Biodiversity and Conservation **11:** 2063–2048, 2002.

Floristic diversity of Mexican seasonally dry tropical forests

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Received 5 July 2001; accepted in revised form 19 November 2001

Key words: Evapotranspiration, Mexico, Rainfall, Seasonally tropical dry forest, Species diversity, Turnover

Abstract. Studies of the variation in tropical plant species diversity and its relationship with environmental factors are largely based on research in tropical moist/wet forests. Seasonally dry tropical forests (SDTFs), in contrast, have been poorly investigated. In this paper we present data from 20 Mexican SDTF sites sampled to describe the magnitude of floristic diversity in these forests and to address the following questions: (i) to what extent is species diversity related to rainfall? (ii) Are there other climatic variables that explain variation in species diversity in SDTFs? (iii) How does species identity vary spatially (species turnover) within the country? We found that species diversity was consistently greater (a ca. twofold difference) than would be expected according to the sites' precipitation. Rainfall did not significantly explain the variation in species diversity. Likewise, the number of dry and wet months per year was unrelated to species diversity. In contrast, a simple measure of potential evapotranspiration (Thornthwaite's index) significantly explained the variation in species diversity. In addition to the great diversity of species per site (local diversity), species turnover was considerable: of a total of 917 sampled species, 72% were present only in a single site and the average similarity (Sorensen's index) among sites was only 9%. These aspects of floristic diversity and the high deforestation rates of these forests in Mexico indicate that conservation efforts should be directed to tropical forests growing in locations of low and seasonal rainfall.

Introduction

An aspect that has generated considerable attention for many years among ecologists, as well as evolutionary and conservation biologists has been the analysis of the patterns, causes and maintenance of biological diversity in the tropics (Gentry 1988; Huston 1994). Tropical forests established in these regions hold a great proportion of the Earth's species richness, a pattern that has been widely recognized (Fisher 1960; Connell and Orias 1964; MacArthur 1965; Pianka 1966; Wilson 1988; Heywood and Watson 1995).

More recently, there has been an awareness of and an increasing interest in understanding the variation in species diversity within the tropics (e.g., Gentry 1982, 1988, 1995). Some studies indicate that the variation in plant species diversity within the tropics can be considerable, sometimes comparable to that found between some tropical and temperate regions (Gentry 1982, 1988; Clinebell et al. 1995). In

general, tropical rain (i.e., wet and moist) forests are the most diverse and, from the floristic point of view, tropical rain forests of the Amazon basin hold the known world records of plant species richness. For example, 1-ha plots in this region can reach a species density as high as 307 tree species with a diameter at breast height (dbh) ≥10 cm (Valencia et al. 1994).

Nevertheless, tropical rain forests are not the only ecosystems present in tropical regions. Tropical forests include a variety of physiognomic entities, including the seasonally dry tropical forests (SDTFs) that extend from equatorial zones up to the subtropical regions of the planet (see Bullock et al. 1995). Moreover, around 42% of the global tropical and subtropical forest coverage corresponds to tropical dry forests (Holdridge 1967; see also Pennington et al. (2000) for a discussion of the differences between SDTF and other similar vegetation types such as woody savannas). Nevertheless, these forests have received considerably less attention than their wet and moist counterparts (Murphy and Lugo 1986), and Janzen (1988) has argued that SDTFs, and not tropical rain forests, are the most endangered tropical ecosystems (see Trejo and Dirzo (2000) for a detailed local example).

Although SDTFs are regarded to be, in general, floristically less diverse than tropical rain forests (Gentry 1995), some sites of SDTF hold a plant species richness comparable to or even higher than that of some moist forests (Hubbell 1979; Gentry 1982, 1988; Janzen 1988). Some pioneer studies (cf. Gentry 1982, 1988, 1995; Janzen 1988) have highlighted the importance of investigations directed to improve our understanding of these tropical forests. Yet information is still very limited regarding even such basic aspects as the range of environmental conditions in which they grow, and the levels and patterns of species diversity of such ecosystems. In this context the extensive field work of Gentry (e.g., 1982, 1988, 1995), using a standardized sampling protocol for the quantification of local plant species diversity, constitutes a valuable approach to studying the patterns of variation in plant diversity in different tropical regions and ecosystems of the world. Gentry has championed the quantification of the number of plant species in a variety of sites, including a few of them with SDTF, at the scale of 0.1 ha, and detected some basic patterns and driving forces of variation in plant diversity. In particular, he found that the variation in species diversity in the Neotropics could be explained by a simple climatic parameter of the study sites: total annual precipitation (TAP) (Gentry 1982, 1988). Gentry found that as TAP increases, local species density also increases. The implication of this pattern is of importance, as it suggests that annual rainfall may be a driving force or, at least, a predictor of local plant species richness in tropical forests. In subsequent studies, Gentry found that this relationship holds for a variety of lowland forests and up to a level of ca. 4.5 m of annual rainfall (Gentry 1988), after which the relationship becomes asymptotic. However, Ter Steege et al. (2000) found that there is no relationship between rainfall and species diversity in Amazonian sites with an annual precipitation ≥2000 mm. Information is very limited for sites located towards the lower part of the precipitation spectrum. Therefore in this paper we attempted to analyze if this pattern holds for SDTFs in Mexico. An important reference is that in an SDTF in western Mexico species richness was higher than would be expected, following Gentry, according to the site's precipitation (Lott et al. 1987).

In this paper we provide a large data set for Mexican SDTFs, in order to describe the variety of ecological settings in which they grow, and to address the following questions. (i) What is the magnitude of floristic diversity of SDTFs at the scale of 0.1 ha within a wide geographic area? Furthermore, following Gentry's (1982) relationship between rainfall and diversity, how does species diversity of Mexican SDTFs compare with that to be expected according to the TAP of the studied sites? (ii) Does variation in floristic diversity significantly correlate with TAP, as proposed by Gentry (1982, 1988)? (iii) Given the climatic seasonality of the areas where these forests grow, are there climatic variables, other than TAP, that better explain the variation in species diversity? (iv) How does species identity vary spatially (i.e., species turnover) within a geographic area (the territory of Mexico) in which SDTF is widely distributed?

The rationale for choosing Mexican SDTFs for this analysis is the following. Mexico has been considered one of the main megadiversity countries (Mittermeier and Mittermeier 1992). From the botanical point of view this is justified, given its great floristic diversity (Rzedowski 1991a; Dirzo and Gómez 1996), its spectacular combination of Nearctic and Neotropical taxa (Sarukhán and Dirzo 2001), and its high concentration of endemisms (Rzedowski 1991b). In addition, the wide geographic distribution of SDTFs in Mexico determines that these forests can be found under a wide variety of environmental conditions (Trejo 1996). Furthermore, the one study available on Mexican SDTFs (Lott et al. 1987) shows an unsually high species diversity and Gentry (1995) highlights such a site as one of the most diverse of its kind in the Neotropics. Even though such environmental heterogeneity is reflected, to some degree, in the variation of the structure of these forests (e.g., height, stratification; Trejo 1998), they present consistent physiognomic and floristic characteristics that typify them as representative SDTFs.

