

Tree species diversity driven by environmental and anthropogenic factors in tropical dry forest fragments of central Veracruz, Mexico

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Abstract We examined vegetation structure and woody species diversity in relation to 14 environmental and anthropogenic factors in ten tropical dry forest (TDF) fragments in central Veracruz, Mexico. The basal area of the canopy (30.2 ± 2.11 m²/ha) and understorey (1.96 ± 0.12 m²/ha) trees was similar, but density ($1,014 \pm 104$ and $2,532 \pm 227$ individuals/ha, respectively) differed among sites. We recorded 98 canopy, 77 understorey, and 60 seedling species. Richness was 24–45 species per site, Fisher's alpha and Shannon's indices increased with site altitude. Chao Jaccard indices revealed high species turnover, and a consistently higher similarity within the sites at the lowest and within the highest elevation sites. Ordination identified altitude, aspect, slope, water proximity, cattle and trails as significant explanatory variables of species patterns, and showed that sites at lower elevations were clearly separated from the other sites. Environmental heterogeneity alone did not control species diversity distribution, but species were affected by environmental filters at different stages in their life cycle, e.g., water proximity was significant for saplings and seedlings but not for adults. Anthropogenic disturbances act synergistically, e.g., trails played a key role in determining structure and tree diversity patterns. An important finding is that human disturbance diminishes species diversity in this TDF, but sites at lower elevations were more disturbed and less diverse, therefore we need to study how environmental factors would act if there were no anthropogenic disturbance.

Keywords Anthropogenic disturbance · Beta diversity · Environmental factors · Tree diversity · Tropical dry forest · Veracruz

Nomenclature Assignment of genera to families follows Angiosperm Phylogeny Group (2003).

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Introduction

Regional (precipitation, temperature, solar radiation) and local environmental variables (elevation, slope, aspect, water proximity), along with anthropogenic disturbances (trails, cattle, fire, wood extraction) have all been linked to spatial changes in tree species diversity in tropical dry forests (Bullock et al. 1995; Gentry 1995; Trejo and Dirzo 2002; Segura et al. 2003; Gordon et al. 2004; White and Hood 2004; Balvanera and Aguirre 2006).

The length of the dry season and the seasonality of precipitation are two of the major causes expected to determine patterns of tree species richness in tropical dry forest (TDF). However, several authors have established that within TDF vegetation there is no significant correlation between species richness and precipitation (Lott et al. 1987; Gentry 1995; Gillespie et al. 2000; Trejo and Dirzo 2002). In contrast, variation in patterns of species diversity has been associated with potential evapotranspiration (Trejo and Dirzo 2002), and differences in water availability (Balvanera et al. 2002; Segura et al. 2003; Balvanera and Aguirre 2006). Balvanera and Aguirre (2006) reported that different species occupy different parts of the spatial heterogeneity along water availability gradients, and that many species are excluded from the driest sites where productivity is lowest. Variables related to water availability are elevation, insolation, slope and soil water-holding capacity (Balvanera et al. 2002). Segura et al. (2003) reported that along a water availability gradient in a 1 km long watershed, tree species richness and species diversity declined as water availability decreased. Live stem density increased substantially along the water availability gradient and the proportion of dead stems increased towards the driest sites.

Many authors have noted the importance of topographic variation, elevation, slope, aspect, and the distribution of plant communities (e.g., Moody and Meentemeyer 2001; Pausas and Austin 2001; Balvanera et al. 2002; Poulos et al. 2007; Mwaura and Kaburu 2009). The timing of solar radiation is an important factor in the topographic distribution of vegetation in drylands (Walton et al. 2005). The mosaic of biotic and environmental conditions found within topographically complex TDF likely play a fundamental role in the maintenance of the elevated species diversity found in these ecosystems (Segura et al. 2003). Other authors have reported that different microhabitat conditions influence species differentiation among canopy and subcanopy trees (Vargas-Rodríguez et al. 2005).

