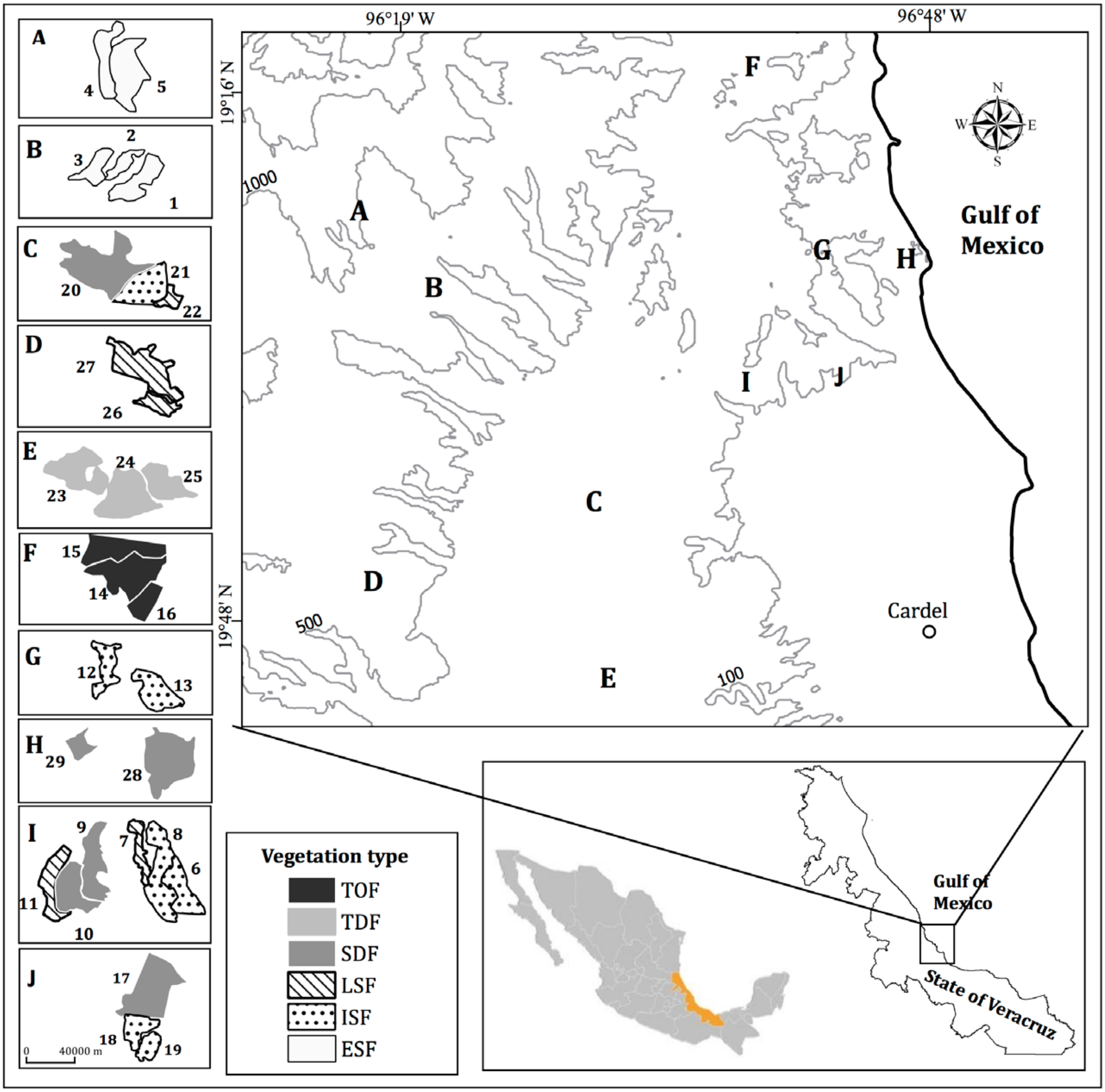

Figure 1. Study area in the seasonally dry tropical region of the Gulf of Mexico, Veracruz, Mexico, showing the location of the 10 sampling sites. Insets to the left of the map are the polygons of the 29 forest fragments (or forested patches) where the vegetation was sampled, the number used to identify each patch sampled within a given site, and its vegetation type (as described in table 1). The numbers over the isolines correspond to the elevation information.

Richness and abundance among vegetation types were compared using generalized linear models (GLMs), with a negative binomial error type due to the overly dispersed nature of our data. When significant differences were detected, a post hoc test (Tukey) was used to determine which vegetation types were different. This analysis was run in R (R Development Core Team, 2015). The dominant species of each vegetation type were determined estimating the Importance Value Index (IVI), which ranks species by the combination of their relative values of abundance, frequency and basal area.

The floristic composition of the 29 forested patches was analyzed with a principal components analysis (PCA) ordination run in PC-ORD, version 6 (McCune & Grace,

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2002). Species abundance data for each patch was log-transformed (log + 1). In order to analyze whether the spatial variation in floristic composition was correlated with environmental variation among the patches sampled, the PCA was complemented with a correlation analysis between the PCA-scores of each patch along each of the 2 main ordination axes and their respective values for elevation, edaphic properties (see above) and climate variables. A cutoff value of $r^2 > 0.2$ was used to decide which environmental variables —climate, edaphology, elevation— would be included in the ordination graph or biplot, and the correlation results were plotted following McCune and Grace (2002). For the climate variables included in our analysis we took the high-resolution (30 arc sec) climate surfaces for Mexico developed by Cuervo-Robayo et al. (2014) and analyzed the collinearity among all of them. This allowed us to select 3 variables: maximum monthly temperature (TMax), mean annual precipitation (PMean) and maximum monthly precipitation (PMax).

Results

In the 29 patches sampled (total sampling area = 8.7 ha) a total of 6,007 plants belonging to 156 species, 113 genera and 43 families were recorded. There were 235 individuals (> 4% of total abundance) that we were unable to identify because they did not have flowers or leaves at the time of sampling and therefore these individuals were excluded from the analysis and the species counts. The richest family was Fabaceae with 31 species, followed by Euphorbiaceae with 8 species (Appendix 2). The 5 most abundant species were: *Quercus sapotifolia* (432 individuals), *Leucaena leucocephala* (388), *Guazuma ulmifolia* (380), *Gliricidia sepium* (292) and *Quercus oleoides* (259). Abundance per patch was 77 to 475 plants, while richness was 3 to 33 species per patch.

The cluster analysis grouped the 29 forest patches into 6 classes or vegetation types(Fig. 2): tropical dry oak forest (TOF), low-statured deciduous forest hereafter tropical deciduous forest (TDF), semi-deciduous forest (SDF), late secondary forest (LSF), intermediate secondary forest (ISF) and early secondary forest (ESF). The first 3 are different types of old-growth forest (TOF; TDF; SDF), while the other 3 are different types of secondary forest (LSF; ISF; ESF) that differed in age, i.e. the time elapsed since agricultural practices were stopped. These secondary forests varied widely in their floristic composition and other community attributes —basal area, canopy height— as a function of their successional age, origin (i.e., type of old-growth forest present before disturbance and in its vicinity), the type of management during agricultural use prior to abandonment, and the surrounding type of agricultural matrix (Appendix 1).