Methods of study

Selection of study sites

For the description of SDTFs and the environmental conditions where they grow in Mexico and to address the questions indicated above, we selected 20 representative sites, located throughout the distribution of SDTFs in the country. For this study we used sites that fulfilled the following requirements. (i) Collectively, they should encompass the geographic range of distribution in Mexico, including the variety of environmental conditions in which they occur in the country (elevation, climate, soil types, and topography). (ii) The minimum size of sites should permit to select, within it, 10 independent plots. (iii) They should be in a satisfactory conservation situation. (iv) There should be meteorological information available to characterize the climate of the area.

In order to select the sites we analyzed the available literature on the distribution of SDTFs in Mexico (mainly Miranda and Hernández-Xolocotzi 1963; Miranda 1942, 1947, 1952; Puig 1976; Rzedowski 1978; SPP (Secretaría de Programación y Presupuesto) 1981; Lundell and Lundell 1983; Rzedowski and Calderón 1987;

Arriaga and León 1989). We also consulted the National Herbarium of Mexico (MEXU) to check the vegetation description and location for specimens of taxa characteristic of SDTFs (e.g., *Bursera, Lysiloma, Jatropha, Juliania, Ceiba*). Besides our own experience with this vegetation type in Mexico, we consulted with national experts as to the distribution and conservation situation of SDTFs throughout the country. From the selected sites we conducted the vegetation sampling and characterization of the climate as follows.

Characterization of SDTFs and magnitude of floristic diversity

This study is based on a standardized sampling protocol of the vegetation directed to quantify plant species diversity at the local level. We used the method proposed by Gentry (1982, 1988), in which all plants with a dbh $\geq$ 2.5 cm present within an area of 0.1 ha are censused. The 0.1 ha area is constituted by 10 transects of 50 $\times$ 2 m (i.e., 100 m^2 each). Transects were located by random selection of coordinates within the area. Typically, we used the longest possible dimension of the area and we established a trail (or used one already established, if possible) along it, and estimated its distance. We then randomly selected 10 positions (defined by meters) along such a trail and randomly selected the direction and distance from such a point, to define the origin of each of the 10 transects. Transects were lined up with a 50-m measuring tape and we censused all plants established (with at least half of the trunk's base) within 1 m on each side of the tape. Each censused individual was identified to species; we also defined its life form (tree, shrub, liana) and measured its diameter. Diameters of all trees and shrubs were measured at the standard height of 1.3 m, while in the case of lianas, following Gentry (1982), diameter was measured at the base of the stem, if they were rooted within the plot. We collected specimens of the censused plants and vouchers were deposited in the National Herbarium of Mexico (MEXU). Our sampling protocol differed from that of Gentry (1982) in that we censused all trees and shrubs with a dbh $\geq$1 cm, instead of 2.5 cm. In addition, all lianas with a basal diameter $\geq$1 cm, instead of 2.5, were considered. This ensured that our sampling included a group of plants that, in the case of SDTFs, constitutes an important component of the plant community (Trejo 1998), and we had a more robust data set to characterize the floristic diversity of our study sites. In addition, because the diameter of all plants was measured, we were able to use the information for plants with dbh (or basal diameter in the case of lianas) $\geq$2.5 cm and make our data set comparable to the data published by Gentry.

With the data and identification of the plants from our study sites we quantified the number of species in three categories of size based on diameter ($\geq$1, $\geq$2.5, $\geq$10 cm) and two life forms (trees, lianas) for each site. We also quantified the number of genera and families present in each site and calculated the indices of diversity of Shannon and Simpson (see Magurran 1988) for each site.

In order to compare the diversity of species (S) of Mexican SDTFs with that to be expected according to the TAP of the sites, we used the regression equation of Gentry (1982) [$S = -1.2 + 0.05676(\text{TAP})$] to predict the expected species diversities.

Relationship of diversity with precipitation

We investigated if species diversity of Mexican SDTFs shows a positive relationship with TAP within the range of rainfall regimes in which they grow. This was examined by calculating regression models for total annual rainfall and species richness for the Mexican data set.

Relationship of diversity with other climatic variables

In order to assess if climatic variables, other than TAP, explain the variation in floristic diversity of SDTFs, we explored if variables related to seasonality had some relationship with species diversity. Following Clinebell et al. (1995), we considered the mean number of dry months per year (dry months being defined as those with less than 60 mm rainfall). Likewise, we used the number of wet months per year (with rainfall $\geq$100 mm). In addition, we considered Thornthwaite's index of potential evapotranspiration. This index takes into consideration potential mean monthly temperature and the duration of solar radiation, corrected by latitude to derive the time course of water availability per year (see details in Thornthwaite 1948). The importance of potential evapotranspiration for vegetation was highlighted in Holdridge's (1967) influential study on plant life zones. In addition, Currie and Paquin (1987) found that variations in annual evapotranspiration describe 76% of the variation in tree species richness in North America. Given the simplicity to derive Thornthwaite's index from climatic data, it is readily used as an indicator of evapotranspiration.

Geographic variation in species identity

We complemented our description of floristic diversity in Mexican SDTFs in terms of species turnover by means of examination of the geographic variations in species density. For this analysis we calculated the floristic similarities between all pairs of sites by using Sorensen's similarity index (Magurran 1988): $S = 2C/A+B$. In this equation C is the number of species common to both sites; A, the number of species present in one of the sites to be compared; and B, the number of species present in the other site. With the calculated values we generated a similarity matrix for both S and C.

Climatic characterization of the sites

For the climatic characterization of the sites we analyzed the data of the meteorological station located closest to each of the studied sites. The information corresponding to each meteorological station was obtained from The National Weather Service of Mexico (Servicio Meteorológico Nacional, www.cna.gob.mx/SMN.html).

Results

Environmental conditions of SDTFs in Mexico

Sites included in this analysis are distributed throughout the geographic range in which these forests occur in Mexico (Figure 1). Hereafter, sites are referred to by their location and/or number, as indicated in Figure 1 and Table 1. The northernmost site is located at 27°15′ LN [Alamos (2)] and the southernmost site at 15°50′ [Copalita (6)]. The former constitutes the northernmost limit of the distribution of SDTF on the continent, while site 19 (La Trinitaria) constitutes the farthest point of southeast Mexico where SDTF can be found, at the Guatemalan border. The elevations at which SDTFs are established in the studied sites range from 60 [Copalita (6)] to 2020 m [C. Zináparo (8)].

Total annual rainfall varies by a factor of 3, from 450 mm [Cosalá (3)] to 1370 mm [Flores (16)]. Mean annual temperature ranges from 19 [C. Zináparo (8)] to 27.4 °C [Infiernillo (9)]. Thermic oscillation ranges from 1.6 [Copalita (6)] to 12.7 °C [Alamos (2)]. The proportion of winter rainfall ranged from 0.8 [Copalita (6)] to 9.6% [Alamos (2)]. Potential evapotranspiration (Thornthwaite 1948) of the study sites varied by a factor of 1.8, from 935.9 [C. Zináparo (8)] to 1691.8 mm [Caleta (5)]. The number of wet months (≥100 mm) per year was small in general, ranging from 0 [Calipam (13)] to 4.7 [Las Flores (16) and El Pensil (17)], and the number of dry months (<60 mm) was high, ranging from 6.0 [Sayil (20)] to 9.2 [La Burrera (1)]. The Mexican SDTFs show a clear affinity with semi-arid climates and with a considerable variation in potential evapotranspiration.

