

## FLORA AND VEGETATION OF THE SEASONALLY DRY TROPICS IN MEXICO: ORIGIN AND BIOGEOGRAPHICAL IMPLICATIONS

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### ABSTRACT

Among the many explanations for the large biological diversity of Mexico is that it is the result of the contact between the Nearctic and Neotropical biotas; however, this contact-related explanation is not fully satisfactory and needs further examination in the light of historical biogeography. We offer newer insights into this issue by examining the history of the flora and the vegetation heterogeneity of the seasonally dry tropics of this country. Several environmental criteria can be used to define the seasonally dry tropical regions, but setting their precise geographical boundaries is not always straightforward. This is largely due to the large vegetation heterogeneity of this region, within which the tropical dry forest (TDF) is prominent. The origin of the TDF flora can be traced back at least as far as 20 million years before present and seems to be associated with the Tertiary North American flora. Available evidence does not support a South American origin of the TDF flora. Similarly, the separation of the TDF and the hot North American desert floras into two different biogeographical realms is not warranted. The history of the seasonally dry tropical flora of Mexico strongly suggests that this biogeographical dichotomy should be replaced by the recognition of the existence of a Pan-American Realm.

Key words: Holarctic Realm, Neotropical Realm, phytogeography, tropical dry forest, vegetation heterogeneity.

### RESUMEN

Entre las diversas ideas que se han propuesto para explicar la gran diversidad biológica de México está la que afirma que ésta es el resultado del contacto de las biotas neotropical

y neártica; sin embargo, esta explicación relacionada con el gran contacto biótico de las Américas no es completamente satisfactoria y necesita ser revisada a la luz de la biogeografía histórica. En este artículo ofrecemos nuevas perspectivas sobre este asunto por medio de una revisión de la historia de la flora y la heterogeneidad vegetacional del trópico estacionalmente seco de este país. Se han usado varios criterios ambientales para definir las regiones tropicales estacionalmente secas, pero ubicar con precisión sus límites geográficos no es siempre fácil. Esto se debe en gran medida a la gran heterogeneidad de la vegetación presente en esta región, entre la que predomina el bosque tropical caducifolio (BTC). El origen de la flora del BTC se remonta, por lo menos, unos 20 millones de años antes del presente y parece estar asociada con la flora del Terciario de Norteamérica. La evidencia disponible no apoya un origen sudamericano para el BTC. Asimismo, no hay razones que justifiquen de forma convincente la separación de la flora del BTC y la de los desiertos calientes de Norteamérica en dos reinos biogeográficos diferentes. La historia de la flora del trópico estacionalmente seco de México sugiere fuertemente que esta dicotomía biogeográfica debería ser reemplazada por el reconocimiento de la existencia de un Reino Panamericano.

Palabras clave: bosque tropical caducifolio, fitogeografía, heterogeneidad vegetacional, Reino Holártico, Reino Neotropical.

## INTRODUCTION

Among the most widespread explanations for the high biological diversity of Mexico is the position of this country more or less halfway between the latitudinal extremes of North and South America; this position makes it easy to conceive the Mexican territory as the natural place for a major contact between the Nearctic and Neotropical biotas, which evolved separated from each other for a very long time. Unfortunately, the general acceptance of the role of this major biological contact is not based on sound analyses. From a floristic perspective, the Mexican vegetation of temperate and cold regions has been traditionally considered Nearctic (assuming a Laurasian origin), whereas the vegetation of the humid tropics is commonly treated as typically Neotropical (possibly of Gondwanan origin; Doyle & Luckow, 2003; Corlett & Primack, 2006; Fiaschi & Pirani, 2009). These biogeographical associations are unclear for the vegetation of other climatic regions in Mexico, in particular, the dry tropical forests. The general assumption is that Mexico's dry forests have a Neotropical origin that is similar to the origins of the humid forests of the Atlantic watershed. Likewise, the xerophytic scrub widespread in central and northern Mex-

ico has been frequently associated with the Nearctic Realm (Cox, 2001; Morrone, 2002). Nevertheless, the floras of these two major plant formations appear to be closely related and thus associating them to two different biogeographical realms is not warranted (Van Devender, 2000). In this paper we examine the history of the flora and the vegetation of the seasonally dry tropics of Mexico in order to gain newer insights on the real role of the contact of the North- and South-American biotas in driving the large plant diversity of its territory. Given the considerable differences in the available information for the various vegetation types occurring in this region, the analysis is undeniably biased towards the tropical dry forest, which is not only the best studied but also the most charismatic ecosystem within this climatic region. Such bias, however, does not imply that the floristic assemblages proper of other vegetation types occurring in this climatic region are less meaningful in searching for answers to this biogeographical question.

#### CIRCUMSCRIPTION OF THE SEASONALLY DRY TROPICS

The term ‘seasonally dry tropics’ (hereafter ‘dry tropics’) refers to low elevation intertropical regions (< 1,400 m a.s.l.) having a well-defined dry season (Gentry, 1995; Mooney et al., 1995). Dry tropics are found on all continents with tropical climates and they cover a larger area than the wet tropics (Mooney et al., 1995). Typically, the dry tropics are a frost-free region (Trejo-Vázquez, 1999). The length of the dry season in the dry tropics is highly variable, but it normally lasts for a period between four and six months. Similarly, the total amount of annual precipitation displays a large inter-annual variability, generally ranging from 500 to 1800 mm (Gentry, 1995), with some reported values as low as 300 mm (Trejo, 1996; 1998). Rainfall is strongly concentrated in summer months due to land over-heating relative to the surface temperature of the sea, which causes the reversal of wind flow patterns (García, 2004). In the Indian subcontinent this phenomenon is known as ‘monsoon’, a term that is increasingly applied to similar ecosystems worldwide (Bowman, 1996). Mean annual temperature ranges between 18 and 26 °C, but more frequently within the much narrower range of 22-24 °C (Trejo, 1996; 2005); sub-zero temperatures are unknown. In Mexico, the prevailing climates in the dry tropics are Aw, Am, Cwa, BSh, and BW (Miranda & Hernández-X., 1963; Rzedowski, 1978; Trejo, 1996; García, 2004).

Despite these apparently simple criteria, circumscription of the dry tropics is not always straightforward. This is due to the increasing duration and intensity of the dry season with increasing distance from the equator. In fact, some areas beyond

the intertropical region share environmental characteristics with the dry tropics; for example, vegetation typical of the dry tropics in Mexico extends north of the limit of the tropical regions, as far as 28° N in San Javier, Sonora (Martínez-Yrizar et al., 2000), and the same is true for dry regions with continental climates and high-elevation (1500-2000 m a.s.l.) areas (Arriaga & León, 1989; Rundel & Boonpragob, 1995; Trejo, 1996; Cerros-Tlatilpa & Espejo-Serna, 1998; Camacho-Rico et al., 2006).

Setting boundaries for the dry tropics in terms of the duration of the season in which plants bear foliage is also troublesome, as varying degrees of deciduousness are difficult to assess in the field (Scariot & Sevilha, 2005). Besides, the precise timing of leaf fall depends on the total amount and distribution of rain in a given year (Martínez & Galindo-Leal, 2002). Nonetheless, even for the most equatorial tropical systems it is generally possible to recognize humid (moist/rain) from dry (deciduous) forests. Therefore, attempting to establish a distinction between these two major ecosystems seems reasonable, while admitting that no single variable of the physical environment will ever allow to unequivocally set a natural, clear-cut limit between them.

Species richness in the dry tropics is generally lower than in tropical humid forests (Gentry, 1995). Species richness peaks near the equator and gradually decreases towards higher latitudes (Gentry, 1995; Gaston, 2000); however, in the dry tropical region of western Mexico, species richness is not only abnormally high, but it also comprises a large endemic component (Lott, 1985; 1993; Lott & Atkinson, 2002).

Some studies allegedly conducted in Mexico's dry tropics have included information for vegetation types that are not really typical of tropical climates, mostly because their boundaries coincided with political-administrative or physiographic units, but not with climatic units (e.g. a volcano [Cedano-Maldonado & Harker, 2000] or a river basin [Camacho-Rico et al., 2006]). The inclusion of non-tropical vegetation types (e.g. temperate pine and oak forests), and of plant communities typical of very particular habitats such as those of coastal areas (mangroves and other halophyllous vegetation), hinders between-locality comparisons and the drawing of general conclusions for the flora and vegetation of the dry tropics. Nevertheless, the presence of several vegetation types coexisting in the same landscape is almost a widespread generalization in the dry tropics, as examined in the following section.

## VEGETATION TYPES IN THE MEXICAN SEASONALLY DRY TROPICS

Perhaps the most striking feature about the dry tropics in Mexico is the large number and variety of vegetation types that they encompass, often under similar

climatic conditions (Table 1). Typical dry tropics vegetation may be dominated by trees (e.g. in the prominent tropical dry forest), or by shrubs or herbs, blurring the correlation between vegetation types and precipitation (Gillespie et al., 2000; Trejo & Dirzo, 2002). The environmental heterogeneity resulting from variations in lithology, relief, soil depth and texture, drainage and water availability, along with diverse disturbance regimes, are the main drivers of such large vegetation variability (Miranda & Hernández-X., 1963; Rzedowski, 1978; Gentry, 1995; Menaut et al., 1995; Trejo, 1996; Pérez-García et al., 2001; 2010).

Dry tropics vegetation may be markedly deciduous, such as the widespread tropical dry forest (TDF) (Miranda & Hernández-X., 1963; Rzedowski, 1978), or decidedly evergreen in the proximity to water sources (Rzedowski, 1978; Lebrija-Trejos, 2001; Camacho-Rico et al., 2006). Moreover, in the dry tropics the phenological behavior of many pachycaulous, sclerophyllous or succulent species does not match that of deciduous plants, particularly in the xerophytic vegetation associated with rocky environments (Toledo Rizzini, 1997; Pérez-García & Meave, 2004). A comparison of the main features of the major vegetation types of the seasonally dry tropics of Mexico is given in Table 2.