The richest vegetation type was SDF with 87 species, followed by ESF with 64, and TOF was the poorest of all forest types, with only 9 species (Fig. 3). The vegetation type with the highest abundance was SDF (1,348 individuals), followed by TDF (1,200 plants). The 95% confidence intervals (CI) on the species accumulation curves per vegetation type indicated no significant differences in richness between SDF and ESF or ISF, but the non-overlapping CIs indicate that SDF was much richer than LSF, TDF and TOF. Diversity profiles indicate that SDF had much higher numbers of typical (q1) and very abundant (q2) species in comparison with the other 5 vegetation types, which in turn had relatively less variation

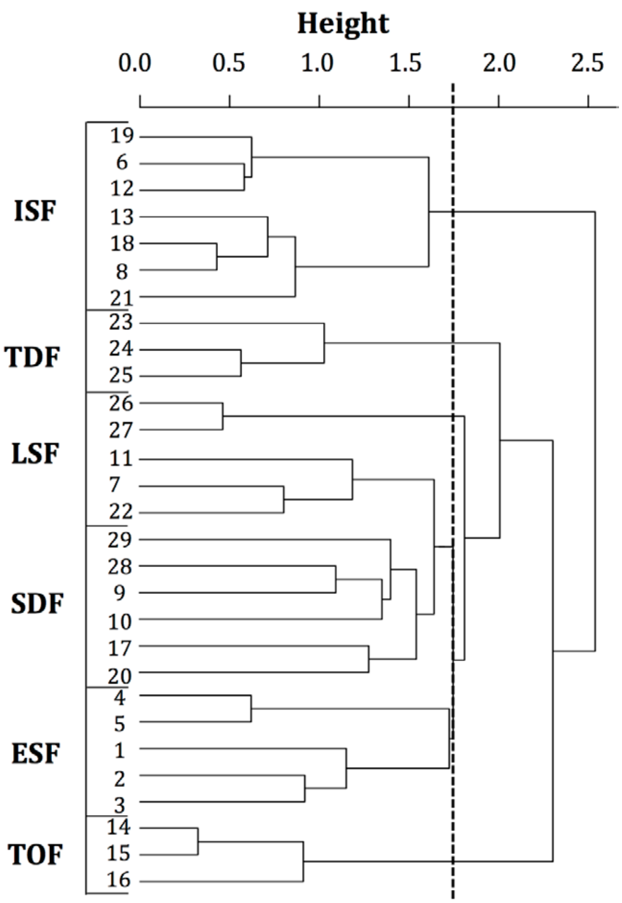

Figure 2. Cluster analysis dendrogram that grouped the 29 sampled patches in 6 vegetation types (patches are numbered as in figure 1). Dotted line represents the cut-off point. For the LSF the cutoff value of the dendrogram was complemented by taking into account the structural (canopy openness and height) similarities of vegetation in the patches and their stand age. The 6 vegetation types are: intermediate secondary forest (ISF), tropical deciduous forest (TDF), late secondary forest (LSF), semi-deciduous forest (SDF), early secondary forest (ESF), and tropical dry oak forest (TOF).

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according to their Hill numbers, except TOF, which had extremely low values (Fig. 3). The species richness of typical species (q1) is equally distributed within most of the vegetation types identified in this study.

Mean species richness (χ^2 = 31.2, d.f. = 5, p<0.001) and mean abundance (χ^2 = 62.6, d.f. = 5, p<0.001) per patch were significantly different among vegetation types (Fig. 4). The TOF was the poorest of all vegetation types, having significantly fewer species than the other 5 types (Fig. 4A). The main differences in mean abundance were between TDF, which had 400 (± 70 s.d.) individuals/patch (Fig. 4B), and the 3 types of secondary forest (LSF, ISF, ESF). ESF had the highest variation in richness and abundance, and the poorest and richest patches of all, as well as some of the least abundant.

There were 16 species with more than 100 plants each within the sampled transects that together accounted for 51.2% of total abundance (Appendix 2). Two of these very abundant species were recorded exclusively in TOF (*Quercus sapotifolia* and *Q. oleoides*). The 2 most widespread species were *Leucaena leucocephala* and *Bursera simaruba*, which were recorded in all but one (TOF) of the vegetation types. The 5 most abundant species in old-growth forest types (i.e., TOF, TDF and SDF) included primary species such as *Q. sapotifolia*, *Byrsonima crassifolia* and *Chloroleucon mangense*,

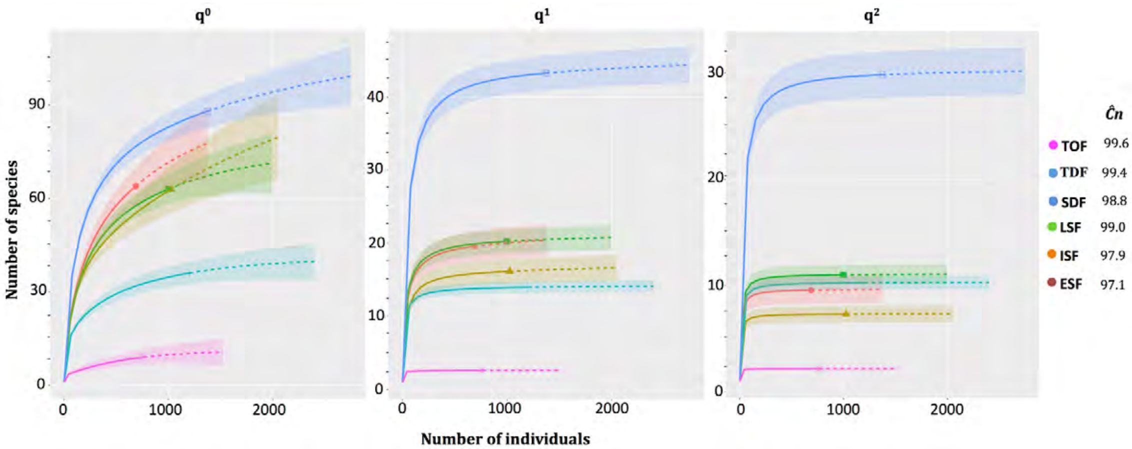

Figure 3. Diversity profile curves (± 95% C.I.) per vegetation type, showing observed richness (Hill number q0), number of typical species (q1), and number of very abundant species (q2). Vegetation types: tropical dry oak forest (TOF), tropical deciduous forest (TDF), semi-deciduous forest (SDF), late secondary forest (LSF), intermediate secondary forest (ISF) and early secondary forest (ESF).