Human activities cause fragmentation, habitat loss and, in general, affect forest structure, composition, diversity, and deplete ecosystem goods and services in forest remnants. Gillespie et al. (2000) reported that in several dry forests of Nicaragua and Costa Rica there was a significant correlation between anthropogenic disturbance (intensity and frequency of fire, wood collection, grazing) and total species richness, tree and shrub species richness, and liana abundance. Sabogal (1992) reported that tree richness is relatively low and tends to decline with increasing stand disturbance in TDF in Nicaragua and because of anthropogenic disturbance, forests have low productivity, lower economic value, and increasing irregularity in the regeneration of commercial species. Gordon et al. (2004) reported that tree and shrub species of limited distribution are very uncommon in disturbed forests, and therefore the higher degree of anthropogenic disturbance may explain the relative lack of restricted range species in southern Honduras in comparison to TDF in coastal Oaxaca, Mexico.

In this paper, we focus on the TDF defined in its simplest terms as forest occurring in tropical regions characterized by pronounced seasonality in rainfall distribution, resulting in several (5–8) months of drought (Mooney et al. 1995). In Mexico and Central America, TDF is characteristic of the Pacific basin regions. The eastern Mexican TDF used to occur in three discontinuous patches: southern Tamaulipas, central Veracruz, and the northern

part of the Yucatan Peninsula (Rzedowski 1978; Challenger 1998; Trejo and Dirzo 2000). TDF has been mostly studied in the Pacific side and on the Yucatan Peninsula, but little is known about the TDF along the Gulf of Mexico coast, particularly in central Veracruz.

Until recently, TDF in central Veracruz, Mexico, was considered to have been practically destroyed because of overexploitation and conversion to agricultural land (Rzedowski 1978; Trejo et al. 2007). However, remnants of dry forest persist and may contribute to the biodiversity of Mexico, even though none of them is under protection. Lopez-Barrera (unpublished data based on INEGI III) reported that 94,372 ha of TDF remained in Veracruz (1.3% of the state's territory) and 35% of that surface is part of our study area.

Since TDF is disappearing at an alarming rate (Trejo and Dirzo 2000), our immediate objective was to record the biodiversity and related attributes of this type of vegetation. This study is part of a long-term multidisciplinary research project (Restoration of Forest Landscapes for Biodiversity Conservation and Rural Development in the drylands of Latin America; ReForLan 2007) focused on identifying and promoting approaches for the sustainable management of dryland forest ecosystems, by researching ecosystem restoration techniques using native species of economic value. Field survey data will be used to identify locations with high species richness or a high density of threatened, endemic or highly valuable tree species, to facilitate the identification of priority areas for conservation and restoration.

The aim of this particular study was to determine the vegetation structure and woody species composition, as well as the alpha and beta diversity patterns of the TDF remnant in central Veracruz, Mexico. Since the effects of environmental heterogeneity and anthropogenic disturbance on TDF are not fully known, the objective was to assess the current patterns of woody plant diversity as a function of a suite of environmental factors and to examine the impact of human activities on variation in tree species composition in this regional dry forest.

Methods

Study area

The study area is located in central Veracruz, Mexico, in the adjacent Municipalities of Comapa and Paso de Ovejas (19° 17' N and 96° 26' W, between 97 and 420 m elevation), covering an area of 300 km², and hereafter referred as PO (Fig. 1). The climate is hot and dry. Mean minimum and maximum temperatures are 19.8 and 30.7°C, respectively. Mean annual precipitation is 966 mm (range: 502–1,466 mm), unevenly distributed through the year. The dry season extends from October to May (data from the nearest meteorological station at Loma Fina; 7–28 km from the study sites). The dominant soil units are Cambisol and Vertisol with exposed rock. The type of vegetation was TDF, and recent research indicates that there is still ~7% of the original forest in the region (López-Barrera personal communication). In this region land is mainly used for cattle ranching, generally on a relatively small scale by private landowners; but for common land tenants (*ejidatarios*) activities are more diverse, and the main activity is growing corn (Gallardo-López et al. 2002).

Ten fragments were selected to characterize the forest of PO (Fig. 1; Table 1). The sites were located 0.55–21.80 km away from each other (mean = 10.67 km), fragment surface area was 1.5–60.1 ha (mean = 14.6 ha), and the fragments were most likely part of a forest that originally covered the region.