The plant communities are present in areas with a combination of climatic

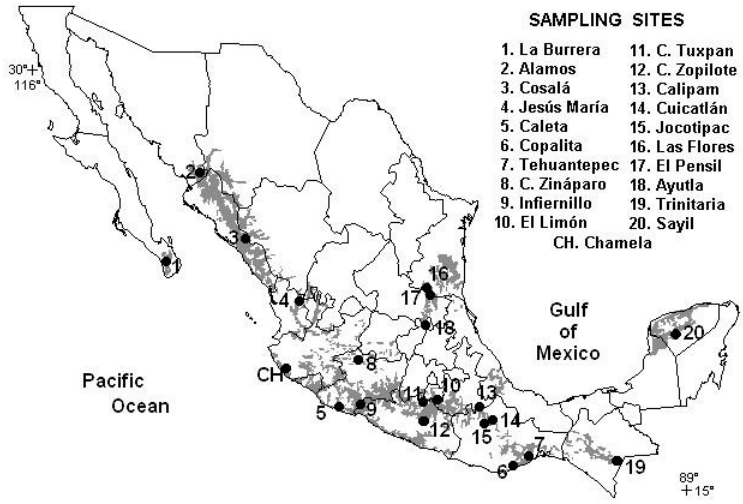

Figure 1. Geographic distribution of SDTFs within Mexico and location of the sampled sites for the present study.

Table 1. Location and climatic characteristics of the 20 study sites of seasonally dry tropical forest in Mexico.

Site	Latitude (North)	Longitude (West)	Elevation (m a.s.l.)	Total rainfall (mm)	Mean temperature (°C)	Number of wet months (>100 mm)	Number of dry months (<60 mm)	Thornthwaite's index (mm)	Köppen's climate type (Garcia 1988)
1 La Burrera, BCS	23°30′	110°02′	538	482	22.0	1.8	9.2	1152.0	BS_0 $(h')hw$ (e)
2 Alamos, Son.	27°15′	108°45′	666	664	23.8	2.2	8.6	1284.8	BS_1 $(h')hw$ $(x')(e')$
3 Cosalá, Sin	24°30′	106°45′	561	900	24.5	3.7	7.6	1335.1	$Aw_0(w)ig$
4 Jesús María, Nay.	22°15′	104°35′	622	855	24.5	3.5	7.6	1379.1	$Aw_0(w)e$
5 Caleta, Mich.	18°07′	102°52′	97	1200	27.0	4.6	6.7	1691.8	$Aw_1(w)I$
6 Copalita, Oax.	15°50′	96°01′	60	800	26.5	4.4	6.8	1608.8	$Aw_0(w)ig$
7 Tehuantepec, Oax	16°21′	95°24′	274	920	26.5	4.3	6.7	1642.2	$Aw_0(w)ig$
8 C. Zináparo, Mich.	20°07′	102°02′	2020	880	19.0	4.1	7.1	935.9	$(A)C(w_1)(w)$
9 Infiernillo, Mich.	18°21′	101°54′	237	640	27.4	3.7	7.3	1735.4	$BS_1(h')w(w)ig$
10 El Limón, Mor.	18°32′	98°57′	1403	870	19.8	3.9	7.2	1060.8	$Aw_0(w)ig$
11 C. Tuxpan, Gro.	18°24′	99°29′	1259	1050	22.9	4.6	6.2	1234.2	$Aw_1(w)ig$
12 C. Zopilote, Gro.	17°45′	99°34′	863	690	25.6	3.7	7.0	1440.4	$BS_1(h')w(w)eg$
13 Calipam, Pue.	18°17′	97°09′	1118	450	24.1	0.0	7.5	1277.4	$BS_0(h')w(w)eg$
14 Cuicatlán, Oax.	17°50′	96°57′	1047	630	22.7	1.7	8.0	1142.2	$BS_1(h')w(w)eg$
15 Jocotipac, Oax.	17°48′	97°01′	897	500	23.8	1.7	8.0	1249.6	$BS_0(h')w(w)eg$
16 Las Flores, Tamps.	22°48′	99°24′	450	1370	23.3	4.7	6.4	1253.1	$(A)Ca(w_2)(w)(e)$
17 El Pensil, Tamps.	22°45′	99°24′	380	1350	23.5	4.7	6.4	1253.1	$(A)Ca(w_2)(w)(e)$
18 Ayutla, Qro.	21°24′	99°35′	670	787	24.1	4.2	7.0	1263.1	$Aw_0(w)(e)g$
19 Trinitaria, Chis.	16°01′	92°01′	890	1000	24.0	4.7	6.6	1259.7	$Aw_0(w)(i)g$
20 Sayil, Yuc.	20°10′	89°38′	100	932	26.5	5.0	6.0	1570.9	$Aw_0(i')g$

Table 2. Floristic diversity of the 20 study sites of seasonally dry tropical forest in Mexico.

Site	Number of species							Number of genera	Number of families	H′ Shannon index	*I*/*D* Simpson index
	Total		Trees	Total		Lianas					
	≥1	≥2.5	≥2.5	≥10	≥30	≥1	≥2.5				
1	56	49	41	22	7	9	*8*	52	29	3.47	24.98
2	46	40	35	25	9	7	5	38	22	2.84	9.97
3	80	70	58	30	9	16	**12**	69	33	3.81	34.58
4	63	45	42	28	6	6	3	55	27	3.50	20.65
5	**123**	**97**	**90**	**51**	11	**17**	7	**105**	45	**4.17**	39.76
6	*107*	86	76	47	**15**	*14*	10	89	**46**	3.98	30.38
7	76	60	58	27	7	4	2	65	*38*	3.65	25.66
8	48	37	34	22	3	5	3	40	24	3.40	36.71
9	115	*78*	*73*	*40*	3	*14*	5	*86*	*38*	*4.07*	30.63
10	76	57	50	27	6	12	7	54	26	3.63	21.57
11	80	66	63	33	6	5	3	67	31	3.74	30.71
12	95	77	75	37	9	9	2	67	32	4.09	**49.28**
13	29	22	22	11	2	1	0	26	15	2.96	13.92
14	90	65	63	32	5	4	2	68	32	3.78	28.94
15	66	53	52	20	3	2	1	54	26	3.54	23.46
16	61	48	41	24	*10*	10	7	55	31	3.37	18.36
17	57	41	33	15	4	*14*	*8*	52	33	3.12	13.33
18	72	47	44	21	4	10	3	64	31	3.80	35.39
19	61	57	52	27	5	8	5	53	34	3.39	20.54
20	83	65	53	19	8	16	**12**	67	*38*	3.91	*36.96*

Numbers in bold face, underlined and italicized in each column indicate the highest, second and third highest values, respectively, for each variable.

variables (cf. Table 1) which sustain plant communities that structurally and floristically can be characterized as SDTF. For instance, in some sites with low precipitation, the presence of low summer temperature promotes lower vegetation evapotranspiration demands and therefore SDTF can be developed there [Tuxpan (11)]. In other cases, a high proportion of winter rainfall (i.e., rainfall in the cold months, January–March) to annual rainfall has the same effect [La Burrera (1), Alamos (2)]. The climatic affinities of the vegetation in the study sites are shown in detail in Table 1.