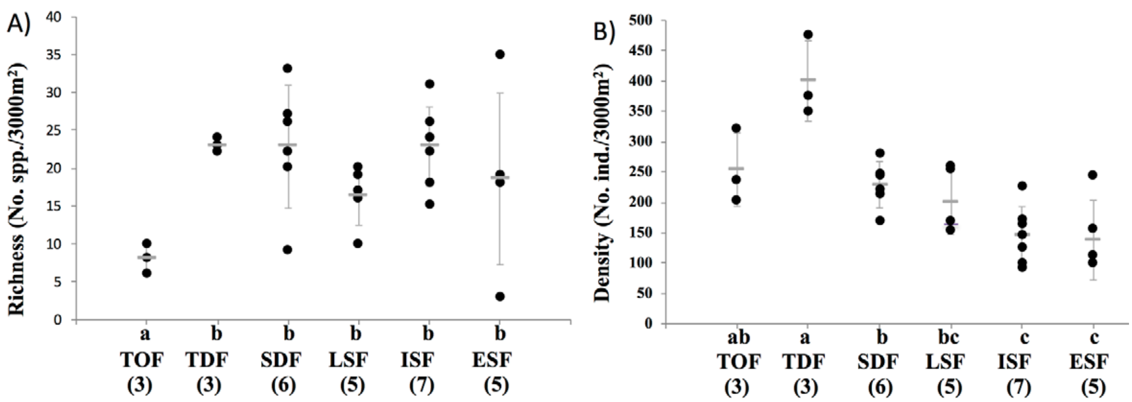

Figure 4. Richness (A) and abundance (B) per vegetation type; showing mean values per patch for each type. Gray dashes represent mean values, and standard deviation is shown as vertical lines. Number of patches sampled per vegetation type is given in parentheses. Identical lower-case letters indicate no significant difference between means (Tukey test; p < 0.05). Tropical dry oak forest (TOF), tropical deciduous forest (TDF), semi-deciduous forest (SDF), late secondary forest (LSF), intermediate secondary forest (ISF) and early secondary forest (ESF).

as well as secondary species like *L. leucocephala* and *Lysiloma divaricata* (Table 2). Some secondary forest types included primary species that were dominant or abundant (e.g., *Aphananthe monoica*, in LSF). However, patches of secondary forest types were mostly dominated by secondary species, such as *L. divaricata*, *Gliricidia sepium*, *L. leucocephala* and *Vachellia pennatula* (Table 2).

The PCA ordination of the 29 patches sampled explained 87% of the variation in floristic composition —38% along axis 1 and 49% along axis 2. The 3 patches of TDF were separated from the other vegetation types on axis 1 (lowest values to the left of Fig. 5). Axis 2 grouped the 3 patches of TOF at the top of Fig. 4 (highest values) and 4 of the 6 patches of SDF at the lowest end of this axis, with most of the patches of secondary forest types grouped in the middle. Species whose presence and abundance in the patches had the highest correlation with PCA scores along axis 1, were *Piscidia piscipula* (r = -0.314), *Licaria capitata* (-0.293) and *Senna pallida* (-0.324); all of which were most abundant in TDF patches. Species whose abundances had the highest correlation with axis 2 scores were: *Q. sapotifolia* (r = 0.37), *Q. oleoides* (0.36) and *Guazuma ulmifolia* (-0.30). These 2 *Quercus* species are dominant in TOF and were exclusively recorded in that vegetation type, while *G. ulmifolia* is widely distributed in the remaining vegetation types and is particularly abundant in some secondary forest types and some SDF patches (Fig. 5).

Table 2

Summary of the 5 most important species, ranked by their importance value index (IVI) in each vegetation type. Vegetation types: Tropical Dry Oak Forest (TOF), Tropical Deciduous Forest (TDF), Semi-deciduous Forest (SDF), Late Secondary Forest (LSF), Intermediate Secondary Forest (ISF) and Early Secondary Forest (ESF).

Vegetation type	Family	Species	IVI
TOF	Fagaceae	*Quercus sapotifolia*	1.58
	Fagaceae	*Quercus oleoides*	1.22
	Malpighiaceae	*Byrsonima crassifolia*	0.87
	Moraceae	*Ficus obtusifolia*	0.22
	Moraceae	*Ficus aurea*	0.22
TDF	Fabaceae	*Senna pallida*	1.27
	Burseraceae	*Bursera simaruba*	1.26
	Fabaceae	*Piscidia piscipula*	1.24
	Fabaceae	*Leucaena leucocephala*	1.11
	Fabaceae	*Eysenhardtia polystachya*	1.07
SDF	Fabaceae	*Lysiloma divaricatum*	0.97
	Fabaceae	*Leucaena leucocephala*	0.77
	Apocynaceae	*Stemmadenia obovata*	0.7
	Fabaceae	*Chloroleucon mangense*	0.62
	Fabaceae	*Coccoloba humboldtii*	0.59
LSF	Cannabaceae	*Aphananthe monoica*	0.47
	Fabaceae	*Leucaena leucocephala*	0.3
	Boraginaceae	*Cordia diversifolia*	0.27
	Fabaceae	*Lysiloma divaricata*	0.22
	Malpighiaceae	*Bunchosia* sp.	0.2
ISF	Fabaceae	*Gliricidia sepium*	1.63
	Malvaceae	*Guazuma ulmifolia*	1.3
	Fabaceae	*Leucaena leucocephala*	0.87
	Malvaceae	*Heliocarpus pallidus*	0.57
	Convolvulaceae	*Ipomoea wolcottiana*	0.49
ESF	Fabaceae	*Vachellia pennatula*	0.93
	Fabaceae	*Leucaena leucocephala*	0.86
	Burseraceae	*Bursera simaruba*	0.75
	Malvaceae	*Guazuma ulmifolia*	0.53
	Fabaceae	*Inga jinicuil*	0.45

Of the 11 environmental variables recorded for each of the 29 patches (7 edaphic, 3 climate and elevation; see Materials and methods), only 5 (all edaphic) were significantly correlated with PCA eigenvectors: pH; soil organic matter; sand and clay content, and the relative content of stones in soil (Fig. 5, Appendix 1). Soil OM, % sand and % stones were positively correlated with PCA scores along axis 2, reaching their highest values in TOF patches and some patches of secondary forest. Clay content was negatively correlated with PCA scores along axis 2, and had the highest values in some SDF patches and some secondary forest patches, while pH was strongly and negatively correlated with both PCA axis, and had the lowest values in the 3 TOF patches (Appendix 1).

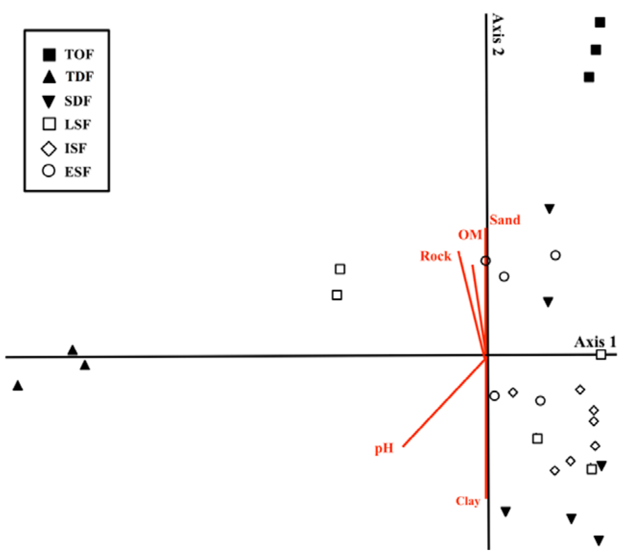

Figure 5. Principal components analysis (PCA) ordination of 29 patches in 6 vegetation types: tropical dry oak forest (TOF), tropical deciduous forest (TDF), semi-deciduous forest (SDF), late secondary forest (LSF), intermediate secondary forest (ISF) and early secondary forest (ESF). Environmental variables shown as vectors had the highest correlation with PCA scores (r2>0.2 with at least one of the axes, following Peck, 2010); OM = soil organic matter, % content of clay, sand and stones in soil samples.