TDF is dominated by relatively short trees, most of which shed entirely their foliage in the dry season (Miranda & Hernández-X., 1963). In this community, herbaceous and thin woody climbers are common, but epiphytes and thick lianas are less abundant and diverse than in humid forests (Challenger, 1998; Pineda-García et al., 2007). Density of multi-stemmed trees tends to be higher than in humid forests (Dunphy et al., 2000), and a wider range of life forms and leaf phenological patterns occurs (Medina, 1995). Diversity is generally high and there is no clear dominance of any species, to the point that many of them are rare (Durán et al., 2006); nevertheless, some genera like *Bursera*, *Lonchocarpus*, *Lysiloma* and *Jatropha* are typically present in these systems. In Mexican TDF communities, emergent columnar cacti are common, conferring them a particular physiognomy (Rzedowski, 1978; Challenger, 1998; Pennington & Sarukhán, 1998). The presence of slow-growing and long-lived plants, such as succulent cacti, suggests that this vegetation is not normally subjected to fire disturbance. Despite these commonalities, TDF is highly variable in structure and composition across the country. This situation has led to the recognition of several community sub-types. In some cases the differences are important at the physiognomic level, but in others these are rather floristic in nature, or a combination of both (Trejo & Dirzo, 2002), even within small geographic areas (Pérez-García & Meave, 2004; Pérez-García et al., 2005; Durán et al., 2006).

Table 1. Comparison of floristic richness between different localities in tropical regions of Mexico. Vegetation type includes a partially standardized classification of the main vegetation types reported at each locality. Secondary vegetation was excluded from this list but plant species occurring in it were considered for floristic richness calculations. S = species richness; G = genus richness; F = family richness; AV = aquatic vegetation; CF = conifer forest (*Abies*, *Juniperus* and *Pinus*); GF = gallery forest (includes 'selva mediana ribereña'); Gr = grassland (includes arid, temperate or secondary grasslands); HV = halophytic vegetation and coastal dunes. Ma = mangrove; MCF = mountain cloud forest; METF = medium-statured evergreen tropical forest; MTF = medium-statured tropical forest (including semi-evergreen forest, sub-deciduous forests, and riparian forests); PG = palm groves; PF = *Pinus* forest; PQF = *Pinus-Quercus* forest; QF = *Quercus* forest; Sv = savanna (tropical grassland); ScS = sclerophyllous scrub ('chaparral'); SeTDF = semi-evergreen tropical dry forest ('tintales' and other flooded forests). SF = spiny forest; SLSTF = spiny low stature tropical forest; SS = spiny scrub; TEF = tropical evergreen forest; TDF = tropical dry forest; XS = xerophytic scrub. For each locality a standard acronym of the Mexican Federal State is given.

Locality	S	G	F	Area (km <sup>2</sup> )	Altitude (m)	Vegetation type	Reference
Calakmul, Cam.	1550	726	147*	23,398	~200-380	METF, Sv, TEF, TDF, SeTDF, MTF, AV	Martínez et al. (2001)
Papalotepec, Gro.	268	203	75	31	700-1350	TDF	Peralta (1995)
Venta Vieja, Gro.	307	222	77*	38	700-1100	TDF	Gual (1995)
Central Veracruz	666	394	104	18.23	400-900	TDF	Castillo-Campos et al. (2007)
Cerro Chiletépetl, Gro.	300	201	72	24.8	540-1260	QF, GF, XS, PG, Sv?, TDF, MTF	Vargas & Pérez (1996)
Chamela-Cuixmala, Jal.	1149	572	125	350	0-500	GF, Ma, SS, TDF, AV, HV	Lott & Atkinson (2002)
Costa Grande, Gro.	1047	527	135	2500	0-300	GF, Ma, XS, TDF, SeTDF, MTF, AV, HV	Peralta-Gómez et al. (2000)
Cozumel, Q. Roo	542	---	105*	490	~0-10	Ma, TDF, SeTDF, AV	Téllez Valdés & Cabrera Cano (1987)
Culiacán, Sin.	1445	623	145	4758.9	0-860	PQF, SF, GF, QF, TDF, MTF	Vega-Aviña et al. (2000)
Upper Tehuantepec River basin, Oax.	448	272	89	≈ 650	700-2100	TDF, PQF, QF, XS, GF	Acosta et al. (2003)

Table 1. Continuation.

Locality	S	G	F	Area (km <sup>2</sup> )	Altitude (m)	Vegetation type	Reference
Balsas River basin, Gro., Jal., Méx., Mich., Mor., Oax., Pue., Tlax. Central Depression, Chis.	4442	1246	202	112,320	0-3100	CF, MCF, QF, TDF, MTF, SS, XS, AV	Fernández et al. (1998)
Gómez Farías, Tam. <sup>1</sup>	998	489	103	9000	200-1500	TDF, SS	Reyes-García & Sousa (1997)
Huatulco, Oax.	286	---	83*§	400	100-900	GF, TDF, MTF, METF, AV	Valiente-Banuet et al. (1995)
Huimanguillo, Tab.	736	391	91*	63.7	0-200	GF, HV, Ma, MTF, TDF, Sv, SLSTF	Salas-Morales et al. (2007)
Lobos Island, Sin.	786	---	---	---	---	QF, Sv, TEF	Puig (1972)
Pájaros Island, Sin.	57	52	27*	0.10	0-141	QF, SS, Gr	Vega-Aviña et al. (2001)
La Vainilla, Gro.	56	50	27*	0.48	0-142	QF, Ma, Gr, HV	Vega-Aviña et al. (2001)
Coyuca Lagoon, Gro.	428	309	98	3.4	250-570	GF, TDF, MTF	Gallardo (1996)
Mitla Lagoon, Gro.	488	--	101	100	0-<100	GF, Ma, TDF, SeTDF, AV	Fonseca & Lozada-Pérez (1993)
Tres Palos Lagoon, Gro.	523	323	99*	225	0-<100	GF, Ma, SS, Sv, TDF, AV	Lozada-Pérez (1994)
Playa Blanca, El Potosí and Salinas del Cuaño lagoons, Gro.	527	329	107	167	0-<100	GF, TDF, SeTDF, AV	Diego-Pérez & Lozada- Pérez (1994)
Upper Mixteca region, Oax., Pue.	382	270	101	219.2	0-180	GF, Ma, XS, TDF, MTF, AV, HV	Diego-Pérez (2000)
Nachititla, State of Méx.	1550	490	132*	8086	1700->3000	CF, PQF, GF, MCF, QF, SS, XS, PG, Gr, TDF	García-Mendoza et al. (1994)
Nizanda, Oax.	288	208	89	13.2	600-1400	GF, TDF	Zepeda & Velázquez (1999)
	746	458	117*	85	90-500	GF, SS, XS, Sav, TDF, MTF, AV	Pérez-García et al. (2001)

Table 1. Continuation.

Locality	S	G	F	Area (km <sup>2</sup> )	Altitude (m)	Vegetation type	Reference
Nizanda, Oax.	922	554	124	90	90-750	GF, XS, Sv, TDF, MSTF, AV	Pérez-García et al. (2010)
Rincón de la Vía, Gro.	498	327	108	78	700-1800	CF, PQF, QF, Sv, MTF, AV	Verduzco & Rodríguez (1995)
Cuchujaqui River, Son.	736	429	736	46	220-400	GF, QF, SS, TDF, AV	Van Devender et al. (2000)
San Juan, Nay.	1200	506	134*	400	~0-2200	CF, PQF, QF, MCF, Gr, TDF, MTF	Téllez Valdés et al. (1995)
Sian Ka'an, Q. Roo.	850	470	112	5280	0-<50	Sv, TDF, SeTDF, AV	Durán & Olmsted (1987)
Huautla Range, Mor.	629	219	83	593	700-2400	TDF, PF, QF, MTF	Maldonado (1997)
Manantlán Range, Jal.	2774	981	181	1400		CF, GF, Gr, MCF, MTF, PQF, PF, QF, TDF, SF, Sv	Vázquez et al. (1995)
Tehuantepec District, Oax.	1720	776	154	6600	0-1800	CF, QF, GF, MCF, SS, XS, Sv, TDF, AV	Torres-Colin et al. (1997)
Tehuacán-Cuicatlán Valley, Pue.	2703	922	189	10,000	~600-2950	CF, PQF, GF, ScS, XS, Gr, TDF	Dávila Aranda et al. (1993)
Tenabo, Camp.	467	322	94*	882	0-100	Ma, TDF, SeTDF, MTF	Zamora-Crescencio (2003)
Tlayacapan, Mor.	368			8500		PF, TDF	Cerros-Tlatilpa & Espejo- Serna (1998)
Ceboruco Volcano, Nay.	369	207	71	4	?-2164	QF, PF, Gr, TDF	Cedano & Harker (2000)
Zimatán, Oax.	1384	668	144*	713	0-2580	PQF, QF, Sv, MTF, TDF, SLSTF	Salas-Morales et al. (2003)

<sup>1</sup> Includes angiosperms only.

\* Family richness considering all legumes (i.e. Caesalpinaceae, Fabaceae and Mimosaceae) as a single family.

§ Some families of monocots are included in Liliaceae.



Table 2. Main vegetation types occurring in the Mexican seasonally dry tropics, with some equivalent names, mostly in Spanish, and a synthesis of their main features.