The sites were established in different lithological substrata, although limestone was the predominant substratum, followed by andesite, schist, gneis, sandstone, argilite and basalt. We found that edaphic characteristics of the study sites are variable, but SDTFs were predominantly established on moderate to steep slopes, in which soils are shallow and with frequent rocky outcrops.

Magnitude of SDTF floristic diversity

The results of the analyses of species richness are shown in detail in Table 2. The total number of species with dbh ≥ 1.0 cm that can be found in Mexican SDTFs at

the 0.1 ha scale ranges over a factor of 4, from 29 in Calipam (13) to 123 in Caleta (5), with an overall mean (±SE) of 74 (±24). Calipam (13), located in the semi-arid region of Tehuacán–Cuicatlán (cf. Figure 1), represents, in various aspects, the extreme distribution of SDTFs, given its climatic conditions and its direct contact with vegetation of xeric affinity. Nevertheless, due to its structural and floristic characteristics this site can be classified as SDTF. The species diversity of this site (13) is 2.6 times lower than the mean of all sites. The sites with the greatest species diversity are located on the Pacific coast [Caleta (5) and Copalita (6)] and in the Basin of the Balsas River [Infiernillo (9) and C. Zopilote (12)].

Species richness for plants with dbh ≥ 2.5 and 10 cm is on average 58 and 28, with ranges of 22–97 and 11–51, respectively. Therefore, site 5 (Caleta), with 97 species of dbh ≥ 2.5 cm, presents a floristic diversity similar to that found in the site with the highest species richness known, Chamela (Lott et al. 1987), where diversity reaches 103 species.

Species diversity considering plants with dbh ≥ 10 cm in 0.1 ha is, on average, 28, ranging from 11 [Calipam (13)] to 51 [Caleta (5)]. Some tree species reach a large dbh (≥30 cm) and, in many cases, these are the emergent trees of the forest. In sites such as Calipam (13), C. Zináparo (8), Infiernillo (9) and Jocotipac (15), there are only two or three species that reach such a size. In other sites such as Las Flores (16), we found 10 species of this size and in Caleta (5) and Copalita (6) we found 11 and 15, respectively. The mean number of species of trees with dbh ≥ 30.0 cm is ~7 species in 0.1 ha.

The presence of lianas varied considerably among sites. In sites like Calipam (13) we found only one species of liana with dbh ≥ 1.0 cm and no species of liana reached a dbh ≥ 2.5 cm. Species of lianas of small diameter are found in numbers of up to 17 in Caleta (5), 16 in Cosalá (3) and Sayil (20), and 14 in Copalita (6), Infiernillo (9) and El Pensil (17). The largest number of species of liana with dbh ≥ 2.5 cm was 12, and it was found in two sites, Cosalá (3) and C. Zopilote (12).

Floristic diversity of these forests is also reflected at the level of genera. In sites such as Caleta (5) the number of genera reaches 105, which means that almost any one of the species of this site belongs to a different genus (ratio species/genera = 1.17). In other sites such as Copalita (6) and Infiernillo (9), we also found high numbers of genera, 89 and 96, respectively. The mean number of genera for the rest of the studied sites was 61.

The number of families ranged between 15 and 46, with an average of 32 (±7.4). Caleta (5) and Copalita (6) had the greatest diversity at this taxonomic level, with 45 and 46, respectively. These numbers correspond to families that include species with small diameters. If we consider the number of families taking into account plants with dbh ≥ 2.5 cm, this value reaches 43 [Caleta (5)]; Copalita (6) has 40 and Sayil (20) and Infiernillo (9) have 33, in contrast with Jesús María (4) with 19, and Calipam (13) with only 10.

In addition to the number of species, we calculated the indices of diversity of Shannon and Simpson (see Methods of study) (Table 2). According to Shannon's index, the sites with the greatest diversity are Copalita (5), C. Zopilote (12) and Infiernillo (9), with values over 4.0, and the less diverse site is Alamos (2), with

Table 3. Spearman's rank correlation (R_s) between species richness and indices of diversity.

Diversity index	All plants ≥1 cm dbh		All plants ≥2.5 cm dbh	
	R_s	P	R_s	P
Shannon	0.9461	<0.0001	0.8788	<0.0001
Simpson	0.6797	0.0009	0.6177	0.0037

2.84. The difference among sites is more evident with Simpson's index (Table 2), which is more sensitive to changes in the abundance of the common species (Peet 1974). In this case the most diverse site is C. Zopilote (12), with 49.28. The lowest diversity according to Simpson's index is found in Alamos (2), with 9.97, El Pensil (17), with 13.33, and Calipam (13) with 13.92. Even though both indices emphasize different aspects of diversity, they are significantly correlated with species richness (Table 3). Nevertheless, Shannon's index shows a much greater correlation with species richness, considering both plants with dbh ≥ 1.0 cm or with dbh ≥ 2.5 cm. This finding is of interest, since all of our results dealing with species richness constitute a good reflection of ecological diversity in terms of Shannon's widely used index of diversity.

Using Gentry's (1982) regression equation to calculate the expected number of species according to the precipitation of the Mexican SDTF sites, we compared these values with the ones we observed in our study sites (Figure 2). This comparison shows that in the majority of the cases (17 out of 23 sites), the species richness we found was higher than expected under Gentry's model. This contrast is

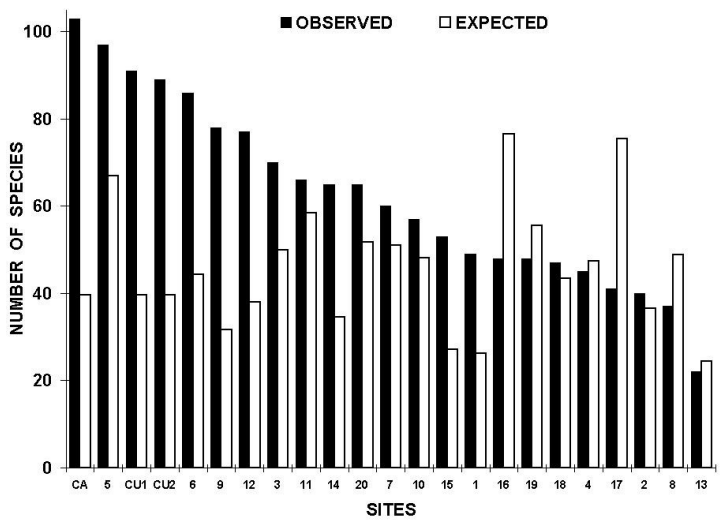

Figure 2. Total number of species (all plants with dbh ≥ 2.5 cm) present in the 20 study sites of Mexican SDTF. Black bars show the number of observed species and white bars the number of expected species, according to Gentry's (1995) regression. Site numbers correspond to the list in Figure 1. C corresponds to sites from Chamela sampled by Lott et al. (1987).

Table 4. Linear regression parameters between total annual precipitation and species richness considering different plant size classes and two life forms.