Discussion

Along the coastal plain of the Gulf of Mexico, the central part of the state of Veracruz together with a portion of the state of Tamaulipas represents the northernmost distribution of the seasonally dry tropics in the Atlantic Basin of the North American continent (Rzedowski & Calderón-de Rzedowski, 2013). The region studied in central Veracruz has been subjected to human disturbance since pre-Hispanic times and currently has close to 12% of its original forest cover (Williams-Linera & Lorea, 2009). In spite of the extensive deforestation underway in the region and the large areas occupied by intensive agricultural activities (mainly sugar cane and cattle pasturing), in this study we detected 6 different types of forest vegetation, 3 types of old-growth forest (tropical dry oak forest, tropical deciduous forest, semi-deciduous forest), and 3 of secondary forest (late secondary forest, intermediate secondary forest and early secondary forest); which together harbor a notable richness of species of trees and shrubs. The presence of distinct forest formations in the study area shows that the prevailing idea of this region having mainly one type of deciduous tropical forest when all of Mexico's vegetation is examined (Rzedowski, 2006; Rzedowski & Calderón-de Rzedowski, 2013; Trejo & Dirzo, 2002) offers a limited view, owing to its coarse cartographic resolution. Our findings, obtained using a much finer resolution, reveal the true heterogeneity and richness of this region. Furthermore, contrary to expectations, based on pervasive habitat loss and the resulting forest fragmentation and deterioration, there is currently a notably high degree of local diversity (α) and even greater diversity on the regional scale (β), with a high proportion of woody species that are not found in other seasonally dry regions of Mexico.

The accurate, up-to-date characterization of the different vegetation and land use types in a region is essential to understanding the state of its conservation and for the maintenance of biodiversity in the long term. The reality is that today's landscapes are shaped by human activities, leading in some cases to extreme transformation, such as that found in our study region. Wherever there are no large tracts of pristine or well-preserved forests, conservation possibilities are considered to be limited or nil. Our results, however, indicate that together, small patches of vegetation can harbor a high degree of diversity and a variety of native species, some of which have restricted geographic ranges. While this may not be the case for all fragmented landscapes, currently the best way to find out is to carry out meticulous plant identification and sampling in the field.

In highly fragmented landscapes the floristic composition of remnant patches might be rich in native species but may also reflect the species composition of their surrounding matrices (Gardner et al., 2009; Melo et al., 2013). To distinguish and categorize vegetation types in these highly fragmented landscapes, in addition to analyzing species composition within the forest patches, it is necessary to take into account, as we did in this study, other attributes or factors that could shape the current composition of the patches such as the physiognomy of the vegetation and the age of the patches (5 years to > 50), with the latter being particularly useful for distinguishing the different types of secondary forest. This type of analysis of forest vegetation and its classification are indispensable for the seasonally dry tropical landscapes of today, since they are very dynamic areas where forest cover and land use are constantly changing (Bonilla-Moheno et al., 2013; Burgos & Maass, 2004; Galicia et al., 2008), which also makes it crucial to identify every landscape element (e.g., remnant vegetation patches, live fences) that may contribute to the maintenance of high regional diversity and the landscape ecological functionality.

It is important to remark that our classification of vegetation types was based mostly on species composition and relative abundance within the patches sampled using a multivariate classification (i.e., Cluster analysis, Fig. 2). This analysis distinguished the 3 types of old-growth forest very clearly from each other and based on their floristic composition we named them TOF, TDF and SDF following Rzedowski (2006) and Castillo-Campos (2006). These 3 old-growth types were also clearly distinguished from secondary forest by the relative abundances of their species, which was also true for early secondary forest less than 10 years old, however for older secondary forest (> 10 years old) the distinction based solely on relative abundances was not as clear. Particularly, for those patches that had undergone more than 20 years of secondary succession we needed to take into account their canopy height and density as well as the size of their trunks (DBH) in order to group them together as LSF, which was the type of secondary forest with the broadest spatial variation in composition. Since the 3 types of secondary forest that we sampled had a greater floristic affinity with SDF (Fig. 5) than with either of the other 2 old-growth forest types, we are certain that they were all derived from this type of forest, which originally was by far the most extensive of the 3 types of primary forest within the region (Castillo-Campos, 2006; Travieso-Bello & Campos, 2006).

In different tropical regions of Mexico it has been observed that the great diversity of plants and the high degree of endemism results from, among other factors, a varied topography, a complex geological and environmental history, heterogeneous soil characteristics, and a wide variety of land use types that generate very heterogeneous agricultural matrices (Balvanera et al., 2002; Méndez-Toribio et al., 2016). In the seasonally dry tropics of central Veracruz on the Gulf of Mexico, the topography includes plains, mountain ranges and steep sided valleys, with elevations ranging from 20 to 1,000 m asl. The heterogeneous topography creates highly variable micro-environments that favor a high degree of richness and spatial heterogeneity in species composition because of its relationship with abiotic factors such as the intensity of solar radiation, the differential impact of wind, and ultimately with biotic factors that include ecological processes such as seed dispersal (Balvanera et al., 2002; Méndez-Toribio et al., 2016). Soil characteristics were the environmental factors most closely related to floristic variation among the different types of vegetation detected in this study; particularly pH, organic matter content, and stones in the soil. This coincides with reports for other seasonally dry tropical regions (Balvanera et al., 2002; Becknell & Powers, 2014; Powers et al., 2009). Although the climate regime prevalent in the region studied set it apart from surrounding areas that are colder and wetter to the west up along the mountains and more humid to the north and south, it is noteworthy that the climate variables did not explain the differences in vegetation found within the region, whose internal variation is closely linked to edaphic properties and with topography (i.e., elevation).

A clear example of how the edaphic characteristics have shaped the distribution of the diversity in the study area is the tropical dry oak forest (TOF) found in the region, which is regarded as a relict forest from the Pleistocene (Arriaga et al., 2000), having maintained its structure and floristic composition without changing. This forest is dominated by tree species of Nearctic origin (*Quercus* spp.) that have not been displaced by Neotropical species, likely owing to the poor, rocky soils they grow on and other edaphic properties (e.g., low pH, Appendix 1) that have prevented the establishment of other tree species. In addition, the poor rocky soils, steep slopes and inaccessible sites where the oak trees grow have protected these forests from deforestation, because the agricultural potential is null or extremely low in these sites. Another example of how soil properties are shaping the distribution of tree species and plant diversity in the study area is manifested in the tropical deciduous forest (TDF), which is the only vegetation type positively correlated with pH. This could explain the dominance of Fagaceae species (i.e., legumes) in TDF, which are well known for fixing nitrogen, a capability that allows them to thrive in relatively alkaline and N-limited soils where other species cannot (Sparling et al., 1999).