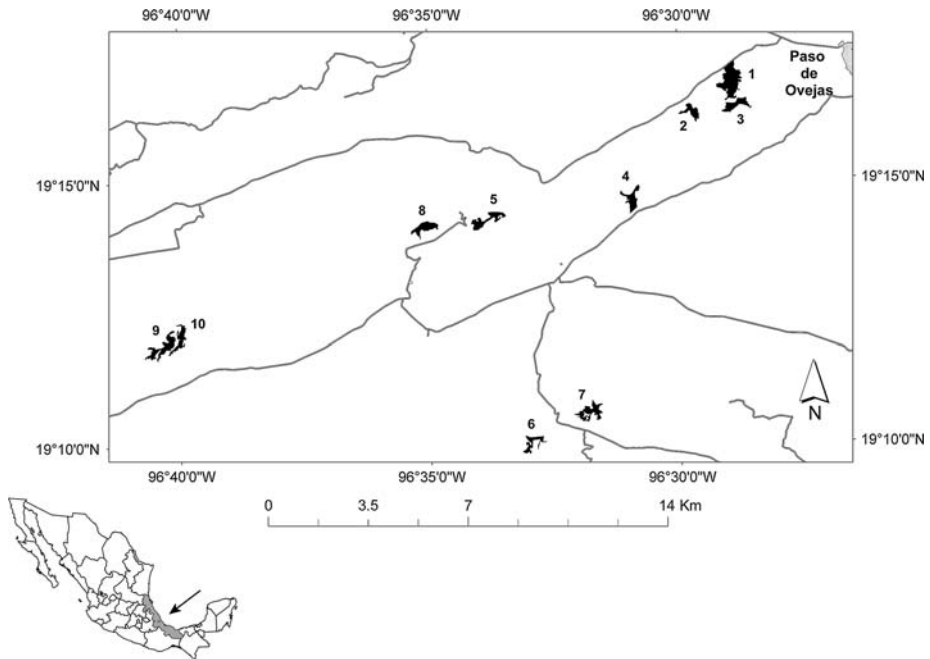


Fig. 1 Location of the ten tropical dry forest fragments used in the study, and roads in central Veracruz, Mexico

Forest structure and floristic composition

At each study site, we set up ten 10×10 m plots for trees ≥ 5 cm in diameter at 1.3 m (dbh) at least 20 m from the fragment edges. Inside each plot we set a 5×5 m subplot for small trees, saplings and shrubs < 5 cm dbh, and a 2×2 m subplot for the advanced regeneration < 2 m height. Henceforth, these three categories are referred to as canopy trees, understory trees, and seedlings, respectively, unless otherwise specified.

In each sampling unit, we measured the diameter and height of canopy and understory trees, and counted the number of seedlings. All plants were either identified in the field or specimens were collected for subsequent identification in the XAL herbarium of the Instituto de Ecología, A.C. The assignment of genera to families follows Angiosperm Phylogeny Group (2003).

In the 100 plots surveyed for each tree size class, richness was calculated as the number of species, and stand structure as basal area (m^2/ha), density (individuals/ha), mean and maximum height (m) of stems for canopy and understory trees, and density for seedlings. Large non-tree plants such as *Beaucarnea recurvata* and *Yucca elephantipes* were recorded in the sampling plots and included in the floristic composition analysis, but were excluded from the structural analyses.

Richness and diversity

Species accumulation curves and the nonparametric estimators, ICE and Chao2, were calculated to assess the completeness of the inventories. Species richness was compared

Table 1 Characteristics of ten fragments of tropical dry forest in central Veracruz, Mexico