Type of plants	F	P	r^2
All plants dbh ≥ 1.0 cm	0.3910	0.5395	0.0212
All plants dbh ≥ 2.5 cm	0.5387	0.5387	0.0290
Trees dbh ≥ 2.5 cm	0.1805	0.6759	0.0099
Trees dbh ≥ 10 cm	0.3046	0.5877	0.0166
Lianas dgl ≥ 1.0 cm	4.7603	0.0426	0.2091
Lianas dgl ≥ 2.5 cm	3.2530	0.0880	0.1530

highly significant (Wilcoxon's Paired Test, $T = 48$; $P < 0.006$). In the Chamela sites (Lott et al. 1987) and in Infiernillo (9), the number of observed species surpasses the expected number by a factor of ~3. In other sites such as Copalita (6), C. Zopilote (12), Cuicatlán (14) and Jocotipac (15), species diversity is about twice that expected. In six sites species diversity is lower than that predicted by the regression. In two of them, Las Flores (16) and El Pensil (17), there is a deficit of species of 40–50% with respect to the expected. In these two sites annual precipitation is the highest among all studied sites (~1350 mm, cf. Table 1). In the two other sites, C. Zinaparo (8) and La Trinitaria (19), the number of species we observed was lower than expected by about 25 and 15%, respectively. C. Zinaparo (8), in particular, has the peculiarity of being situated at an unusually high elevation (2020 m, Table 1) for the typical altitudinal distribution of SDTFs. Calipam (13), with a species richness slightly below the expected diversities for its annual precipitation, is somewhat peculiar also, in that it is located directly adjacent to a major arid zone in Central Mexico and, accordingly, is the driest of all sampled sites. In general, this comparison shows that Mexican SDTFs do not fit to the expected diversities, according to the original model of Gentry. It appears that, with the exception of sites 16, 17, 8 and 13, located towards the climatic limit of distribution of the SDTFs, the great majority of the Mexican sites have floristic diversities that surpass the expected.

Relationship of diversity with precipitation

Although we found that Mexican SDTFs tend to have higher values of species richness than expected, it is conceivable that their species diversity may still show a relationship with annual precipitation within the range of rainfall regimes in which they grow (see Methods of study). To analyze this we conducted regression analyses between TAP and species diversity for the studied sites. This analysis shows that annual precipitation did not significantly explain the variation in species richness in the Mexican sites (Table 4). This was the case for linear regressions considering all species with either dbh ≥ 1.0 or 2.5 cm; trees with DBH ≥ 1.0 cm or with dbh ≥ 2.5 cm; or lianas of basal diameter ≥2.5 cm. The only marginally significant relationship was that of lianas with a basal diameter ≥1.0 cm. Nevertheless, in this case the proportion of the variance in species richness explained by TAP is quite small ($r^2 = 0.209$).

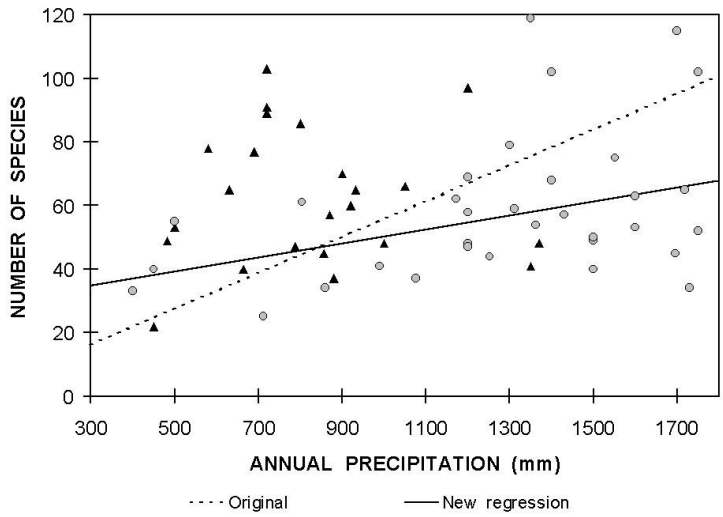

Figure 3. Species diversity of Mexican SDTF sites (▲) and other, non-Mexican, SDTF sites in the Neotropics (●), within a range of 350–1750 mm TAP. Data points explore the relationship between rainfall and species diversity by means of the equation $S = 0.05676 * PP - 1.2$ (– – –) and a regression calculated for SDFTs of the Neotropics ($S = 0.0221 * PP + 28.05$) (——), excluding Mexican sites.

Our data set clearly indicates the lack of a relationship between species diversity and total precipitation for the Mexican sites. This poses the question of whether the lack of such a relationship is peculiar to our study sites in Mexico or is a more general feature of SDTFs. To address this issue, we calculated a new regression, specific for SDTFs, using the more recent data set of Gentry (1995) and his associates (Clinebell et al. 1995; see also Gillespie et al. 2000). We then assessed if this regression was significant and compared the Mexican sites in the context of such known floristic diversities for Neotropical SDTFs. This new regression (Figure 3) was statistically significant ($F = 8.0242$; $P = 0.0084$), although the explained variance is considerably lower (22.2%) than in the original model of Gentry (1982) (i.e., 93%). For comparison, we have drawn the extrapolated regression line of the original model of Gentry in Figure 3. This shows that most of the known Neotropical SDTFs, disregarding the Mexican sites, fall below the original regression line. Finally, the Mexican SDTF sites show a striking contrast with respect to the other Neotropical SDTF sites. As Figure 3 shows, and in concordance with Figure 2, most Mexican sites are located above the regression line of the SDTFs. Furthermore, when the Mexican sites are included in the regression, the model becomes non-significant ($F = 0.5229$; $P = 0.4728$).

Relationship with other climatic variables

Linear regression equations of the relationship between species richness and the mean number of dry months per year had negative slopes in all cases. However, the

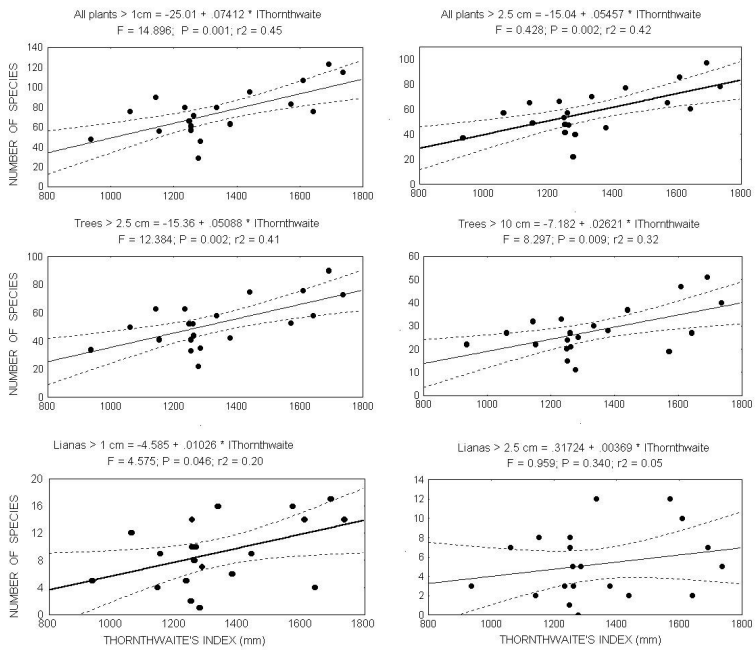

Figure 4. Relationship between species number and Thornthwaite's index of potential evapotranspiration (see text for details) for each of the life forms and dbh categories found at the Mexican SDTFs.