Even though most of the forest patches found in the seasonally dry tropical region of the Gulf of Mexico are small (range: 3 - 118 ha, with a mean area of 25 ha, with 85% smaller than 50 ha; Appendix 1) secondary forest, their importance to regional diversity is clearly shown by our results. Given their rich and heterogeneous vegetation, and their critical role in enhancing landscape connectivity and species turnover, the importance of small-forested patches in deforested landscapes, including secondary

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forest, has been recognized by numerous authors (Arroyo-Rodríguez et al., 2009; Castillo-Campos et al., 2008). Moreover, the presence and wide distribution of relatively rich, dense secondary forest in the region clearly shows that forest regeneration has not been halted, and thus that forest recovery is still possible in spite of the intense degree of fragmentation (Mesa-Sierra & Laborde, 2017). Additionally, the diversity profiles of the 6 forest types (Fig. 3) also show that in spite of widespread deforestation, the region studied is not currently dominated by a handful of very abundant species and thus, it is not under a process of biotic homogenization (sensu McKinney & Lockwood 1999; Olden & Rooney, 2006).

In this study, some of the tree species that are common in pastures or man-disturbed sites —forest edges with open areas, secondary vegetation— were recorded in old-growth forest patches (e.g., *Leucaena leucocephala* in TDF and SDF), but there were also some late-successional or primary species within the patches of secondary forest (e.g., *Aphananthe monoica* in LSF). The relatively high degree of similarity in species composition between old-growth patches of SDF and some of the patches of secondary forest that have undergone several years of succession (LSF but also ISF) is indicative of intense and dynamic seed dispersal across the landscape, which is particularly important for forest recovery, landscape restoration, maintenance of viable populations, and ecosystem services (Chazdon, 2014; Mesa-Sierra & Laborde, 2017). The latter along with the heterogeneity of the agricultural matrices that surround these patches have lessened the harmful effects of habitat fragmentation on the many native woody species that grow in these patches (Chazdon, 2014). Among these native species are several drought-resistant trees such as *Leucaena leucocephala*, *Tecoma stans*, *Gliricidia sepium*, *Senna pallida* and *Bonellia macrocarpa* (Williams-Linera & Álvarez-Aquino, 2016; Williams-Linera & Lorea, 2009), whose presence across the region is crucial to mitigating the effects of climate change. In addition, these tree species and others recorded in this study with particular functional attributes (e.g., nitrogen fixation by some Fabaceae species, several trees and shrubs that produce edible fruit for frugivorous vertebrates) are also crucial to ameliorating the long-term detrimental effects of forest fragmentation and degradation in the region due to human activities.

In general, secondary succession in tropical dry regions is assumed to be slow, complex and difficult, depending on both stochastic and deterministic processes (Lebrija-Trejos, Meave et al., 2010). It is mainly limited by the extreme climate conditions during the dry season (niche limitation; Norden et al., 2009). It can also be a process dominated by anemochorous secondary species (Janzen, 1988) given that the dispersal failure of zoochorous late successional species across and towards the agricultural matrix (dispersal limitation; Norden et al., 2009) can interrupt or change the trajectory of succession, preventing the recovery of species composition and vegetation structure (e.g., arboreal strata) of the original old-growth forest. Both, niche and dispersal limitation can also reduce the variability in species composition of the forest patches surrounded by an agricultural matrix (Lebrija-Trejos, Pérez-García et al., 2010). That being said, in this study we recorded several patches of secondary vegetation (LSF and ISF) with a floristic composition relatively similar to that of mature seasonally dry forest (old-growth SDF), indicating a successional trajectory towards the original forest, a result also found in other studies of secondary succession within the dry tropics (Chazdon, 2014; Williams-Linera et al., 2011). The latter supports the idea of "guild turnover" proposed by Lebrija-Trejos, Meave et al. (2010), in which pioneer species with anemochorous dispersal facilitate the arrival of mature forest species with longer life spans. The latter establish under the pioneers' canopy and start to grow until they become part of a relatively high canopy, which in turn encourages visits by seed dispersers such as frugivorous birds and bats, and maintains the diversity of different groups of forest animals (Guevara & Laborde, 1993; Borges, 2007).

Historically, a considerably less importance has been given to floristic studies and conserving the biodiversity of seasonally dry tropical regions than that given to more humid tropical regions (Quesada et al., 2009). However, there have been increasingly more ecological studies of the seasonally dry tropical regions in Mexico in the last 20 years (2000-2018), and these have focused mainly on the regions of Chamela (Jalisco), Nizanda (Oaxaca) and the Yucatán Peninsula. In contrast, the few studies done in the dry forests of the Gulf of Mexico have been limited to small areas of this region usually along the coast (Castillo-Campos et al., 2008; Moreno-Casasola & Paradowska, 2009; Williams-Linera & Álvarez-Aquino, 2016). Our study has addressed this lack of information for the region by sampling several sites that still have forested patches. It is worth mentioning that each of these regions borders a different biome, and this has favored the enrichment of different lineages and their differentiation (Rzedowski & Calderón-de Rzedowski, 2013; Trejo & Dirzo, 2002).

The seasonally dry tropical region of the Gulf of Mexico is bordered by cloud forest at the highest elevations of the study region, more evergreen tropical forest to the south and north, and coastal dune scrub along the coast. As proposed by Powers et al. (2009) and Banda et al. (2016), the presence of different types of vegetation in the periphery of seasonally dry regions may have a strong influence on the tree and shrub species that we recorded in the sampled patches. For instance, *Diphysa americana* a tree species strongly associated with coastal dune scrub, was abundant in patches of SDF in our study and found in all 3 stages of secondary forest. Other abundant species in our study such as *Quercus* spp. and *Inga* spp. are also abundant in forests at higher elevations (*Inga* trees are also favored as shade for coffee in the upper limits of our study region), and lastly some species such as *Brosimum alicastrum, Nectandra salicifolia* and *Terminalia amazonia* are typical of more humid evergreen forest (Castillo-Campos, 2006; Travieso-Bello & Campos et al., 2006). The comparison of the species richness found in our study (156 woody species in 8.7 ha sampled) with similar regions in Mexico, is complicated by the differences in objectives and sampling effort among studies. However, in Chamela, Jalisco, Balvanera et al. (2002) found 119 tree species in 2.4 ha of sampling area; in Nizanda, Oaxaca, Silva-Aparicio et al. (2018) reported 90 species of woody plants in only 0.45 ha sampled, and lastly in Yucatán, López-Martínez et al. (2013) reported 200 species of woody plants in 5.5 ha. In general terms, there are similarities in composition among the 4 regions, mainly owing to species that are widely distributed in the Neotropics (e.g., *Bursera simaruba*, *Leucaena leucocephala*), and that are considered oligarchs (sensu Williams et al., 2017) or winners (sensu McKinney & Lockwood, 1999) because of their high abundance values in the anthropic landscapes of these regions (Berdugo-Lattke & Rangel, 2015; Carbonó & García, 2010).

The seasonally dry tropical region that abuts the Gulf of Mexico in central Veracruz has undergone severe deforestation, and its current forest cover continues to be under threat because the unbridled expansion of sugarcane crops and cattle pastures continues. However, the results of this study demonstrate that the region has a high diversity of woody plants at the local scale (i.e., in each patch), but more notably at the regional scale (across the entire landscape) that is not only rich but unique and worth preserving. This is why it is essential to acknowledge the biodiversity value of this region and the urgency of developing and implementing protection and management policies that ensure its long-term conservation. We would like to highlight that any management plan or policy implemented for this region should start by aiming to protect a minimum area of forest cover to preserve the diversity and the ecological functions of the landscape. It is also vital to recognize that the current patches of woody vegetation, including those of secondary forest are highly valuable and should be protected for the future. The development of this type of management should be a priority for decision makers and different social sectors, given the current worldwide trends of land degradation in anthropic landscapes.