<i>Site characteristics</i>										
Site	1	2	3	4	5	6	7	8	9	10
Location	Hato Marines 1	Mata Mateo	Hato Marines 2	El Limon	Acazonica Pepesca	Xocotitla Ranch	Xocotitla Road	Acazonica Cantaranas	Caminos Stream	Caminos Top
N Latitude	19°16'12"	19°16'30"	19°16'33"	19°14'31"	19°14'18"	19°10'4"	19°10'37"	19°14'5"	19°11'59"	19°11'49"
W Longitude	96°29'39"	96°28'52"	96°28'53"	96°30'55"	96°33'40"	96°33'0"	96°31'53"	96°35'12"	96°40'13"	96°40'12"
Area (ha)	21.1	1.5	60.1	2.0	2.4	1.5	2.6	2.1	32.6	19.5
Total no. species	28	29	24	29	40	26	40	37	41	45
<i>Explanatory variables</i>										
Altitude	97 (3)	101 (3)	117 (2)	170 (0)	172 (4)	221 (3)	230 (0)	244 (9)	393 (6)	420 (2)
Slope	26 (6)	41 (5)	49 (3)	20 (4)	31 (5)	35 (1)	3 (3)	21 (2)	56 (6)	48 (2)
Aspect	102 (19)	207 (7)	68 (8)	199 (14)	243 (25)	293 (21)	279 (27)	306 (8)	171 (23)	207 (28)
Radiation	0.90 (0.07)	0.76 (0.04)	0.80 (0.07)	0.93 (0.08)	0.76 (0.09)	0.65 (0.08)	0.99 (0.44)	0.70 (0.03)	0.72 (0.12)	0.70 (0.11)
Exposed rock	15 (2)	23 (7)	29 (9)	19 (5)	27 (9)	59 (7)	4 (2)	3 (2)	4 (1)	31 (10)
Stoniness	9 (5)	20 (4)	18 (5)	7 (2)	28 (9)	37 (4)	2 (1)	29 (9)	15 (6)	27 (7)
Canopy	11 (2)	8 (2)	7 (1)	5 (1)	4 (0)	5 (0)	5 (0)	3 (0)	6 (1)	6 (1)
Bare soil	17 (5)	21 (5)	17 (5)	4 (1)	9 (4)	1 (0)	0 (0)	14 (7)	1 (0)	1 (1)
Herb cover	60 (9)	40 (7)	62 (6)	21 (8)	5 (2)	1 (0)	28 (10)	52 (13)	28 (11)	4 (1)
Water	0	1	2	1	1	1	0	0	1	2
Trails	2	1	2	2	0	0	1	0	2	0
Cattle	1	0	1	1	0	0	0	1	1	0
Cut	0	0	5	2	0	2	0	1	4	1
Dead	2	0	7	4	5	4	2	3	2	7

Explanatory variables are: means (±1 SE) of altitude (m), slope (°), aspect (°), radiation (MJ/cm²/year), exposed rock (%), stoniness (%), canopy openness (%), bare soil (%), herbaceous cover (%); modes for water proximity and trail categories; presence or absence data is given for cattle; number of cut and dead are individuals/0.1 ha

among the ten study sites after reducing the number of individuals to a common abundance level using rarefaction curves with the S_{obs} Mau Tao function. We used EstimateS version 7.5 software (Colwell 2005).

Fisher's alpha and Shannon's diversity index were calculated for each site, and for the region. Fisher's alpha is the preferred diversity estimator because it is independent of the number of individuals sampled, and assumes a log-normal distribution of relative abundances for the population from which the sample is drawn. The Shannon index has been widely used in ecological studies, it has been criticized because it confounds species richness and evenness in a single number, but we coincide with several authors in taking this as an advantage rather than a problem (see Magurran 2004; Jost 2007).

Beta diversity was also analyzed at a regional scale using Chao's Jaccard abundance-based similarity index (Chao et al. 2005; Colwell 2005). This similarity index includes not only species matching but also similarity of relative abundances, with a value of 1 for identical assemblages and tending toward 0 for increasingly dissimilar assemblages. It is nonparametric in the sense that there is no need to postulate any particular species abundance distribution to derive the estimators. The derivation assumes that the number of species is finite (Chao et al. 2005).

Explanatory variables

A suite of ten environmental and four human activity-related variables were measured in each 10×10 m plot. Environmental variables were elevation, slope, aspect, incident radiation, stoniness, rockiness, canopy openness during the wet season, percent of bare soil, herbaceous cover, and water proximity. Anthropogenic variables were trails, livestock presence, and dead trees (cut and natural). Fire was planned to be recorded as number of burnt stumps and presence of ashes on the floor but we did not find signs of recent fires in the forest interiors.