Vegetation type	Equivalent names	Main features	References
Tropical dry forest	Selva baja caducifolia, bosque tropical caducifolio, and caatinga, cerradão, miombo (in part)	Dominated by trees, generally < 15 m tall; few emergents; flat crowns. Mostly deciduous; herbaceous and woody climbers common; few epiphytes. Multi-stemmed trees common. Canopy cover usually > 350%; unclear stratification. Columnar cacti frequent in the canopy; many trees with exfoliating and bright-colored bark. Characteristic species: <i>Bursera</i> spp., <i>Jatropha</i> spp. <i>Jacaratia mexicana</i> A.DC., <i>Lysiloma divaricatum</i> (Jacq.) J.F.Macbr., <i>Plumeria rubra</i> L., <i>Pachycereus pecten-aboriginum</i> (A.Berger) Britton et Rose	Miranda & Hernández-X. (1963), Rzedowski (1978), Trejo (1996, 1998, 2005), Pérez-García et al. (2001), Gallardo-Cruz et al. (2005), Durán et al. (2006), Pineda-García et al. (2007)
Sub-tropical scrub	Matorral subtropical	Dominated by small trees, generally < 7 m tall; few emergents, flat crowns. Mostly deciduous, trees sometime spiny. Intermediate position between tropical dry forest (TDF) and pine and pine-oak forest or xerophytic scrub. Characteristic genera: <i>Ipomoea</i> , <i>Bursera</i> , <i>Eysenhardtia</i> , <i>Acacia</i> , <i>Forestiera</i> , <i>Erythrina</i> , <i>Tecoma</i> .	Rzedowski & Calderón (1987)
Thorn woodland	Selva baja espinosa, mezquital	Spiny, low stature tropical forest. It varies from <i>Prosopis</i> -dominated communities to scrub vegetation, which is transitional to semi-arid zones. In these forests, small-leaved, hard-wooded, and deciduous legumes are widespread, particularly <i>Parkinsonia florida</i> (Benth. ex A. Gray) S. Watson, <i>Lysiloma divaricatum</i> (Jacq.) J.F.Macbr., and <i>Prosopis glandulosa</i> Torr.	Miranda & Hernández-X. (1963), Rzedowski (1978), Sánchez-Mejía et al. (2007), Búrquez & Martínez-Yrizar (2010)
Xerophitic scrub	Matorral xerófilo, matorral crasirosulifolio con crasicaules áflos, saxicolous vegetation	Open vegetation growing on rocky localities within the SDT region, usually on limestone outcrops or basaltic rocks. Succulents, cacti, and rupicolous and epiphytic plants are common. Representative genera: <i>Agave</i> , <i>Cyrtopodium</i> , <i>Hechtia</i> , <i>Mammillaria</i> , <i>Pseudosmodingium</i> , <i>Tillandsia</i>	Perez-García et al. (2001, 2007), Pérez-García & Meave (2004).

Table 2. Continuation.

Vegetation type	Equivalent names	Main features	References
Medium-statured tropical dry forest	Selva mediana caducifolia	Canopy 15-30 m tall, more than 75% of individuals are deciduous. Epiphytes less diverse and scarcer than in humid forests. Representative genera: <i>Bursera</i> , <i>Cochlospermum</i> , <i>Cordia</i> , <i>Jacaratia</i> , <i>Lonchocarpus</i> , <i>Pachycereus</i> , <i>Piptadenia</i>	Salas-Morales (2002), Salas-Morales et al. (2003), Salas-Morales & Casariego-Madorell (2010)
Medium-statured tropical moist forest	Selva mediana subperennifolia, selva mediana subcaducifolia, bosque ribereño, gallery forest (in part), semi-evergreen seasonal forest	Canopy 15-30 m tall, > 50% of trees are perennial. Epiphytes less diverse and scarcer than in humid forests. Characteristic species: <i>Brosimum alicastrum</i> Sw., <i>Enterolobium cyclocarpum</i> (Jacq.) Griseb., <i>Ficus insipida</i> Willd., <i>Hymenaea courbaril</i> L., <i>Inga vera</i> Willd., <i>Tabebuia heterophylla</i> (DC.) Britton., <i>Andira inermis</i> (W. Wright) Kunth ex DC., <i>Cynometra oaxacana</i> Brandegee, <i>Licania arborea</i> Seem.	Rzedowski (1978), Lebrija-Tejos (2001), Camacho-Rico et al. (2006)
Gallery forest	Bosque de galería	Canopy 10-25 m tall. Usually evergreen and dominated by few species, such as <i>Astianthus viminalis</i> (Kunth) Baill., <i>Salix humboldtiana</i> Willd. and <i>Licania arborea</i> Seem.	Lebrija-Tejos (2001), Pérez-García et al. (2001)
Savanna	Sabana, vegetación sabanoide, cerrado (sensu stricto), tropical grassland	Dominated by graminoids (Poaceae and Cyperaceae). Driven by climatic and/or edaphic factors; related to recurrent fires. May completely lack trees or harbor some sparse individuals and shrubs. Two major variants: very dry savannas mostly on hilltops with shallow soils, and flooded savannas in flat areas. Characteristic species: <i>Byrsonima crassifolia</i> (L.) Kunth, <i>Crescentia alata</i> Kunth, <i>C. cujete</i> L., <i>Curatella americana</i> L., in some cases with <i>Pinus</i> and <i>Quercus</i> spp.	Miranda (1998), Puig (1972), Rzedowski (1975, 1978), Meave & Kellman (1994), Kellman (1984), Pennington et al. (2000), López-Olmedo et al. (2006, 2007)

Table 2. Continuation.

Vegetation type	Equivalent names	Main features	References
Palm grove	Palmares	Dominated by Areaceae, almost always mono-specific in the upper stratum. Usually on sandy soils with shallow water tables, with <i>Orbignya guacuyule</i> (Liebm. ex Mart.) Hern.-Xol., <i>Sabal guatemalensis</i> Becc., <i>S. mauritiformis</i> (H.Karst.) Griseb. et H. Wendl., and <i>S. mexicana</i> Mart. Additionally, <i>Brahea dulcis</i> (Kunth) Mart and <i>B. nitida</i> André stands are mainly found on drier areas, at 600-2,250 m a.s.l.	Miranda & Hernández-X. (1963), Eiten (1972, 1997), Toledo Rizzini (1997), Torres-Colín (2004), Hągsater et al. (2005)
Tropical oak grove	Encinares tropicales Sabanas con encinos	Physiognomic dominance of <i>Quercus oleoides</i> Schltdl. et Cham. In tropical moist sites with distinctive edaphic conditions, usually along ravines in savanna landscapes. Mid-elevation <i>Quercus</i> stands often forming ecoclines with TDF in mountain ranges.	Pennington & Sarukhán (1998), Hągsater et al. (2005)
Tropical pine grove	Pinares Sabanas con pinos	Very open and discontinuous tree stratum to rather closed canopy, mostly of <i>Pinus oocarpa</i> Schiede ex Schltdl. Understorey dominated by graminoid herbs, with some Asteraceae, Polygalaceae, Scrophulariaceae, and terrestrial orchids ( <i>Bletia</i> ). Sometimes forming ecoclines with TDF on mountains ranges or in lowland areas in the Isthmus of Tehuantepec.	Kellman (1984), Kellman et al. (1994), Hągsater et al. (2005), Correa-Metrio et al. (2012)

Undoubtedly, TDF is the most widely studied vegetation type in Mexico's dry tropics. Available studies encompass a wide array of approaches, ranging from basic floristic and structural analyses (Trejo, 1996; 1998; 2005; Trejo & Dirzo, 2002; Gallardo-Cruz et al., 2005; Pineda-García et al., 2007; see Table 1) to the examination of species spatial patterns (Pérez-García & Meave, 2004; Durán et al., 2006; Padilla-Velarde et al., 2006; Gallardo-Cruz et al., 2009; 2010). Other commonly examined topics are biogeographical relationships (Cué-Bär et al. 2006; Lott & Atkinson, 2006), degree of biological differentiation (Balvanera, 1999; Balvanera et al., 2002; Pérez-García & Meave, 2006), functioning (Martínez-Yrizar et al., 2000; Maass et al., 2005), successional patterns (Burgos & Maass, 2004; Romero-Duque et al., 2007; Lebrija-Trejos et al., 2008; 2010; 2011; Gallardo-Cruz et al., 2012), seed banks (Rico-Gray & García Franco, 1992; Miller, 1999; Maza-Villalobos et al., 2011), or the evolutionary history of its flora (Becerra, 2005).

For several dry tropical regions in Mexico, particularly in mountainous areas, the existence of a sub-tropical scrub has been reported. However, there are doubts whether this is a natural or an anthropogenic community (Rzedowski & Calderón, 1987). In other areas of the country's dry tropics there also are communities dominated by spiny, short trees; they are usually classified as 'spiny low stature tropical forest' or thorn woodland (in part), although they actually form a heterogeneous group as they may be either evergreen or deciduous (Miranda & Hernández-X., 1963). This vegetation type ranges from *Prosopis*-dominated communities (mezquital) to scrub vegetation which is transitional to semi-arid zones (Miranda & Hernández-X., 1963; Challenger, 1998; Sánchez-Mejía et al., 2007). In these forests, small-leaved, hard-wooded, and deciduous leguminous species are widespread, particularly of the genus *Parkinsonia*, *Lysiloma*, and *Prosopis*. Other common genera are *Acacia*, *Amphipterygium*, *Bursera*, *Chloroleucon*, *Croton*, *Jatropha*, and *Tabebuia* (Miranda & Hernández-X., 1963; Sánchez-Mejía et al., 2007). In the Isthmus of Tehuantepec (Oaxaca), a low spiny tropical forest exists with a very characteristic floristic composition (Torres-Colín et al., 1997), although structural data supporting its segregation from the TDF are lacking.