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Appendix 1. Summary of the variables for each of the vegetation patches sampled (patches are numbered as in Figure 1). Vegetation type: Tropical Oak Dry Forest (TOF), Tropical Deciduous Forest (TDF), Semi-deciduous forest (SDF), Late Secondary Forest (LSF), Intermediate Secondary Forest (ISF) and Early Secondary Forest (ESF). Surrounding matrix abbreviations: pasture (P), secondary vegetation (SV). Variable abbreviations: organic matter (OM), temperature maximum (Tmax), mean annual (Prec. Mean), maximum monthly precipitation (Prec. Max). Climate variables from Cuervo-Robayo et al. (2014).

Patch	Vegeta. type	Eleva. (m asl)	Surrounding matrix	Stand age (yrs)	Previous use	Area (ha)	OM (%)	pH	Clay (%)	Silt (%)	Sand (%)	Stones (%)	Tmax (ºC)	PrecMean (mm)	PrecMax (mm)
14	TOF	436	P, SV	Mature	None	25.65	28.6	4.5	37.8	25.6	36.6	80	30.6	1,220.5	220.0
15		436	P, SV			20.05	26.4	4.6	32.5	22.2	41.2	80	30.6	1,220.5	220.0
16		436	P, SV			9.46	27.4	4.8	32.2	25.0	42.9	80	30.6	1,220.5	220.0
23	TDF	259	P	Mature	None	6.66	17.2	7.4	54.8	22.3	22.9	70	34.2	949.4	211.8
24		259	P			10.14	15.4	7.6	51.5	22.0	26.5	32	34.2	949.4	211.8
25		259	P			12.12	11.5	7.8	47.5	21.3	31.2	70	34.2	949.4	211.8
9	SDF	279	P, SV	Mature	None	60.55	4.2	6.6	57.4	27.6	14.9	7	32.7	1,052.7	224.1
10		265	P, SV			52.81	6.2	6.7	46.8	19.6	33.6	7	32.7	1,052.7	224.1
17		103	P, SV			118.52	10.4	6.7	53.5	32.3	14.2	26	33.1	1,100.5	244.6
20		227	Various crops			29.90	10.3	7.7	66.2	22.3	11.5	26	33.6	1,019.9	221.5
28		483	Dunes			26.31	8.3	7.3	24.8	13.3	61.8	2	33.3	1,158.4	249.7
29		483	Various crops			5.30	4.8	7.9	21.5	7.3	71.2	2	33.3	1,158.4	249.7
26	LSF	702	P, Citrus orchard	22	Crops	7.77	38.5	7.2	47.5	18.0	34.5	7	31.7	1,021.7	196.0
27		702	P, Citrus orchard	22	Crops	29.73	29.6	7.3	50.8	20.7	28.5	7	31.7	1,021.7	196.0
7		135	P, SV	23	P	22.93	12.3	6.1	63.8	19.0	17.2	30	33.1	1,071.0	232.8
11		265	P, SV	21	P	40.85	7.1	6.6	63.4	23.6	12.9	7	32.7	1,052.7	224.1
22		184	Various crops	20	P	3.03	7.1	7.5	62.8	23.6	13.5	7	33.6	1,019.9	221.5
12	ISF	78	P	15	P	7.90	10.0	6.4	47.1	30.3	22.6	7	32.9	1,137.9	245.0
13		108	P	17	P	11.17	5.0	6.3	42.5	13.5	23.2	7	32.9	1,137.9	245.0
19		64	P, Sugarcane	14	P	22.95	8.1	6.5	78.2	17.6	4.2	26	33.1	1,100.5	244.6
6		161	P, SV	15	P	43.98	11.8	6.4	62.3	28.4	6.2	10	33.1	1,071.0	232.8
8		133	P, SV	15	P	71.86	5.7	6.2	65.8	17.6	16.6	30	33.1	1,071.0	232.8
18		73	P, SV	14	P	34.64	9.2	6.8	67.5	22.3	10.2	26	33.1	1,100.5	244.6
21		184	Various crops	10	Crops	13.84	6.0	7.7	68.8	20.3	10.9	7	33.6	1,019.9	221.5
1	ESF	730	P	7	P	6.51	10.5	6.2	43.4	31.0	25.6	15	31.1	1,070.2	204.8
2		730	P, Mango orchard	7	P	4.16	7.2	7.1	42.8	33.0	24.3	30	31.1	1,070.2	204.8
3		841	P, Mango orchard	10	P	10.56	14.8	6.3	54.8	26.3	18.9	15	31.1	1,070.2	204.8
4		1,045	Shaded coffee	8	Shaded coffee	22.49	6.2	6.3	34.8	25.0	40.3	15	26.7	1,563.7	279.5
5		1,045	Shaded coffee	8	Shaded coffee	37.68	6.8	5.8	31.4	24.3	44.3	15	26.7	1,563.7	279.5

Appendix 2. Plant species recorded in the seasonally dry tropical region of the central Veracruz, Mexico on the Gulf of Mexico, and their respective abundance in each vegetation type: Tropical Oak Forest (TOF), Low-statured Deciduous Forest (LWF), Semi-deciduous Forest (SDF), Late Secondary Forest (LSF), Intermediate Secondary Forest (ISF) and Early Secondary Forest (ESF).

Species			Vegetation type					
	Most-known synonym	Family	TOF	TDF	SDF	LSF	ISF	ESF
Achatocarpus nigricans Triana		Achatocarpaceae	0	0	7	1	0	0
Acrocomia aculeata (Jacq.) Lodd. ex Mart.		Arecaceae	0	0	30	0	0	0
Alchornea latifolia Sw.		Euphorbiaceae	0	4	0	2	0	0
Amphilophium paniculatum (L.) Kunth		Bignoniaceae	0	0	2	0	0	0
Annona muricata L.		Annonaceae	0	0	0	0	0	1
Annona reticulata L.		Annonaceae	0	1	5	5	0	1
Aphananthe monoica (Hemsl.) J.-F. Leroy	*Mirandaceltis monoica*	Cannabaceae	0	4	0	209	0	0
Astronium graveolens Jacq.		Anacardiaceae	0	5	0	0	0	0
Astronium sp.		Anacardiaceae	0	0	0	2	0	0
Bauhinia divaricata L.		Fabaceae	0	46	0	0	1	0
Bernardia sp.		Euphorbiaceae	0	0	0	0	0	1
Bonellia macrocarpa (Cav.) B. Ståhl & Källersjö		Primulaceae	0	1	0	0	0	0
Brosimum alicastrum Sw.		Moraceae	0	0	50	0	0	1
Bunchosia sp.		Malpighiaceae	0	2	0	83	0	0
Bursera graveolens (Kunth) Triana & Planch.		Burseraceae	0	0	17	19	0	0
Bursera simaruba (L.) Sarg.		Burseraceae	0	151	17	34	12	35
Byrsonima crassifolia (L.) Kunth		Malpighiaceae	69	0	0	0	0	0
Caesalpinia cacalaco Bonpl.		Fabaceae	0	40	0	1	0	0
Caesalpinia mexicana A. Gray		Fabaceae	0	0	0	0	14	0
Calliandra sp.		Fabaceae	0	0	4	0	0	0
Calliandra tergemina (L.) Benth.		Fabaceae	0	0	0	0	0	1
Calophyllum brasiliense Cambess.		Clusiaceae	3	0	0	0	0	0
Carica papaya L.		Caricaceae	0	0	2	0	0	0
Casearia aculeata Jacq.		Salicaceae	0	1	3	2	23	9
Casearia guevarana Cast.-Campos & E. Medina		Salicaceae	0	0	1	0	0	0
Casearia nitida Jacq.	*Casearia corymbosa*	Salicaceae	0	0	8	1	0	6
Casearia sp.		Salicaceae	0	0	48	6	2	0
Castilla elastica Sessé ex Cerv.		Moraceae	0	0	1	19	0	0