The position (latitude, longitude) of each sampling plot was located precisely using a global positioning device (GPS Garmin III Plus, Garmin Corporation, Kansas, USA), and the altitude measured using an altimeter (Thommen Classic, Switzerland). Aspect and slope were estimated using a compass and clinometer, respectively. Aspect is a poor variable for quantitative analysis, since 1° is adjacent to 360° —the numbers are very different even though the aspect is about the same. So aspect was transformed to folded aspect (McCune and Keon 2002). Stoniness and rockiness were estimated as the percentage of the surface covered by stones or exposed rock. To estimate the potential annual direct incident radiation ($\text{MJ}/\text{cm}^2/\text{year}$) based on topographic variables, we used the equations proposed by McCune and Keon (2002), with the correction of McCune (2007). Percent canopy openness was determined using a crown densiometer during the rainy season. For water, categorical values were assigned according to permanent or intermittent streams and their proximity (0 for no water, 1 for a permanent stream < 10 m away, 2 for a stream > 10 m away or an intermittent stream). For trails, we assigned a categorical value based on proximity observations (0 for no trail, 1 for a trail < 10 m away, and 2 for a trail > 10 m away). Livestock was ranked as 0 for no evidence of any cattle and 1 if dung was present. Dead trees resulting from natural or anthropogenic causes were counted.

Data analyses

An analysis of variance (ANOVA; with post hoc Tukey's honestly significant difference test) was used to analyze differences in vegetation structural variables among study

sites. Prior to the ANOVA, structural data were tested for normality with the Shapiro–Wilk W test and for homogeneity of variance with the Levene test; non-normal data were log transformed. The correlation between pairs of richness with structural variables and between pairs of explanatory variables were determined using Spearman's rho correlation coefficients. The statistical software package used was JMP, version 3.2 (SAS 1997).

A canonical correspondence analysis (CCA) was used to facilitate the interpretation of the relationship between species composition of the study sites and the 14 explanatory variables. The three species matrices (canopy, understory and seedling) contained tree counts per species, per plot. The matrix for environmental variables included altitude, slope, aspect, incident radiation, stoniness, rockiness, canopy openness, percent bare soil, herbaceous cover, water proximity, trails, cattle, dead trees and stumps. CCA is able to summarize the relationships between response variables (species abundances) and one or several explanatory variables. CCA was appropriate because the objective is to describe community variation with respect to a particular set of environmental variables (see McCune 1997). We used the program CANOCO, version 4.5 (ter Braak and Smilauer 1998), and the forward selection for ranking environmental variables in order of importance for determining the species data, for reducing the large set of environmental variables, and to determine the statistical significance of each selected variable judged by a Montecarlo permutation test.

Results

Forest structure and floristic composition

The vegetation structure of the PO TDF was estimated for three strata. Canopy trees had an average basal area of 30.2 (se = 2.11) m²/ha, tree density of 1,014 (104) individuals/ha, mean and maximum height were 10 (0.5) and 15 (0.7) m, respectively. For understory trees, average basal area was 1.96 (0.12) m²/ha, density of 2,532 (227) individuals/ha, mean and maximum height were 3.7 (0.2) and 5.4 (0.3) m, respectively. Seedling density was 28,715 (1,507) individuals/ha. The results of the ANOVAs indicated that basal area was similar among study sites for canopy and understory trees, however, for both tree size classes, density, and mean and maximum canopy height varied among study sites (Fig. 2). Seedling density was statistically similar among study sites.

A total of 122 species, 82 genera and 40 families (119 taxa identified at least to family and 3 morphospecies) were recorded in one sampled ha for the three strata surveyed in ten TDF fragments. We recorded a total of 1,019 canopy trees belonging to 98 species, 634 understory trees belonging to 77 species, and 1,154 seedlings belonging to 60 species (see Appendix).