The shrub-dominated vegetation in the dry tropics may be classified as spiny or semi-spiny scrub or thorn woodland -in part- (Rzedowski, 1978; Pennington & Sarukhán, 1998; Pérez-García et al., 2001). However, it is often difficult to distinguish the different low deciduous forests given the gradual variation between these two vegetation types (Trejo, 1996; Pennington & Sarukhán, 1998). This difficulty is particularly strong when attempting to differentiate low spiny deciduous forests from the scrub vegetation in marginal areas (Sánchez-Mejía et al., 2007; Búrquez &

Martínez-Yrizar, 2010). A further type of open vegetation with short-stature plants of the dry tropics is the xerophytic scrub. This community type usually covers small areas, as they are constrained to rocky substrates, e.g. limestone outcrops (Pérez-García & Meave, 2004) or lava fields (Castillo-Campos et al., 2007).

Moist forest or medium-stature tropical forests (canopy height between 15 and 30 m) in dry tropics may be sub-deciduous or semi-evergreen (Miranda & Hernández-X., 1963). Medium deciduous forest was not included in the classification scheme of Miranda & Hernández-X. (1963) apparently because of the very limited distribution of this community type. In areas with a higher or better-distributed rainfall, tall semi-evergreen (> 25 m) or sub-deciduous forests may be found. Medium-stature forests are common in the Pacific Coastal region (Miranda & Hernández-X., 1963; Gallardo, 1996; Peralta-Gómez et al., 2000), as well as in the Atlantic watershed from Hidalgo and Tamaulipas to the Yucatán Peninsula (Ibarra-Manríquez et al., 1995; Martínez & Galindo-Leal, 2002). This vegetation type also covers significant areas of Central America (Janzen & Liesner, 1980). Epiphytes in medium-stature forests are neither as diverse nor as abundant as in humid forests. In Huatulco (Oaxaca), a medium stature deciduous forest was described based on the height and phenology of dominant trees (Salas-Morales, 2002; Salas-Morales et al., 2003; Salas-Morales & Casariego-Madorell, 2010). This forest occurs in areas spanning from sea level to 500 m elevation, and the most frequent families in its canopy are Fabaceae, Euphorbiaceae, Boraginaceae, and Burseraceae. Medium-stature forests often have the largest species richness in the dry tropics because they receive the largest precipitation in the region (Gentry, 1995). Descriptions of medium-stature forests usually include gallery forests (Miranda & Hernández-X., 1963; Pérez-García et al., 2001). These may be highly diverse communities similar to sub-deciduous or semi-evergreen forests, or low diversity communities such as gallery forests (Rzedowski, 1978; Lebrija-Trejos, 2001; Camacho-Rico et al., 2006).

Comparisons of upland vegetation with riparian medium-stature forests have revealed that the latter usually harbors a higher plant species richness (Lott et al., 1987; Gentry, 1995). Typical medium-stature forest genera in riparian vegetation include *Andira*, *Brosimum*, *Cynometra*, *Enterolobium*, *Ficus*, *Hymenaea*, *Inga*, and *Tabebuia*. Riparian communities have gained recognition, mainly because of their potential role as reservoirs of forest species during long dry periods (Kellman et al., 1994; Meave & Kellman, 1994), as biological corridors (Bonesso et al., 2000), and their ability to regulate the hydrological cycle (Lebrija-Trejos, 2001).

Coastal sand dune vegetation, open savannas, and aquatic and halophytic vegetation are examples of typical dry tropics plant communities dominated by small-

sized, generally herbaceous plants (Flores, 1992; Zizumbo & Colunga, 1980; Peralta-Gómez et al., 2000; López-Olmedo et al., 2006; 2007). Palm groves may also be included here, although palms usually reach large heights (Eiten, 1972; 1997; Toledo Rizzini, 1997) (Table 2).

Savannas are plant communities dominated by graminoids (Poaceae and Cyperaceae). These communities occupy vast areas in Africa and South America (Menaut et al., 1995; Eiten, 1997; Furley, 2006), but significant areas with this vegetation type also occur in Australia (Furley, 2006), Mexico, and Central America (Puig, 1972; Meave & Kellman, 1994; López-Olmedo et al., 2006). Climate, soils, and recurrent fires are the main drivers of savanna presence in some regions (Kellman, 1984; Pennington & Sarukhán, 1998; Pennington et al., 2000; Guindão Cruz et al., 2002; Furley, 2006). These communities are not exclusive of the dry tropics since they also occur in more humid climates. In these cases, however, they are associated with oligotrophic soils (Kellman, 1984) or to senescent phases of a limnological development series (Hágsater et al., 2005). In Mexico, this vegetation type is generally related to poorly drained soils, particularly in the Yucatán Peninsula (Miranda & Hernández-X., 1963; Martínez & Galindo-Leal, 2002), although they are also common at sites with rather shallow, well-drained soils (Pennington & Sarukhán, 1998; Pérez-García et al., 2001; López-Olmedo et al., 2006; 2007).

Savannas may completely lack trees or, conversely, they may harbor sparse individual trees and shrubs. In Mexico and Central America, savanna trees often belong to the genera *Pinus* or *Quercus*, leading to their classification as pine or oak open woodland, respectively. Nonetheless, according to Miranda & Hernández-X. (1963), the most common trees in Mesoamerican savannas are *Byrsonima crassifolia* (L.) Kunth (Malpighiaceae), *Crescentia alata* Kunth, *C. cujete* L. (Bignoniaceae), and *Curatella americana* L. (Dilleniaceae).

Despite the ample recognition of the antiquity of savannas worldwide (Eden, 1974; Haffer, 1982), in Mexico and other areas its potential anthropogenic origin has been recurrently discussed (Furley, 2006). For example, Puig (1972) concluded that there is no sufficient evidence to recognize a natural origin for savannas in the southern State of Tabasco. Conversely, López-Olmedo et al. (2007) reported for the savannas of the Isthmus of Tehuantepec the presence of slow-growing plants and a large ensemble of species exclusive of this vegetation type; along with the constancy of their boundaries through time, this finding supports the alternative view that they are a primary vegetation type (López-Olmedo et al., 2007). Moreover, as early as the first half of the 20th century, when human activ-

ity was not yet very intense in the region, the presence of savanna vegetation on the Trans-Isthmian Mountains was reported (Williams, 1939; Goldman, 1951), and paleogeographical and paleozoological data suggest that savannas or analoge grasslands were already present in Mexico since Middle or even Early Tertiary (Rzedowski, 1975). Yet the presence of some grasslands and savanna-like vegetation (*sensu* Rzedowski, 1978) may be the outcome of human activities in several regions in the country.

Palm groves are communities dominated by species of *Arecaceae*, almost always monospecifically, in the upper stratum. Although palm groves are generally recognized as a distinct vegetation type, they are usually associated with the humid tropics and are seldom listed as a typical dry tropics community in Mexico. Additionally, its floristic relevance has been greatly overlooked. In Mexico, palm groves, oak groves and tropical pine groves have been classified together as one type of savanna (Hágsater et al., 2005). In Mexico, palm groves occur along the Pacific coast, from Oaxaca to Sinaloa, frequently on sandy soils with shallow water tables (Miranda & Hernández-X., 1963). At some localities, palm groves of *Sabal mexicana* Mart. and *Brahea dulcis* (Kunth) Mart. are favored by human disturbance through recurrent fires (Miranda & Hernández-X., 1963). Stands of *Brahea dulcis* and *B. nitida* André are mostly found on calcareous soils, at elevations ranging from 600 to 2,250 m a.s.l., and in semi-warm to temperate semi-arid climates (Torres-Colín, 2004).

Tropical oak groves, mostly of *Quercus oleoides* (Fagaceae), are normally associated with typical humid forest climates, but they grow at sites with distinct edaphic conditions (Pennington & Sarukhán, 1998). In southern and western Mexico, tropical oak groves occur intermittently from Nayarit to Oaxaca, frequently adjacent to treeless savannas, low deciduous forests, and medium-stature forests (Pennington & Sarukhán, 1998). These oak-dominated communities are highly fragmented and do not cover large continuous areas (Rzedowski, 1978). Perhaps this has led to their disregard in descriptions of the Mexican dry tropics (e.g. Challenger, 1998). However, they were recently acknowledged as an important vegetation type for the Mexican orchid flora (Hágsater et al., 2005). In the mountains of Mexico's dry tropics gradual transitions between TDF and oak forest are common, and species of both vegetation types may coexist in ecoclines.

Tropical pine groves are characterized by a very open and discontinuous tree stratum, whilst graminoids and numerous shrubs of the *Fabaceae*, *Melastomataceae*, and *Myrtaceae* families dominate the understory. Even though this vegetation type is more typical of humid climates, it is also transitional with TDF, particularly in the lowlands of the Isthmus of Tehuantepec.

## PHYTOGEOGRAPHY OF THE MEXICAN SEASONALLY DRY TROPICS

Notwithstanding the proposal that western Mexico is an area of diversification for plant species of the dry tropics (Rzedowski, 1962; 1991), the limits of this area of endemism apparently extend to the central portion of the Mexican Pacific coast (Lott & Atkinson, 2002). Around 40% of all species in the modern flora of the Chamela-Cuixmala (Jalisco) region are endemic to the dry tropics of the Pacific watershed (Lott, 1993), with 17% of the flora shared with Central America and 36% with South America. It has been suggested that the distribution of part of the TDF flora from this Mexican region expanded southwards, in exactly the opposite direction that supposedly followed the Amazonian flora along the Atlantic watershed. Given the uncertainty around these distribution models, the floristic links of the typical TDF requires further analysis (Lott & Atkinson, 2002; 2006).