Table 5. Linear regression parameters for the relationship between dry and humid months and species richness considering different size classes and two life forms.

Type of plants	Dry months (<60 mm)			Humid months (>100 mm)		
	F	*P*	r^2	*F*	*P*	r^2
All plants dbh ≥ 1.0 cm	1.629	0.218	0.032	4.049	0.059	0.184
All plants dbh ≥ 2.5 cm	1.450	0.243	0.074	4.384	0.051	0.196
Trees dbh ≥ 2.5 cm	1.217	0.284	0.063	2.882	0.107	0.138
Trees dbh ≥ 10 cm	0.335	0.569	0.018	2.408	0.138	0.118
Lianas dgl ≥ 1.0 cm	2.130	0.161	0.106	9.993	0.005	0.357
Lianas dgl ≥ 2.5 cm	0.604	0.447	0.032	5.019	0.037	0.218

analyses of variance of the regressions yielded non-significant relationships (Table 5), considering all categories of size of (i) all species together, (ii) trees alone, or (iii) lianas. Linear regressions of species richness and the number of wet months were, again, non-significant, with the exception of lianas of both classes, although the proportion of explained variance is rather low (Table 5). In contrast, regression analyses of species richness with Thornthwaite's evapotranspiration index yielded significant relationships in all (but one) cases of plant size and life form (Figure 4). Lianas in general are not an important floristic component of these forests (see Table 2) and this may explain the relatively poor (or lack thereof) relationship with this climatic variable. Furthermore, in the case of lianas with a basal diameter ≥1.0 cm,

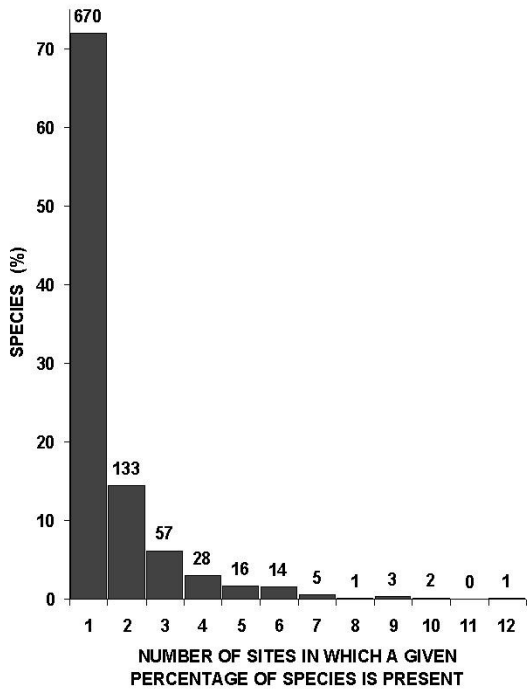

Figure 5. Frequency distribution of species according to the number of sites in which they occur. Numbers of species found within each category are shown above each bar.

which includes a slightly larger floristic contingent, the relationship is significant ($P = 0.0464$), although the proportion of explained variance is relatively small ($r^2 = 0.2025$). Apart from the case of lianas, species diversity of trees and trees plus lianas was significantly explained by Thornthwaite's evapotranspiration index with regression coefficients ranging from 32 to 45%. Thus species diversity of woody plants from Mexican SDTFs predictably increases as the potential for water availability increases in these forests.

Geographic variation in species identity

The floristic composition of the 20 studied sites is represented by 917 species. The frequency distribution of the number of species found in 1, 2, or *n* sites was very skewed (Figure 5). A great majority of the species (72%) was sampled only from a single site, and 85% of the species were present in only two of the 20 sites (Figure 5). There was not a single species that was found in all 20 sites. The most widely distributed species, *Lysiloma divaricata* (Leguminosae: Mimosoidae), was found in 12 of the studied sites. This was followed by *Plumeria rubra* f *acutifolia* (Apocynaceae) and *Juliania adstringes* (Julianaceae), which were found in 10 sites, and *Euphorbia schlechtendalii* (Euphorbiaceae), found in nine sites.

The floristic similarity among sites, calculated by Sorensen's coefficient (S),

Table 6. Floristic similarity index (Sorensen's index and number of shared species) between 20 study sites of SDTF in Mexico.

Site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
	Sorensen similarity index (%)																			
1		8	4	2	6	4	3	4	0	2	3	0	0	1	2	4	4	2	3	3
2	4		**27**	15	8	11	10	2	9	10	10	3	0	9	4	4	8	2	8	2
3	3	17		14	9	11	12	2	5	6	11	5	0	7	3	10	10	7	9	4
4	1	8	10		11	9	14	4	14	17	17	14	4	12	8	3	7	9	13	1
5	5	7	9	13		21	16	2	18	8	10	6	0	5	4	8	6	4	9	7
6	3	8	10	8	24		22	3	19	14	9	6	4	7	7	6	5	2	10	8
7	2	6	9	11	16	20		5	15	13	13	10	6	17	13	6	9	8	7	6
8	2	1	1	2	2	2	3		2	8	5	0	0	7	0	7	11	5	0	6
9	0	7	5	12	21	21	14	2		19	14	21	6	19	17	2	4	6	6	6
10	1	6	5	12	8	11	10	5	18		19	12	0	16	10	6	9	7	9	4
11	2	6	9	12	10	8	10	3	14	15		**27**	**28**	**24**	18	6	6	7	11	3
12	0	2	4	11	7	6	9	0	22	10	24		19	**28**	25	1	4	10	9	1
13	0	0	0	2	0	3	3	0	4	0	3	12		**24**	**40**	0	0	4	2	2
14	1	6	6	9	5	7	16	5	19	13	20	26	14		**44**	5	8	6	9	2
15	1	2	2	5	4	6	6	0	15	7	13	20	19	35		3	7	7	6	1
16	2	2	7	2	7	5	6	4	2	4	4	1	0	4	2		**46**	**28**	7	10
17	2	4	7	4	5	4	6	6	3	6	4	3	0	6	4	27		**23**	7	9
18	1	1	5	6	4	2	6	3	5	5	5	8	2	5	5	18	15		6	3
19	2	4	6	8	8	8	11	0	5	6	8	7	1	7	4	4	4	4		1
20	2	1	3	1	7	8	5	4	6	3	2	1	1	2	1	7	6	2	1	
	Number of shared species																			

demonstrates the existence of distinct floristic contingents in the different sites (Table 6). The overall mean of *S* is just 9.0 ($\pm$7.8). The greatest similarity was 46%, between Las Flores (16) and El Pensil (17), with 27 shared species (Table 6). Although geographically contiguous (see Figure 1), these two sites hold a moderate degree of similarity, and this underscores a high degree of environmental heterogeneity. For example, Las Flores is located on a substrate with profuse limestone outcrops and El Pensil grows on a substrate with basaltic outcrops. Sites Cuicatlán (14) and Jocotipac (15) are also geographically adjacent (cf. Figure 1), in the Tehuacán Valley, and they share 35 species, with an *S* value of just 44%. With the exception of cases like these two pairs of sites, floristic similarities among sites are very low in general and *S* values are zero in 7% of the cases (Table 6).