Appendix 2.
Continued

Species			Vegetation type					
	Most-known synonym	Family	TOF	TDF	SDF	LSF	ISF	ESF
Cecropia sp.		Urticaceae	0	0	0	0	0	1
Cedrela odorata L.		Meliaceae	0	0	84	0	0	6
Ceiba pentandra (L.) Gaertn.		Malvaceae	0	5	1	0	0	0
Ceiba sp.		Malvaceae	0	0	0	0	1	0
Celtis caudata Planch.		Cannabaceae	0	0	0	3	16	2
Celtis iguanaea (Jacq.) Sarg.		Cannabaceae	0	0	4	0	1	0
Cestrum dumetorum Schltdl.		Solanaceae	0	0	5	4	0	4
Cestrum racemosum Ruiz & Pav.		Solanaceae	0	73	0	0	17	0
Chiococca coriacea M. Martens & Galeotti		Rubiaceae	0	0	1	0	0	0
Chloroleucon mangense (Jacq.) Britton & Rose		Fabaceae	0	0	27	2	9	0
Citrus maxima (Burm.) Merr.	*Citrus* × *aurantiifolia*	Rutaceae	0	0	0	0	0	3
Citrus reticulata Blanco		Rutaceae	0	0	0	0	0	1
Cnidoscolus aconitifolius (Mill.) I.M. Johnst.		Euphorbiaceae	0	19	7	35	0	20
Coccoloba barbadensis Jacq.		Polygonaceae	0	0	8	0	0	0
Coccoloba humboldtii Meisn.		Polygonaceae	0	0	55	2	4	0
Coccoloba liebmannii Lindau		Polygonaceae	0	0	9	0	0	0
Cochlospermum vitifolium (Willd.) Spreng.		Bixaceae	0	0	15	0	6	0
Comocladia macrophylla (Hook. & Arn.) L. Riley		Anacardiaceae	0	2	5	9	1	14
Condea verticillata (Jacq.) Harley & J.F.B. Pastore	*Hyptis verticillata*	Lamiaceae	0	0	13	1	0	0
Cordia dentata Poir.	*Cordia alba*	Boraginaceae	0	1	3	4	15	0
Cordia diversifolia Pav. ex A. DC.		Boraginaceae	0	0	12	117	17	0
Coulteria velutina (Britton & Rose) Sotuyo & G.P. Lewis	*Caesalpinia velutina*	Fabaceae	0	0	0	1	10	0
Crateva tapia L.		Capparaceae	0	0	12	0	0	0
Crescentia cujete L.		Bignoniaceae	0	0	4	0	1	0
Crossopetalum gaumeri (Loes.) Lundell	*Myginda gaumeri*	Celastraceae	0	0	1	0	0	0
Croton ciliatoglandulifer Ortega		Euphorbiaceae	0	0	1	41	1	3
Croton cortesianus Kunth		Euphorbiaceae	0	0	0	0	0	2

Appendix 2.
Continued

Species	Most-known synonym	Family	Vegetation type					
			TOF	TDF	SDF	LSF	ISF	ESF
Croton guatemalensis Lotsy		Euphorbiaceae	0	112	9	3	9	1
Cupania dentata DC.		Sapindaceae	0	0	2	0	0	1
Dalbergia brownei (Jacq.) Schinz		Fabaceae	0	0	3	0	0	0
Dalbergia sp.		Fabaceae	0	0	0	5	0	0
Desmopsis trunciflora (Schltdl. & Cham.) G.E. Schatz		Annonaceae	0	0	1	0	13	0
Diospyros acapulcensis subsp. *veraecrucis* (Standl.) Provance, I. García & A.C. Sanders		Ebenaceae	0	0	11	0	10	0
Diphysa americana (Mill.) M. Sousa		Fabaceae	0	0	40	14	3	3
Ehretia tinifolia L.		Boraginaceae	0	0	39	6	0	0
Elaeodendron xylocarpum (Vent.) DC.	*Cassine xylocarpa*	Celastraceae	0	0	3	0	0	0
Enterolobium cyclocarpum (Jacq.) Griseb.		Fabaceae	0	0	7	0	1	1
Erythrina leptorhiza DC.	*Erythrina herbacea*	Fabaceae	0	0	0	0	1	8
Erythroxylum areolatum L.		Erythroxylaceae	0	0	1	1	0	2
Erythroxylum havanense Jacq.		Erythroxylaceae	0	0	2	0	1	0
Erythroxylum sp.		Erythroxylaceae	0	0	35	1	1	0
Esenbeckia berlandieri Baill.		Rutaceae	0	0	4	0	0	0
Eugenia acapulcensis Steud.		Myrtaceae	0	0	1	0	0	0
Eugenia capuli (Schltdl. & Cham.) Hook. & Arn.		Myrtaceae	0	0	0	4	0	0
Euphorbia schlechtendalii Boiss.		Euphorbiaceae	0	0	39	8	0	0
Eysenhardtia polystachya (Ortega) Sarg.		Fabaceae	0	102	0	8	1	2
Ficus aurea Nutt.		Moraceae	2	0	0	0	0	0
Ficus cotinifolia Kunth		Moraceae	0	0	2	1	0	7
Ficus insipida Willd.		Moraceae	0	0	0	1	0	0
Ficus obtusifolia Kunth		Moraceae	2	0	2	0	0	0
Fraxinus dubia (Willd. ex Schult. & Schult. f.) P.S. Green & M. Nee		Oleaceae	0	0	0	0	0	1
Genipa americana L.		Rubiaceae	1	0	0	0	0	0
Ginoria nudiflora (Hemsl.) Koehne		Lythraceae	0	0	1	6	2	3