At smaller geographical scales, biogeographical patterns in the dry tropics are also complex; for example, a preliminary phytogeographical analysis of the savanna flora in the Nizanda region (Oaxaca), showed that species of this vegetation type have stronger affinities with the Pacific watershed than with the Atlantic watershed. For the same locality, it was found that the xerophytic vegetation, gallery forest and secondary vegetation have larger similarities with localities in semi-arid areas, such as the Tolantongo Gorge and the Tehuacán-Cuicatlán Valley in central Mexico. This finding is similar to that reported by Acosta-Castellanos (1992) for the vegetation of the upper Tehuantepec River basin, as he identified the strongest floristic similarity of his study area with the Tehuacán-Cuicatlán Valley (Puebla-Oaxaca). Thus, the hypothesis that a much more extended arid region existed in the past that encompassed the Balsas river basin and the Tehuacán-Cuicatlán Valley, south to the Tehuantepec river basin, is further supported (González-Medrano & Chiang, 1988; Acosta-Castellanos, 1992; 1995; Acosta et al., 2003). In contrast, Lebrija-Trejos (2001) reported stronger affinities between the riparian vegetation of Nizanda and the Atlantic humid forests, which may be due to the fact that many species in his study system are riparian habitat specialists adapted to frequent flooding, or at least to permanently high water availability.

Pine savannas provide a different example of the complex biogeographical and ecological relationships for the dry tropics flora (Correa-Metrio et al., 2012). Pines have a clear Holarctic origin, whilst the floristic elements of the understorey supposedly have Neotropical affinities. Interestingly, for a specific plant group such as the orchids the ambiguity holds, given that the orchid flora of these pine savannas is more similar to the tropical oak groves and the sub-deciduous medium-



stature forests surrounding them (Hágsater et al., 2005). Other epiphytic components of the *Pinus-Quercus* savannas, like some *Tillandsia* species, are also considered Neotropical taxa. Under the traditional biogeographical classification of Mexico, the canopy of these savannas may be seen as an example of the mixture of Nearctic and Neotropical plants, though some epiphytes are nearly pine-specific (e.g. *Mormodes lineata* Bateman ex Lindl. [Orchideaceae]).

## ORIGIN OF THE MEXICAN SEASONALLY DRY TROPICAL FLORA

Given the location of the Mexican territory on the North American tectonic plate, its biota may be reasonably associated with that of the Nearctic Realm, or more broadly, to the Holarctic Realm (sensu Cox, 2001). Despite this basic geographical principle, the floras of the tropical, subtropical and arid climates of the country have been often related to the Neotropical Realm (Rzedowski, 1991). This broad phytogeographical dichotomy of the country's territory is widely accepted, as exemplified by the prevailing dogma which states that "Mexico is a floristically megadiverse country due (among other causes, such as a highly heterogeneous territory, both climatically and geomorphologically, as well as high speciation rates) to the fact that it is a contact zone between the Nearctic and Neotropical Realms". Although the basic tenets of this statement are unquestionable (the large richness and the biogeographical contact), this idea also seems to be an oversimplification of a history that is actually much more complex. A clear understanding of the origin and evolution of the Mexican flora is still lacking.

The study of plant palaeo-communities, including both xeric and mesic systems, has shown the role of geomorphology as a driver of various biological processes (Cevallos-Ferriz & González-Torres, 2005; Castañeda-Posadas & Cevallos-Ferriz, 2007). For example, temporal patterns of formation, origin and constituent elements are different between the country's two large Sierras Madre (Eastern and Western), and understanding their history is essential if we are to fully comprehend the biogeography of the modern flora.

The Mexican territory and its geologic history are particularly complex. This problem is evidenced by discussions over the origins of the ancestors of the taxa occurring in this country (Diego-Pérez, 2000; Diego-Pérez et al., 1996/97). Floristic assemblages of Mexico's tropical regions display floristic affinities with Central and South America (Rzedowski, 1991), and to a lesser extent with the remaining of North America and the Caribbean region (Diego-Pérez et al., 1996/97; Wendt, 1993;

Burnham & Graham, 1999). In fact, with the exception of Oceania, the modern flora of Mexico shows relationships with the floras of all other continents where vascular plants are found (Cevallos-Ferriz & Ramírez, 2004).

The complexity of the biogeographical identities increases when incorporating the temporal scale. This exercise has resulted in a plethora of proposals for the origin of the Mexican tropical flora including Boreotropical, Austrotropical, Arcto-Tertiary, Madro-Tertiary, Gondwanan, Laurasian, Neotropical-Tertiary and Neogene-North American (Axelrod, 1950a; 1950b; 1975; 1979; Rzedowski, 1970; Wolfe, 1975; Wendt, 1993; Cevallos-Ferriz & Ramírez, 2004; Calvillo-Canadell & Cevallos-Ferriz, 2005). Also, diverse relationships with the modern flora have been proposed, including both with the Holarctic and the Neotropical floras, and to a lesser extent with the Pantropical Realm (Rzedowski, 1962; 1970; 1978; 1991; Chiappy-Jhones et al., 2001). In addition, the presence of palaeo- and neo-endemic Mexican components (Rzedowski, 1991; Rzedowski & Palacios-Chávez, 1977; Soto & Salazar, 2004; Cevallos-Ferriz & Ramírez, 2004) makes it more difficult to establish floristic relationships with other regions of the world.

Disentangling the history of the biogeographical relationships of the Mexican flora is still a challenge, and all proposed models lack full testability to date. The fossil record, albeit incomplete, is the only evidence capable of showing directly which plants grew in Mexico, and sedimentology and taphonomy may help reconstruct the environments in which they lived. With a perspective that integrates geological time, several aspects of the history of Mexican vegetation may be applicable to this country's dry tropics (Calvillo-Canadell & Cevallos-Ferriz, 2005; Castañeda-Posadas & Cevallos-Ferriz, 2007). Among the most striking ones is the finding that some of the genera occurring in the Mexican dry tropics at present occurred in North America since at least 65 million years before present (Ma b.p.).

Oligocene fossil plants from Tepexi de Rodríguez (Puebla) suggest that 30 Ma b.p. a community analogous to modern TDF (or maybe some kind of chaparral) existed in this locality (Ramírez & Cevallos-Ferriz, 2002; Beraldi-Campesi et al., 2005). The species present in this community may have derived from species of tropical humid forests of Eocene age that occurred at higher latitudes (Cevallos-Ferriz & Ramírez, 2004). During the Miocene (ca. 23.5-5.3 Ma b.p.), the tropical humid forest from the El Cien formation (ca. 20 Ma b.p.), Baja California Sur, apparently formed a belt of this vegetation type along the old coastline. As a consequence of volcanic and tectonic activity during the Oligocene-Miocene, new areas of rain shadow appeared, and tropical sub-humid communities replaced the moist vegetation (Castañeda-Posadas & Cevallos-Ferriz, 2007).

Lineages that are present in the various modern communities typical of dry tropics occurred in tropical wet and moist floras since at least some 20 Ma b.p., but this does not imply that modern vegetation types existed through all this time. For example, the floristic composition for the El Cien formation is thought to have been very similar to the recent TDF of Chamela, Jalisco, with the Miocene plants having a larger physiologic ability to transport water, and the Miocene dry season, if there was any, being much shorter (Martínez-Cabrera et al., 2006). Some plant species from the El Cien formation display affinities with western Africa and eastern Brazil (*Copaifera*), whilst other taxa (e.g. *Tapirira*) occurring today in the Isthmus of Tehuantepec have affinities with northern South America (Cevallos-Ferriz & Barajas-Morales, 1994). From this information we can conclude that plants presently considered typical of Neotropical communities, such as *Andira*, *Ficus*, *Maclura*, and *Tetragastroxylon*, grew in Mexico at least since some ca. 20 Ma (Martínez-Cabrera et al., 2006).

Angiosperms made their evolutionary appearance at 167-199 Ma b.p. at the end of Jurassic (Bell et al., 2010), and underwent important diversification and radiation processes during the Cretaceous (Sims et al., 1999; Magallón & Sanderson, 2005), particularly ca. 102-130 Ma b.p. (Barremian-Uppermost Albian, Lower Cretaceous; Magallón & Castillo, 2009). In the Late Cretaceous, two distinctive floristic provinces existed in the Northern Hemisphere. One of them included eastern North America and Europe (Normapolles flora), whereas the other comprised most of Asia and western North America (Aquilapollenites flora; Raven, 1975; Wolfe, 1975). For Mexico, a third province was identified for the same period, namely the Monocolpates province, which was established in the southern part of the country (Martínez-Hernández & Ramírez-Arriaga, 1996). Palynological information demonstrates that the Mexican territory has an ancient influence of Laurasian elements, but with an important presence of Gondwanan plant groups like *Afropollis*, *Proxapertites* and *Nothofagidites* since Late Cretaceous (Martínez-Hernández & Ramírez-Arriaga, 1996).

One of the first alternative explanations for the presence of a Mexican tropical flora showing biogeographic relationships with several parts of the world is centered on the Geoflora hypothesis (Chaney, 1959). The basis for this hypothesis was the notion of a flora distributed around the Arctic Ocean that later began to migrate southwards as a whole, known as the Arcto-Tertiary flora (Axelrod, 1975; Wolfe, 1975; Tiffney, 1985a,b). The concept was later expanded, giving way to the notions of Neotropical Tertiary Geoflora and Madro-Tertiary Geoflora. Apparently, however, the fossil record has not supported any of the proposed migration routes (Tiffney, 1985b).