Fabaceae and Euphorbiaceae were the most diverse families, with 22 and 14 species, respectively, and accounted for 30% of the species identified. The genera *Acalypha* and *Bursera* had more species (four species each) than the other genera. Canopy tree species contribute 80% of the species richness. Only eighteen of the recorded understory tree species differed from the canopy tree species (e.g., *Acalypha alopecuroides*, *A. arvensis*, *Achatocarpus nigricans*, *Annona reticulata*, *Eugenia mozomboensis*, *Euphorbia tithymaloides*, *Hippocratea celastroides*, *Malvaviscus arboreus*). This means that nearly 77% of the understory species were young individuals of the canopy tree layer. Six species <2 m height category (*Bucida buceras*, *Capparis frondosa*, *Chamaecrista nictitans*, *Coursetia*

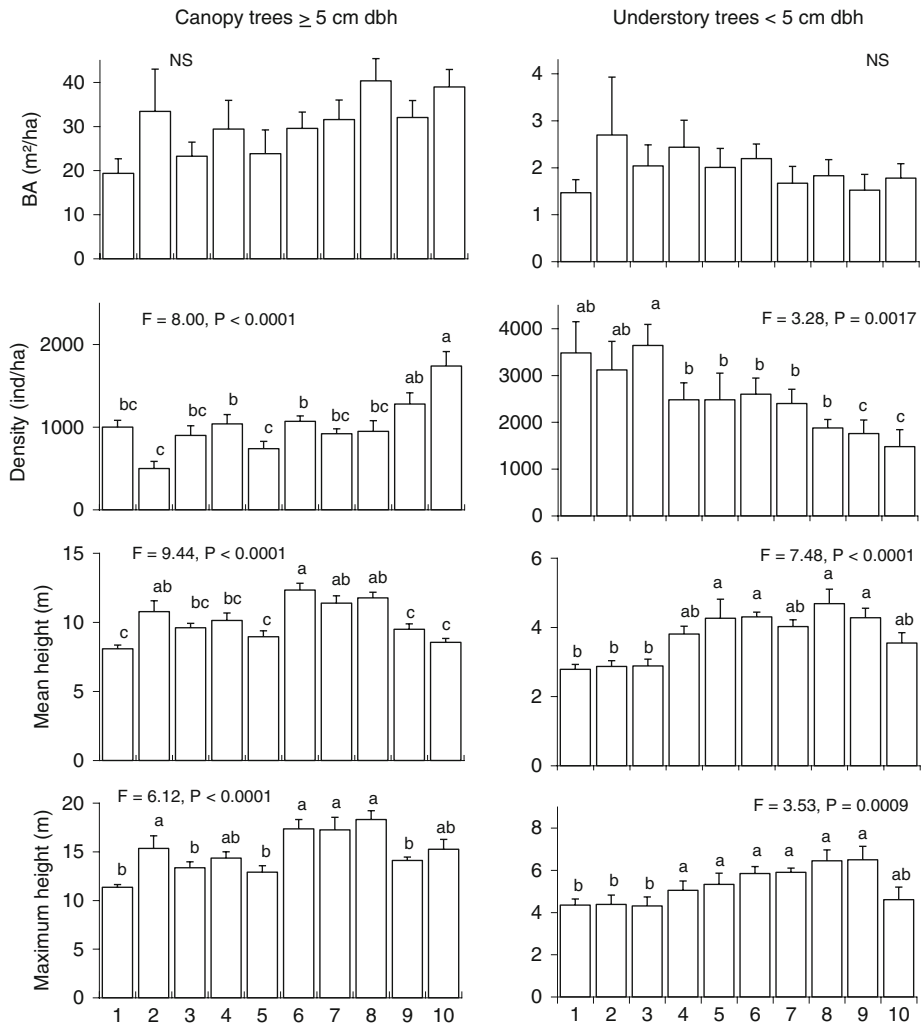


Fig. 2 Vegetation structure of ten tropical dry forest fragments in central Veracruz, Mexico

carbaea, *Piper hispidum* and an unidentified legume) were not found in the canopy and understory layers because they were not tree seedlings, but rather small woody plants of the forest understory (see Appendix).

In the forest canopies, one species, *Heliocarpus donnellsmithii*, was present at all the sites, followed by *Luehea candida* and *Tabebuia chrysantha*, which were found in nine and eight of the sites, respectively. Almost 46% of the species were found in just one of the ten sites. The most common understory species were *Ayenia adenostachya*, *Croton cortesianus*, *Heliocarpus donnellsmithii*, and *Luehea candida*. As found for canopy trees, the percentage of understory species at a single site was high (44%). The species most frequently recorded as seedlings were *Leucaena lanceolata*, *Luehea candida*, and *Randia aculeata*, but of all the species 53% was specific to one of the ten sites.