Appendix 2.
Continued

Species	Vegetation type							
	Most-known synonym	Family	TOF	TDF	SDF	LSF	ISF	ESF
Gliricidia sepium (Jacq.) Kunth ex Walp.		Fabaceae	0	0	31	0	257	4
Guazuma ulmifolia Lam.		Malvaceae	0	1	48	16	258	57
Guettarda macrosperma Donn. Sm.		Rubiaceae	0	0	0	3	0	0
Gyrocarpus jatrophifolius Domin		Hernandiaceae	0	0	3	0	0	0
Hamelia patens Jacq.		Rubiaceae	0	0	0	0	0	1
Handroanthus chrysanthus (Jacq.) S.O. Grose		Bignoniaceae	0	1	36	6	34	0
Heliocarpus pallidus Rose		Malvaceae	0	0	18	12	27	7
Hyperbaena jalcomulcensis E. Pérez & Cast.-Campos		Menispermaceae	0	0	1	0	2	0
Inga jinicuil Schltdl.		Fabaceae	0	0	0	0	0	34
Inga vera Willd.		Fabaceae	0	0	0	0	0	24
Ipomoea wolcottiana Rose		Convolvulaceae	0	0	4	8	30	2
Jatropha sp.		Euphorbiaceae	0	0	0	0	0	4
Karwinskia humboldtiana (Schult.) Zucc.		Rhamnaceae	0	39	3	0	1	0
Leucaena lanceolata S. Watson		Fabaceae	0	0	0	0	1	0
Leucaena leucocephala (Lam.) de Wit		Fabaceae	0	50	58	129	61	90
Leucaena macrophylla Benth.		Fabaceae	0	0	0	0	0	41
Licaria capitata (Schltdl. & Cham.) Kosterm.		Lauraceae	0	109	0	0	0	0
Lippia myriocephala Schltdl. & Cham.		Verbenaceae	0	0	0	2	0	0
Luehea candida (DC.) Mart.		Malvaceae	0	0	0	0	0	4
Lycianthes sp.		Solanaceae	0	0	0	0	0	3
Lysiloma divaricatum (Jacq.) J.F. Macbr.		Fabaceae	0	0	46	28	23	0
Maclura tinctoria (L.) D. Don ex Steud.		Moraceae	0	2	8	0	13	0
Mangifera indica L.		Anacardiaceae	0	0	0	0	0	7
Manilkara zapota (L.) P. Royen		Sapotaceae	0	0	3	0	0	0
Mimosa tricephala Schltdl. & Cham.		Fabaceae	0	0	0	0	10	0
Nectandra salicifolia (Kunth) Nees		Lauraceae	0	0	78	0	3	0
Nectrandra sp.		Lauraceae	0	0	0	0	0	1
Parmentiera aculeata (Kunth) Seem.		Bignoniaceae	0	0	0	0	0	14

Appendix 2.
Continued

Species			Vegetation type					
	Most-known synonym	Family	TOF	TDF	SDF	LSF	ISF	ESF
Persea sp.		Lauraceae	0	0	0	0	0	1
Piper amalago L.		Piperaceae	0	0	10	0	0	3
Piscidia piscipula (L.) Sarg.		Fabaceae	0	113	11	8	4	0
Pisonia aculeata L.		Nyctaginaceae	0	21	104	30	13	0
Pistacia sp.		Anacardiaceae	0	0	0	1	0	0
Pithecellobium dulce (Roxb.) Benth.		Fabaceae	0	3	0	0	7	0
Pithecellobium insigne Micheli ex Donn. Sm.		Fabaceae	0	0	18	0	1	0
Protium copal (Schltdl. & Cham.) Engl.		Burseraceae	0	0	0	6	0	0
Protium sp.		Burseraceae	0	0	0	0	0	4
Psychotria costivenia Griseb.		Rubiaceae	0	0	15	0	0	0
Quadrella incana (Kunth) Iltis & Cornejo		Capparaceae	0	2	0	0	0	0
Quercus oleoides Schltdl. & Cham.		Fagaceae	259	0	0	0	0	0
Quercus sapotifolia Liebm.		Fagaceae	432	0	0	0	0	0
Randia monantha Benth.		Rubiaceae	0	5	0	0	0	3
Rochefortia lundellii Camp		Boraginaceae	0	0	14	0	1	3
Ruprechtia chiapensis Lundell		Polygonaceae	0	0	0	1	0	0
Sabal mexicana Mart.		Arecaceae	0	0	1	0	1	0
Sapindus saponaria L.		Sapindaceae	0	1	0	0	0	3
Sapranthus microcarpus (Donn. Sm.) R.E. Fr.		Annonaceae	0	0	1	0	3	4
Savia sessiliflora (Sw.) Willd.		Phyllanthaceae	0	0	0	15	0	0
Schaefferia frutescens Jacq.		Celastraceae	0	0	7	0	0	0
Senna atomaria (L.) H.S. Irwin & Barneby		Fabaceae	0	19	3	3	10	5
Senna pallida (Vahl) H.S. Irwin & Barneby		Fabaceae	0	235	3	0	0	0
Senna pendula (Humb. & Bonpl. ex Willd.) H.S. Irwin & Barneby		Fabaceae	0	5	0	0	0	0
Sideroxylon celastrinum (Kunth) T.D. Penn.		Sapotaceae	0	6	4	1	3	0
Solanum erianthum D. Don		Solanaceae	0	0	0	0	0	2
Solanum sp.		Solanaceae	0	0	0	0	0	1

Appendix 2.
Continued

Species	Most-known synonym	Family	Vegetation type					
			TOF	TDF	SDF	LSF	ISF	ESF
Spondias mombin L.		Anacardiaceae	0	0	0	35	1	9
Tabernaemontana alba Mill.		Apocynaceae	0	0	1	0	0	1
Tabernaemontana litoralis Kunth		Apocynaceae	0	0	0	1	0	0
Tabernaemontana odontadeniiflora A.O. Simões & M.E. Endress	*Stemmadenia obovata*	Apocynaceae	0	0	96	5	13	0
Tecoma stans (L.) Juss. ex Kunth		Bignoniaceae	0	0	10	2	8	0
Terminalia amazonia (J.F. Gmel.) Exell		Combretaceae	0	0	0	0	1	0
Thevetia peruviana (Pers.) K. Schum.		Apocynaceae	0	0	0	2	3	0
Thouinidium decandrum (Bonpl.) Radlk.		Sapindaceae	0	0	8	3	25	2
Tithonia sp.		Compositae	0	0	0	0	0	6
Trichilia havanensis Jacq.		Meliaceae	0	0	0	5	0	2
Trichilia hirta L.		Meliaceae	0	0	0	0	1	0
Vachellia campechiana (Mill.) Seigler & Ebinger	*Acacia cochliacantha*	Fabaceae	0	0	12	0	1	0
Vachellia cornigera (L.) Seigler & Ebinger	*Acacia cornigera*	Fabaceae	1	3	1	1	5	1
Vachellia farnesiana (L.) Wight & Arn.	*Acacia farnesiana*	Fabaceae	1	2	8	5	6	24
Vachellia pennatula (Schltdl. & Cham.) Seigler & Ebinger	*Acacia pennatula*	Fabaceae	0	0	0	0	2	177
Varronia macrocephala Desv.	*Cordia pringlei*	Boraginaceae	0	0	1	0	0	0
Vitis bourgaeana Planch.		Vitaceae	0	0	9	0	0	0
Xylosma panamensis Turcz.		Salicaceae	0	0	4	3	0	0
Xylosma sp.		Salicaceae	0	0	0	0	0	4
Zanthoxylum sp.		Rutaceae	0	0	6	0	1	0

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