A second hypothesis states that during the Paleogene (ca. 65-23 Ma b.p.) the world's tropical flora was partitioned between the Northern and Southern Hemispheres, that is, a Boreotropical Realm versus an Austrotropical Realm (Wolfe, 1975; Tiffney, 1985a,b). The Boreotropical flora may have colonized and radiated within the emerging Mexican territory (Cevallos-Ferriz & González-Torres, 2005; Calvillo-Canadell & Cevallos-Ferriz, 2005). The expansion model for the Boreotropical flora assumes migrations along the coast of the Tethys Sea and later along the North Atlantic Ocean, or else across the Bering land-bridge, when the climate in North America was warmer than today (Wolfe, 1975; Tiffney, 1985b). The Boreotropical flora hypothesis seems to offer a better explanation for the strong floristic relationships between eastern North America (including Mexico) and eastern Asia (Tiffney, 1985b; Smedmark & Anderberg, 2007). Further, this hypothesis does not conceive the flora as a fixed, unchangeable entity; rather, it recognizes that its composition varies depending on its geographical coordinates, and that species migrate across the territory at different rates and through different routes. In addition to the fossil record, the proposed migration of the Boreotropical flora has been supported by biogeographical analyses for several taxonomic groups, such as amphibians, reptiles, spiders, bees, beetles and other invertebrates, as well as for modern plants (Lavin & Luckow, 1993; Smedmark & Anderberg, 2007).

At present the largest differences in tropical vegetation and floras occur between the Paleotropics and the Neotropics (Wolfe, 1975). Despite the striking ecological and geological similarities between Africa and South America (Wolfe, 1975), a clear differentiation between the floras of these two continents has long existed (Burnham & Graham, 1999). There is an almost passionate controversy as to whether the flora of Mexico came from the north, either from the North American Eocene floras that are part of the Boreotropical flora (Wolfe, 1975; Tiffney, 1985a; Wendt, 1993; Cevallos-Ferriz & Ramírez, 2004), or from Central- and South America (Rzedoswki, 1991). This controversy is further complicated by the fact that to any given flora having a single biogeographical origin several dispersal routes may be attributed. For example, Gondwanan plants are likely to have arrived to Mexico via South America or via Africa-Europe-North America (Wendt, 1993). The controversy on the origin of the tropical Mexican flora makes much sense because of the geographical proximity of Mexico to Central and South America, and given the similarities between modern biotas present in these regions. Nonetheless, the fossil record suggests that the flora of Mexico is much older than previously thought (Tiffney, 1985a; Cevallos-Ferriz & Ramírez, 2004; Calvillo-Canadell & Cevallos-Ferriz, 2005). For the case of Mexico it is true that fossil plants related to

Southern Hemisphere lineages have been identified, but the oldest records for these plants suggest that their origin was rather in Mexico and that they dispersed from this country into South America (Cevallos-Ferriz & Ramírez, 2004). Thus, based on direct evidence we now know that at least some elements of the flora (e.g., *Andira*, *Copaifera*, *Hymenaea*, *Inga*, *Pithecellobium* [Leguminosae], *Tetragastroxylon* [Burseraceae], *Haplorhus*, *Loxopterigium*, *Tapirira* [Anacardiaceae], and *Ficus*, *Maclura* [Moraceae]), traditionally linked to the Mexican Neotropical biomes, occurred in Mexico much before than originally thought, to the point that it is necessary to conclude that these 'Neotropical' components became part of the tropical flora via the Northern Hemisphere rather than via the Southern Hemisphere (Calvillo-Canadell & Cevallos-Ferriz, 2005).

According to Lavin & Luckow (1993), the Boreotropical origin hypothesis for the tropical North American flora (including Mexico) has a testable prediction: any taxon having its diversification center in Mesoamerica and being represented in the fossil record in the region since the Tertiary, should have its sister groups in the Old World tropics, whereas the derived groups should occur in South America. After testing this prediction through a molecular phylogenetic analysis for two modern groups of legumes, these authors obtained results consistent with the Boreotropical hypothesis. Similarly, in Mexico there are several taxa thought to be ancestral of groups that radiated later in South America (Rzedowski, 1991), with examples provided by species of Burseraceae (Becerra, 2003; Dick & Wright, 2005; Weeks et al., 2005), Orchidaceae (Cox et al., 1997; Van den Berg et al., 2000; Soto & Salazar, 2004; Hágsater et al., 2005), Anacardiaceae, Berberidaceae, Cactaceae, parts of Moraceae and Asteraceae (Cevallos-Ferriz & Ramírez, 2004; Edwards & Donoghue, 2006), as well as for *Leucaena* and *Ateleia* (Leguminosae, Pennington et al., 2006a).

Based on new fossil record, it has been proposed that Burseraceae made its first appearance in North America since the Late Paleocene/Early Eocene (Becerra et al., 2012), and that by the beginning of the Late Oligocene (23 Ma b.p.) this family dispersed into other parts of the World (Weeks et al., 2005; Dick & Wright, 2005). Weeks et al. (2005) suggested that *Beiselia mexicana* Forman, the only representative of this monotypic genus and discovered recently in the TDF of western Mexico, diverged early within the family, and that its sister clades presently occur both in America and the Old World tropics. Based on the taxa used by these authors, the positions occupied by modern Mexican species indicate an early separation, both in *Bursera* and in *Protium*, whilst South American and African groups are less differentiated from each other; Weeks et al. (2005) go as far as proposing that *Commiphora* is a subgroup derived from *Bursera*. Similarly, there is evidence that the genus *Bursera*

has undergone an intense diversification in Mexico for over 50-57.1 Ma (Becerra, 2005; Becerra et al., 2012), and that its sister groups are basically African (the genera *Commiphora* and *Boswellia*), with the exception of the South American species, *Commiphora leptophloeos* (Mart.) J.B. Gillett (Becerra, 2003), and a new species from limestone outcrops in Central Brazil (A.C. Sevilha, pers. comm.; Weeks et al., 2005). For these two species, the possibility of long-term dispersal has received wider acceptance (Weeks et al., 2005). In addition, based on molecular information, Becerra et al. (2012) established links between the orogeny in Mexico, the radiation of the genus *Bursera* and the possible origin of tropical dry forest in the country, placing the origin of this vegetation type some 30 to 37 Ma b.p. In fact, it has been proposed that ca. 50 Ma b.p., at the end of the Early Eocene, the New World experimented changes that promoted seasonality as less water evaporated from the sea, causing a reduction of the range of the wet tropical vegetation (Graham, 2011).

Much information related to the Orchidaceae family supports the presence of very old orchid lineages in Mesoamerica. For example, Mesoamerica and the Caribbean are thought to be the centers of origin of Laelinae and Pleurothallidinae. Particularly for Laelinae (a subtribe comprising 43 genera and 1,466 species), it has been proposed that the basal lineages of numerous taxa occur in Mexico, whereas the most derived groups are present in South America (Van den Berg et al., 2000). This pattern was observed for several groups in this family, such as *Arpophyllum*, *Bletia*, *Chysis*, *Coelia*, *Hexalectris*, *Isochillus* and *Ponera*, and for one of the oldest groups in Orchidaceae, namely the subtribe Cyripedioideae. The oldest groups of this subtribe with a distichous phyllotaxy (e.g. *Mexipedium* and *Selenipedium*) occur in Mesoamerica, and the range of one of the oldest species in the entire subtribe, *Cyripedium irapeanum* La Llave et Lex., is currently restricted to Mexico (Cox et al., 1997). As far as the understanding of the group's biogeography goes, the idea of a Boreotropical flora widely distributed in the Northern Hemisphere during the Palaeogene and Early Neogene is again central. Later on, the contraction of its geographical range in the continent would result from the widespread impact of Pleistocene climatic changes (Cox et al., 1997; Wendt, 1993).

The information examined so far provides stronger support to the hypothesis of a Boreotropical origin for the Mexican flora than to alternative Geofloras hypotheses (Lavin & Luckow, 1993), particularly than to the one claiming a recent migration from South America (Pennington et al., 2006a). Therefore, one may reasonably assume that part of the ancestral Mexican flora expanded southwards, also into the Antilles, where it diversified and persisted to present day, conferring a distinctive character to the American tropical regions (Cox, 2001). The Boreotropical hypoth-

esis is also compatible with the presence of antique taxa in the Antilles (Santiago-Valentin & Olmstead, 2004) and with the large generic similarity between western Mexico and Cuba (Borhidi, 1996; Diego-Pérez et al., 1996/97).

More phylogenies of Mexican species and their sister groups occurring beyond the country's borders are needed in order to determine the ultimate sources and relative ages of the components of this diverse biota (Lavin & Luckow, 1993; Cevallos-Ferriz & Ramírez, 2004; Calvillo-Canadell & Cevallos-Ferriz, 2005). Of course, one must not overlook the possibility that Mexico has functioned as a zone of biogeographical contact for a long time, and not only after the recent establishment of the Central American landbridge (Pennington et al., 2006a). It is likely that since the Early Eocene, migrations from the Southern Hemisphere had provided a 'recent Neotropical' character to the vegetation of the Mexican tropics (Graham, 1993; Wendt, 1993), in particular to the wet tropics since the Pliocene. The palaeopalynological records from Central and South America suggest that tropical elements from the Neotropical Realm arrived in Mexico from the Miocene onwards (Burnham & Graham, 1999). If this is true, it would be necessary to quantify better the relative contribution of each biogeographic component to the Mexican flora, as well as its timing.

A panbiogeographic study of genera of the Euphorbiaceae family suggested a Gondwanan origin, with a later Neotropical radiation (Martínez-Gordillo & Morrone, 2005). Besides, for Mexican and Central American species of *Ruprechtia* (Polygonaceae), robinoid legumes, *Chaetocalyx* and *Nissolia* (Fabaceae), and *Loxopterygium* (Anacardiaceae), an important diversification process took place both during and before the Pleistocene from taxa with previous (Mid-Miocene to Pliocene) existence in South America (Pennington et al., 2004; Lavin, 2006). Moreover, it has been proposed that the Bromeliaceae family probably originated in the Guiana Shield ca. 100 Ma b.p. (Givnish et al., 2011).