The tendencies in the species similarity among sampled sites are clearly depicted in Figure 6, showing the frequency distribution of *S* values. The class intervals between 0.1–13.5% include practically 75% of all possible paired comparisons among sites. The highest frequency corresponds to the class interval 4.6–9%, which includes 34% of the cases, and only in 1.6% of the paired comparisons is similarity greater than 36%.

Discussion

The most distinguishable aspect of the environmental conditions in which SDTFs

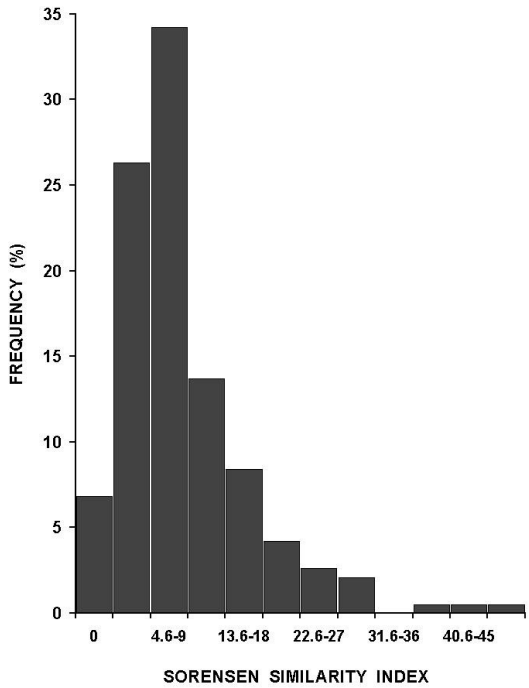

Figure 6. Frequency distribution of the value of Sorensen's similarity index for the 20 Mexican SDTF sites.

grow in Mexico is the marked seasonality in rainfall, with mean numbers of 7.2 dry months and 5.5 wet months per year. However, the seasonality was considerably variable across sites (the coefficient of variation in mean monthly rainfall ranged from 79 to 145%). In addition to variation in seasonality, variation in total annual rainfall was also considerable. Most of the sites showed a clear affinity with semi-arid climates; however, there were extreme variations, demonstrated by the fact that some sites hold a SDTF directly adjacent to major desertic areas, while others grow under very mesic rainfall regimes.

Likewise, although sites were in general associated with conditions of high potential evapotranspiration (mean = 1275.8 mm), this environmental feature had a 1.9-fold variation. Another remarkable aspect of variation in environmental conditions of Mexican SDTFs was that of elevation. While most sites (15) were located in lowlands (<900 m), four sites were established in localities of elevations >1000 m and one area held a distinct SDTF at 2020 m a.s.l. Regarding edaphic conditions, we found that Mexican SDTFs were predominantly established on moderate to steep slopes, with shallow soils and rocky outcrops. This may reflect an affinity of SDTFs for these edaphic conditions, or the fact that these topographic conditions are restrictive for agricultural activities and therefore currently SDTFs are restricted to such conditions. Studies on SDTF distribution in Mexico prior to extensive

anthropogenic disturbance show that other types of thorny forests (Rzedowski 1978) largely occupied lowlands with deeper soils. This suggests that our findings reflect an affinity of SDTFs for moderate/steep slopes with shallow, rocky soils. Other authors have found that variation in edaphic conditions may be an important driving factor of variation in species composition in samples from the Brazilian cerrado (Ratter and Dargie 1992; Ratter et al. 1996). The relationships between soil characteristics and variation in species diversity in Mexican SDTFs have been analyzed elsewhere (Trejo 1998).

Such a remarkable range of environmental conditions and the wide latitudinal range (16° to 27°15′) in which SDTFs occur in Mexico is unusual for other tropical ecosystems or for other SDTFs in tropical countries (see Mooney et al. 1995). The variety of ecological settings in which Mexican SDTFs grow anticipates that the magnitude of floristic diversity should be considerable. Collectively, the study sites include a total of 917 species, 368 genera and 76 families in the cumulative 2 ha that we sampled. If we add the Chamela sites studied by Lott et al. (1987), the total floristic contingent rises to 975 species in 21 localities sampled at the scale of 0.1 ha. The modification of the sampling protocol of Gentry (1982) to include smaller plants (2.4 $\geq$ dbh $\geq$ 1.0 cm) was helpful to characterize the floristic diversity of Mexican SDTFs given the fact that small trees, small lianas and shrubs were found to be the predominant life forms of the forests. This modification allows us to gain insights regarding the patterns of variation in floristic diversity across sites within Mexico, as described in our results. However, in order to put our data set into perspective with what is known for other tropical forests, we need to restrict our results to those plants with dbh $\geq$ 2.5 cm (cf. Gentry 1982, 1988).

The mean number of species with dbh $\geq$ 2.5 cm for all Mexican sites was 58 (range 22–97). This number is 30% larger than the expected average, according to Gentry's (1982) relationship between rainfall and species diversity, for sites of equivalent precipitation. If we include the data of the Chamela site sampled by Lott et al. (1987), we find that in 74% of the cases the diversity of Mexican SDTF sites is greater than expected, with eight sites showing values of species diversity 2–3 times greater than would be predicted by the species–rainfall relationship of Gentry. It is worth noticing that, although six of our sites had values lower than expected, most of them were distributed under extreme environmental conditions for SDTFs. Two of them grow in the wettest localities we studied. One was located at a very unusual elevation (2020 m) for this type of tropical forest (Rzedowski and Calderón 1987), and one was the driest location in the direct vicinity of the Tehuacán Valley, an area of Central Mexico with a strong rainshadow effect that defines the establishment of one of the major desertic zones of Mexico (Villaseñor et al. 1990). Aside from these exceptional sites, we found that in only three cases were the expected values greater than 25% from what we found. The trend of greater floristic diversity for Mexican SDTFs is statistically significant, as revealed by a pairwise comparison with the expected diversities according to the TAP of the localities of study.

The significant trend of higher species diversity in the Mexican sites may not necessarily invalidate the relationship of rainfall and local plant diversity uncovered by Gentry (1982, 1988). However, our regression analyses revealed that total annual

rainfall did not significantly explain the variation in species diversity across sites. It would seem that the significant correlation of diversity and precipitation that Gentry (1982, 1988) found for moist and wet tropical forests is not applicable to the SDTFs of Mexico.

This finding leads to the question of whether this is a general feature of SDTFs or if it is more specific to the Mexican sites. When we developed a new regression for the SDTFs, using the most complete data set available for this type of forest (Clinebell et al. 1995; Gentry 1995; Gillespie et al. 2000), but excluding the Mexican sites, we found that the relationship is highly significant, although with a more limited predictive power (22.2%) than the original model (93%). Largely this appears to be so because the SDTF data points fall below the original regression. In addition, when the Mexican data points were included, the regression becomes non-significant because these sites lie predominantly above the regression line. In sum, in the context of the floristic diversity known for other sites in the Neotropics, Mexican SDTFs are unusually diverse and their variation in species richness is not explained by TAP.