Contradictory information has been published about migration routes for some taxonomic groups; for example, Melastomataceae are thought to have originated in North America (Early Eocene fossils from Dakota) and to have dispersed later into Central and South America (Oligocene), and subsequently to Africa and Asia (12 to 14 Ma b.p.; Renner et al., 2001). However, the almost exactly opposite pattern for this family was proposed by Morley & Dick (2003), who contend that Melastomataceae has a Gondwanan origin, and that this family should have dispersed into North America through Central America a long time ago.

The evidence examined so far suggests that the origin of the Mexican tropical flora, as we know it today, began in the Upper Cretaceous and that some elements tra-

ditionally considered Neotropical were already in the country at that time. Although the full explanation of how they arrived in Mexico that long ago remains a challenge, the Boreotropical flora hypothesis faces this problem reasonably well. Apparently, radiation, speciation and diversification processes were very active in Mexico during Cenozoic due to a fragmented topography caused by active geological evolution that continues to date (Cevallos-Ferriz & González-Torres, 2005; Calvillo-Canadell & Cevallos-Ferriz, 2005).

#### THE IMPORTANCE OF SEASONALLY DRY TROPICS IN THE MAINTENANCE AND DIVERSIFICATION OF THE XEROPHYTIC FLORA

North American deserts are relatively recent in geological time (Briones, 1994), according to their suggested age of ca. 8 Ma b.p. (Van Devender, 2000). Much of the Mexican territory presently occupied by deserts was mountain-free until relatively recent times (Ferrusquía-Villafranca, 1993; Cevallos-Ferriz & Ramírez, 2004; Cevallos-Ferriz & González-Torres, 2005). For example, heights at the Sierra Madre Occidental peaked between 38 and 20 Ma b.p. (Ferrari et al., 2005), and maximum elevation in the Sierra Madre Oriental occurred roughly at the same time, that is ca. 28.4-37.2 Ma b.p. (Upper Eocene to Lower Oligocene; Eguiluz de Antuñano et al., 2000). Before the Upper Paleocene (ca. 55.8 to 58.7 Ma b.p.), there were nearly no emerged lands in the southern part of the North American tectonic plate. Consequently, there were no strong biological connections between North and South America, despite the existence of archipelagos that could have served as stepping stones (Santiago-Valentin & Olmstead, 2004), creating a weak link between these two continental land masses, particularly for animals (Pennington et al., 2006b).

It has been repeatedly pointed out that the fossil record supports the idea of an evolutionary route for Mexican vegetation starting from the tropical wet, through the tropical sub-humid, to the xerophytic vegetation (Rzedowski, 1978; 1991; Cevallos-Ferriz & Ramírez, 2004). Also, the cores of the ranges of those species that are shared between TDF and the deserts of northern Mexico suggest that the latter systems derived from the dry forests (Lott & Atkinson, 2002), despite the large diversity of Mexican deserts and their high level of endemism both at the genus and family levels (Rzedowski, 1962; Lavin et al., 2003).

In Mexico, topographically rocky systems (e.g. outcrops, karst terrain, lava fields) where xerophytic communities thrive are common, though they are quite dis-



tant from the core of Mexico's large arid and semiarid regions. Such xerophytic communities are often patchily distributed within a matrix of mesophytic vegetation. Consequently, these communities have been referred to as 'xerophytic vegetation enclaves' (Pérez-García & Meave, 2004). Edaphic aridity imposes similar constraints on plants as those derived from desert climates, which leads to ecological similarities between these environments. González-Medrano (1996) suggested that an important step in the colonization of arid zones was the previous adaptation in island-like xerophytic environments, particularly in rocky habitats with limestone and basaltic substrates.

The vegetation of rocky environments is very heterogeneous regarding species richness. For example, 66 species of vascular plants occur in such habitats in Ivory Coast (Porembski et al., 1996), 86 in Rio de Janeiro, Brazil (Meirelles et al., 1999), between 100 and 200 in Córdoba Province, Argentina (Cabido et al., 1990), 232 in Serra dos Carajas, Brazil (Silva et al., 1996), ca. 538 in the Pedregal (lavafield) of San Ángel, Mexico (Rzedowski, 1954), and 614 in southern Venezuela (Groeger & Barthlott, 1996). Although some of these systems harbor relatively few species, they commonly contain a large number of endemic taxa (Porembski et al., 1994; González-Medrano, 1996; Groeger & Barthlott, 1996; Silva et al., 1996; Porembski, 1996; Palvetic & Trinajstić, 1997; González-Medrano & Hernández Mejía, 1998; Porembski et al., 1998; Danin, 1999; Meirelles et al., 1999). In some places the presence of paleo-endemics is notorious (Soto et al., 1990; Porembski et al., 1994; Fleischmann et al., 1996). For example, in dry areas of Cuba, the largest species richness and densities are concentrated in the *mogotes* or limestone outcrops (Borhidi, 1996).

Habitat islands may be relicts of formerly more widespread communities that underwent spatial contraction because of climate changes, as suggested for some montane (Rzedowski & Palacios-Chávez, 1977; Danin, 1999; Watson & Peterson, 1999) and lowland communities (Eden, 1974; Meave & Kellman, 1994). In this context, plant communities that develop on rock outcrops generally represent habitat islands which differ considerably from their biological surroundings, both in terms of their floristic composition and their physiognomy (Porembski et al., 1997). These habitats are characterized by thin and discontinuous soils (Silva et al., 1996), associated to a low water retention capacity and low fertility (Groeger & Barthlott, 1996; Porembski et al., 1996; Porembski et al., 1998; Szarzynski, 2000). A distinctive feature of such vegetation is the prevalence of herbs over trees, among which monocots are noteworthy (Porembski et al., 1998). In turn, and depending on the specific location, abundance of succulent and poikilohydric plants is very variable (Porembski, 1996; Porembski et al., 1995). A remarkable feature common to most rocky systems is their

relative stability through time (Porembski et al., 1998; Burke, 2003), and therefore characterizing these systems as successional is unjustified (Ehrendorfer, 1962).

A related example includes those plants thriving on karstic terrains. Frequently, these habitats harbor endemic plants (Borhidi, 1996; Pérez-García & Meave, 2004), for example *Beaucarnea sanctomariana* L. Hernández in Los Chimalapas (Hernández-Sandoval, 2001), and *Agave guiengola* Gentry on Mt. Guiengola (Torres-Colín, 1989), both of them being endemic taxa to the Isthmus of Tehuantepec, Oaxaca. The presence of the palaeoendemic *Mexipedium xerophyticum* (Soto Arenas, Salazar et Hågsater) V.A. Albert et M.W. Chase (Orchidaceae; Soto et al., 1990) at Los Chimalapas region suggests that at least some elements of the karstic flora are very old, as this species diverged from its sister group, the Asiatic genus *Paphiopedillum*, at 16.4 to 23 Ma b.p. (Albert, 1994). The degree of endemism and the taxonomic composition of the xerophytic vegetation typical of limestone outcrops suggest that they represent relict communities embedded within a mesophytic environment (Pérez-García et al., 2001).

The existence of arid environments within mesophytic ecosystems in Mexico is documented in the fossil record. For instance, at Los Ahuehuetes, near the fossiliferous locality of Tepexi de Rodríguez (Puebla), volcanic ash and associated sandstones formed soils with low water retention capacity, resulting in edaphic aridity. Moreover, the hydrographic conditions at this locality changed drastically, including the disappearance of rivers and lakes, an indication that the region became drier. Such environmental development is likely to have selected against taxa that presumably derived from tropical humid vegetation, giving way to a tropical sub-humid type represented by the fossils studied to date (Ramírez & Cevallos-Ferriz, 2002; Cevallos-Ferriz & Ramírez, 2004; Calvillo-Canadell & Cevallos-Ferriz, 2005). Similarly, it was recently shown how vegetation could have evolved in Panotla (Tlaxcala), central Mexico, from the Miocene to the present, changing from a tropical rain forest to the modern grasslands that characterize the area. Apparently, these changes are also intimately linked to processes of edaphic aridity and changes in the region's hydrologic regime, all because of the limited capacity of volcanic soils to retain water (Castañeda-Posadas et al., 2009).

There is reliable information that during glaciation events in the Late Pleistocene a large proportion of the territories presently corresponding to the Chihuahuan and Sonoran deserts were covered by oak or juniper forests, which thrived in a dry but temperate climate (Bryant, 1974; Wells, 1977; Valiente-Banuet, 1995; Van Devender, 2000; Van Devender et al., 2000). Similarly, based on the first fossil record of a giant anteater (*Myrmecophaga tridactyla*) for North America (dating from Early

Pleistocene), it may be inferred that at that time savannas occurred along the coast of the Gulf of California (Webb & Rancy, 1996). This is interesting because recurrent fires characterize this vegetation type, a feature that is incompatible with the most representative xerophytic forms typical of Mexican deserts (succulents, leafless crassicauls, spiny succulent rosettes, etc.). Although it is likely that in this region xerophytic plants existed, to the best of our knowledge there are no fossil records older than 10,000 years for the most xerophilous species, such as *Larrea*, *Fouquieria*, and *Hechtia* (Wells, 1977; Schultheis & Baldwin, 1999).

Pleistocene refugia have been proposed as a maintenance mechanism for xerophytic vegetation. According to Wells (1977), such refugia should have the following features: (a) a location at tropical latitudes; (b) protection from the effects of polar air masses; and (c) present regional or local aridity. These three prerequisites are met in the southernmost regions of the Chihuahuan desert, such as the Estórax river basin (Querétaro), the Mezquitlán Gorge (Hidalgo) and the Tehuacán-Cuicatlán Valley (Puebla-Oaxaca). The high biological richness and degree of endemism at these sites support this idea; however, this Pleistocene refuge model may suffer from similar criticisms as those expressed against the tropical moist forest refuges (Amarin, 1989; Meave & Kellman, 1994; Meave, 2001; Jaramillo et al., 2006). Many plants endemic to the North American deserts are absent from the southernmost deserts, which are allegedly refuge areas. Yet the largest problem continues to be that a Pleistocene (or even a slightly older) age for these refuges would be insufficient to explain the intense radiation of the Mexican xerophytic flora. Moreover, this hypothesis fails to explain the routes and modes of plant colonization between North and South America.

Hypotheses concerning patterns of morphological evolution for Cactaceae have been proposed based on *Pereskia*, a genus displaying some of the most plesiomorphic traits in the family. Apparently, *P. lychnidiflora* diverged earlier than other species of this genus and of the family in general (Edwards & Donoghue, 2006). In a comparative study of morpho-architectonic and distributional patterns of Cactaceae in a dry tropical landscape of southern Mexico (where *P. lychnidiflora* and other 18 cactus species occur), spatial patterns of vegetative characters matched the family's molecular phylogeny, and those plants having the most derived traits grew on limestone outcrops, the most xerophytic habitats in the region (Tovar-Romero, 2005).

It is surprising that rupicolous vegetation has received so little attention despite its large biological importance (Meirelles et al., 1999; Burke, 2003); however, it was recently suggested that these communities occur in habitats that are analogous to those where the process of adaptation to xerophytic conditions may have arisen

(Pérez-García & Meave, 2004). It is assumed that these habitats host plants whose ancestors occupy a basal position in the phylogeny of their respective groups, thus some systematists argue that the taxa diverged long ago, and the rupicolous floras are relict communities. Furthermore, the high degree of plant endemism in these habitats suggests that some taxa have maintained their individuality for a very long time.

## THE PAN-AMERICAN BIOGEOGRAPHICAL REALM

In tropical dry regions, the precipitation regime is highly seasonal and there is a considerable diversity of plant communities. Such variation in composition, phenology, and structure is reflected in the existence of many vegetation types whose floristic elements display a large variation in their morphology and physiology. With some exceptions, soil fertility is high in these environments, and water is the most limiting factor (Pennington et al., 2006a). Plants respond to the variation in water availability with the same intensity along a climatic gradient within a large region and within a single landscape. The complex responses of vegetation to environmental heterogeneity are central in understanding the high species diversity that characterizes the dry tropics, especially by allowing the coexistence of species typical of moist habitats with those clearly adapted to xeric conditions.

The presence of fire or highly specific soil characteristics such as low fertility, in some portions of this climatic region has led to the development of savanna-like communities, with very unique floristic components. Typical TDF trees and succulent plants are fire intolerant, so that the presence of these plants suggests that TDF is not subjected to much fire disturbance. In fact, this vegetation type might well be much more locally persistent than other vegetation types. The spiny low stature tropical forest, perhaps a marginal variety of TDF, as well as plant communities on rocky outcrops, share many taxa with deserts, and the ancestors of the highly diverse modern desert plants are likely to have first evolved in this types of communities.

Graham (2011) suggested that the study of modern communities that are adjacent or close to each other in space is useful for understanding how different plant communities have replaced each other through time. The intermediate position of the dry tropics between humid and arid ecosystems (Trejo, 1996) bestows upon it a large biological value, particularly from a biogeographical perspective (Pennington et al., 2000). Additionally, this ecosystem boasts an important endemic component, which gives the TDF vegetation an identity in its own right. Both the fossil record

(Cevallos-Ferriz & González-Torres, 2005) and the molecular evidence point to the antiquity of the history of Mexican dry tropical vegetation (> 20 Ma b.p.; Becerra, 2003; 2005; Weeks et al., 2005). There is a relative consensus that the tropical floras from the Cenozoic that occurred at higher latitudes of North America (where this vegetation is lacking at present) may be important precursors of the Mexican tropical biota. Its marginal character and relative isolation (given the peninsular position of the Mexican territory on the North American plate) may have caused Mexico to act as a refuge for the Boreotropical flora, but also as an ecological island, while permitting an active differentiation process in its flora (Cevallos-Ferriz & González-Torres, 2005). Based on these considerations, we conclude that treating TDF as a plant community that has a prominent South American component is not warranted, and thus this plant formation cannot be considered as being part of the Neotropical Realm.

The floristic similarities between TDF and the typical vegetation of the arid regions of Mexico and southern United States, along with the different forms of transitional vegetation between them, lead to the idea that the xerophytic vegetation of the hot North American deserts shares a common biogeographical origin with TDF (Van Devender, 2000), although the latter seems to have an older origin. Many representative plant species of the hot North American deserts have been traditionally associated with the Neotropical Realm, including the genera *Agave*, *Hechtia*, *Larrea*, *Opuntia*, *Prosopis*, and others that are more typical of the Mexican TDF like *Bursera*, *Fouquieria*, and *Pachycereus*. Therefore, and in agreement with Rzedowski (1978), we argue that the biogeographical classification of the TDF and the hot North American deserts (Sonoran, Chihuahuan and Mohave) as belonging to two different biogeographical realms does not make sense, at least from a floristic perspective. Besides, the prevalence of Agavaceae and Cactaceae in these deserts is inconsistent with a true Gondwanan origin, as these families are quasi-endemic to the Americas. Likewise, the Fabaceae component of these deserts does not match the Gondwanan origin hypothesis (Doyle & Luckow, 2003). In particular, apparently Agavaceae originated in North America ca. 20-26 Ma b.p., and *Yucca* seems to be one of the basal clades of this family (Good-Avila et al., 2006).

If TDF is not Neotropical, and the North American hot deserts are not Nearctic, what are they? There is no easy answer to this question, as the elements comprised in each of these two floras could have its own, different geographical origin, and if they originated outside of this region, they could have migrated into it at different times. In our view, the distinction between the Nearctic and the Neotropical floristic Realms needs to be revised in the light of a historical biogeographical perspective.

The evolutionary history of the seasonally dry tropical flora of Mexico strongly suggests that the traditional Neotropical vs. Nearctic biogeographical dichotomy should be replaced by the recognition of the existence of a Pan-American Realm.

A Pan-American Realm would result from the merging of two previously recognized and widely accepted realms, and thus its high-ranking position is warranted. Moreover, this biogeographical realm as a natural entity is strongly supported by the existence of numerous endemic taxa, particularly of higher rank. In the case of plants, well-known examples of such Pan-American endemic or nearly endemic higher taxa are Agavaceae, Bromeliaceae, Cactaceae, Cannaceae, Crossosomataceae, Heliconiaceae, Fouquieriaceae, Limnanthaceae, and Simmondsiaceae. Notable endemic animal taxa include Ramphastidae, Tinamidae, Trochilidae and Troglodytidae among birds, as well as the mammalian groups Didelphidae, the Platyrrhini monkey families, and the superorder Xenarthra (Edentata). Further examples of animal Pan-American endemics are *Agkistrodon*, *Crotalus*, *Bothrops*, and other snake genera in the Viperidae family, as well as the Phrynosomatidae family and the Liolaeminae subfamily of lizards.

We suspect that the term ‘tropical’ within the word ‘Neotropical’ is to some extent responsible for the widespread tendency to associate the Neotropical Realm with tropical climates, on the one hand, and by default the Nearctic Realm with temperate and cold climates, on the other. In fact, in Mexico the line separating frost-free from frost-prone areas is frequently used as an indication of the location of the major biological frontier separating two biogeographical realms. Although even a superficial look of modern climatic heterogeneity throughout the Americas would prove this idea incorrect, the mistake becomes colossal when palaeoclimatic heterogeneity is considered.

## FINAL REMARKS

Undoubtedly, numerous aspects of the dry tropics of Mexico remain poorly known, especially those related to regeneration, dispersal, and phytogeography. Our knowledge of the dry tropics flora is uneven; while there are localities for which inventories are very complete and reliable, for many others there is virtually no available information, particularly areas along the coasts of Michoacán, Oaxaca and Chiapas, despite significant efforts to overcome this deficiency (Zizumbo & Colunga, 1980; Pineda-García et al., 2007; Salas-Morales et al., 2003; 2007).

At some localities, mostly in western Mexico, TDF has an important endemic component (Lott, 1985; 1993; Lott & Atkinson, 2002). This feature alone justifies not

treating the dry tropics flora as a depauperate subset of the humid tropics flora (Toledo Rizzini, 1997; Gentry, 1995; Becerra, 2005). Conversely, it is more reasonable to recognize both ecosystems as distinct entities with a partially shared history: the tropical humid vegetation contributes lushness and biodiversity, whereas the vegetation of the dry tropics contributes a complex history and a large share of endemic species. Unfortunately, the vegetation in the dry tropics, particularly the forest communities, is threatened worldwide due to human activities (Gillespie et al., 2000; Miles et al., 2006; Pennington et al., 2006a; Maass et al., 2010), and in Mexico annual rates of TDF deforestation are very high (Mooney et al., 1995; Trejo & Dirzo, 2000). The transformation of dry tropical ecosystems may have consequences not only for biodiversity maintenance, but also for ecosystem functioning (Maass, 1995) and future climate change (Miles et al., 2006). The exclusivity of the dry tropics flora should be better appreciated, and this character should suffice to encourage the establishment of nature protection areas in this biome of large contrasts and spectacular colors.

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