A few additional sites sampled by Gentry (1995) in South America share the unusual diversity of the Mexican sites. Sites Perseverancia, Yanaigua and Curuyuqui in Bolivia, and Tarapoto in Peru, have diversity levels that surpass those expected by Gentry's original equation. With the exception of the Peruvian site, the others as well as the Mexican sites are located in latitudinal positions that challenge the well-established pattern of decrease in species diversity with latitude (Pianka 1966; Gentry 1988; Huston 1994). With his usual insightful vision, and being aware of the remarkable values of species diversity in Chamela, Mexico (Lott et al. 1987), Gentry (1995 and personal communication to R.D.) suggested that the unusually high species diversity of SDTFs may be a general subtropical phenomenon. Clearly, the study of the factors responsible for this apparent pattern is an aspect of tropical conservation biology that warrants further research.

The lack of a significant relationship of species diversity of SDTFs and annual rainfall in Mexico was consistent when we considered all plants (trees plus lianas) with dbh $\geq$ 1.0 or 2.5 cm, trees of both size classes and lianas with basal diameter $\geq$2.5 cm. This lack of relationship challenges the widely known, simple and most attractive pattern described by Gentry (1982, 1988) and later supported by Clinebell et al. (1995). The fact that a predominant driving force of the ecology of plants and animals from this type of forest is seasonality (see Mooney et al. 1995) led us to explore climatic variables related to the time course of water availability for plants throughout the year. Surprisingly, the mean number of dry months per year did not significantly explain the variation in species diversity of all plant size classes and life forms. The same situation was found in the case of the mean number of wet months for all plants (trees plus lianas) and trees (alone) of all sizes and only in the case of lianas alone did we find a significant relationship, although with a very limited predictive value. This result contrasts with that of Clinebell et al. (1995), who found that the numbers of dry and wet months were significantly correlated with species diversity (Pearson's $\rho = -0.706$ and 0.715, respectively; $P = 0.0001$ in both cases) for a large data set including 69 Neotropical forests, most of which were moist/wet sites.

In contrast to precipitation, with the exception of lianas with diameter ≥2.5 cm, Thornthwaite's index of potential evapotranspiration was highly significantly related to species diversity, with predictive values that range between 32 and 45%. Thornthwaite's index (1948) is an environmental parameter that is widely used in climatological studies (Alley 1984); however, it is seldom used in ecological research, despite the fact that it can be readily computed from meteorological and climatological data. Given the fact that this index takes into consideration solar radiation, monthly temperature and precipitation to derive the potential time course of water availability for a given site, it may be useful in studies of seasonal ecosystems. The generality of its predictive value for species diversity in SDTFs and its potential for application to other types of forest needs to be tested with other data sets. Interestingly, Currie and Paquin (1987) found that species diversity in North American forests is significantly explained by variation in evapotranspiration. The fact that the large data set of Gentry can be obtained, upon request, from the Missouri Botanical Garden (http://www.mobot.org/mobot/research/gentry) provides an opportunity to validate the usefulness of Thorntwaite's index in studies of tropical forest diversity.

The lack of a relationship between the diversity of species of lianas and climatic variables we observed in this study was not consistent with the response of other life forms. We speculate that the low number of species per site (1–17 for plants ≥1.0 cm, and 0–12 for plants ≥2.5 cm basal diameter) may be at least partly responsible for this lack of relationship. Clearly, this is an aspect that warrants further work.

In addition to the information provided by our data set to characterize plant species richness at the local (α) level in Mexican SDTFs, we used specific identities to explore the patterns of species turnover throughout the 20 localities. Strikingly, 72% of the 917 species we sampled was present only in a single site and not one single species was present in all 20 sites, while only one species was present in 60% of the sites and only two species were distributed in 50% of the sites. In addition to this, the matrix of pairwise comparisons of all sites in terms of shared species and Sorensen's similarity indices underscore the fact that species turnover in Mexican SDTFs is very high. The mean number of shared species among all possible pairs of sites was 7 and only in 5.8% of the cases was the number of shared species ≥20. Likewise, the overall mean similarity (S) was only 9.0% and only directly adjacent sites had a moderately high similarity (44 and 46%). Similarly, Ratter et al. (1996) found that in the Brazilian cerrado and Amazonian savanna, out of 534 species sampled in 98 sites, 158 (i.e., 30%) occurred at a single site only and only 28 species were found at 50% or more sites.

The high turnover rate of species in Mexican SDTFs leads to the occurrence of very distinct floristic assemblages at the species level and this suggests the existence of processes of high local diversification (see Kohlman and Sánchez-Colón 1984), possibly due to particular historical processes. For example, Pennington et al. (2000) suggest that processes of fragmentation and expansion of tropical dry forests during the Pleistocene may have driven plant speciation in these forests.

The fact that floristic diversity of Mexican SDTFs is rather high, both at the local (α diversity) and regional (β diversity) levels, has an important implication from the conservation point of view: the protection of this type of forest in Mexico will

require a network of numerous reserves distributed throughout the country. The criticality of this issue is underscored by the fact that SDTFs of Mexico are particularly rich in endemisms. Rzedowski (1991a, b) estimates that Mexican SDTFs hold a contingent of 60 and 11% of endemic species and genera, respectively. At the local level information is still very limited, but available information highlights the situation. For example, the Balsas River Basin (where sites 9, 10, 11 and 12 are located) has as much as 20 endemic species of the genus *Bursera* (Toledo 1982) and this area is undoubtedly an important center of speciation of this evolutionary lineage (Miranda 1947; Toledo 1982; Rzedowski 1991b). Sampled sites such as C. Zopilote (12), Infiernillo (9), Cuicatlán (14) and Jocotipac (15) contain 45, 30, 35 and 39% of endemic species, respectively (Trejo 1998).

Against this scenario of high significance of biological diversity in Mexican SDTFs we must observe the fact that current rates of deforestation of SDTFs in the country are alarmingly high. Trejo and Dirzo (2000) have estimated that only 27% of SDTF coverage in Mexico remains in a relatively satisfactory condition of forest structure and integrity. In addition, the same authors have estimated deforestation rates of up to 1.4% per year for some specific localities, such as the state of Morelos (where site 10, El Limón is located). All of this underscores the criticality of delineating comprehensive, long-term and effective plans for the conservation of SDTFs in Mexico.

Several important studies on Neotropical plant diversity (e.g. Clinebell et al. 1995) claim that forests with plentiful and year-round moisture supply are the most diverse and that, therefore, conservation efforts should be directed to these ecosystems. The present investigation indicates that conservation efforts should be directed, also, to tropical forests growing in locations of relatively low and seasonal rainfall.

The different facets of the remarkably high floristic diversity of Mexican SDTFs documented in this study, their high levels of endemism and the current threats to their survival due to land use patterns clearly constitute an issue of local and global concern for biodiversity conservation.

Acknowledgements

This study was supported by the Pew Scholars Program in Conservation and the Environment (R.D.), by a grant from the National Geographic Society (no. 4875-92) to R.D., and by a CONACYT grant to I.T. Pedro Tenorio and Germán Avila-Sakar assisted with field work. Néstor A. Mariano, Toby Pennington and Lourdes Rico read a previous draft and made useful comments.

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