Richness and diversity

Overall, the total number of tree species per site ranged from 24 to 45 (Table 1). Canopy tree species per site ranged from 17 to 35; there were 10–21 understory species, and 8–19 seedling species (Table 2). The total number of species in each site and stratum was compared using individual-based rarefaction curves with the S_{obs} Mao Tau (Colwell 2005) and standardized to a minimum number of individuals to estimate richness for each site. Rarefaction curves indicated a trend toward higher richness in sites located at higher elevations. Rarefaction curves for canopy trees (49 trees) revealed that sites 7, 5, 9, and 10 are richer than the other sites. Furthermore, they indicated that sites 10, 9, 8, and 5 for understory trees (37 trees), and sites 8, 5, 10, and 4 for seedlings (93 seedlings) are richer in species than the other sites (Fig. 3).

The species accumulation curves for the three forest strata showed no indication of reaching an asymptote, and therefore the non-parametric indicators of diversity indicated that many more species are likely to be found. ICE and Chao2 suggested that 52–64 more species are needed to complete the inventories for canopy trees, between 25 and 35 for understory trees, and 16–14 for seedling species, respectively (Table 2). Fisher's alpha was high for canopy and understory trees but relatively low for seedlings, whereas the Shannon index was high and similar for the three strata (Table 2).

Tree species abundance varied from one site to another; therefore, turnover was high for canopy tree, understory and seedling species in the study area. The abundance-based Jaccard index (1 indicates identical composition) was 0.08–0.62 for canopy tree species, 0.01–0.56 for understory, and 0.00–0.52 for seedlings. Similarity was consistently higher for the sites at the lowest (sites 1, 2, 3) and those at the highest (9 and 10) extremes of the altitudinal gradient for the three tree size classes (Table 3). High species turnover was indicated by a larger difference in beta diversity between lower altitude and higher altitude sites. In general, seedling species turnover was the highest, and compared with all the other sites, sites 1, 2, and 3 had the lowest similarities with values mostly <0.09 in their species composition and abundance (Table 3).

Direct gradient ordination analysis

The CCA was carried out for 100 plots and abundances of canopy trees (98 species), understory trees (77 species), and seedlings (60 species) with 14 explanatory variables in each case. All the CCA models retained four significant environmental variables for the three tree size categories: altitude, aspect, trails and cattle. The gradient established along the first ordination axis was mostly related to altitude and the presence of trails and cattle for the three tree size classes. Additionally, the model for canopy trees and seedlings retained slope, and the model for understory trees and seedlings retained water proximity as significant explanatory variables (Figs. 4, 5, 6; Table 4).

For canopy trees, axis 1 (eigenvalue = 0.52) and axis 2 (eigenvalue = 0.406) described 17.3 and 13.6% of the species-environment relationship (Monte Carlo test, first axis $F = 2.89$, $P = 0.01$; all canonical axes $F = 1.53$, $P = 0.005$). Ordination of plots according to species abundance data showed a separation of groups of sites. CCA results show that sites 1, 2, and 3 were clearly separated from sites 9 and 10, and both groups were separated from the other sites along the first canonical axis. Several species exhibited a strong association with a particular group of sites. For instance, *Brosimum alicastrum*, *Bursera fagaroides*, *Calypttranthes schiediana*, and *Stemmadenia pubescens* were strongly associated with the 1-2-3 site group. *Comocladia engleriana*, *Luehea candida*, *Senna*

Table 2 Richness and diversity of tropical dry forest fragments arranged by altitude, from lowest to highest

Site	Ind	S_{obs}	ICE	Chao2	α	Shannon
A						
1	99	17	22	22	5.91	2.44
2	49	17	22	20	9.23	2.51
3	89	15	20	18	5.17	2.09
4	104	22	46	33	8.53	2.56
5	74	26	58	40	14.27	2.90
6	107	22	26	25	8.39	2.77
7	92	34	73	142	19.5	3.07
8	95	20	27	25	7.73	2.59
9	136	35	63	54	15.26	3.07
10	174	34	44	40	12.6	3.06
Total	1,019	98	150	162	26.77	3.76
B						
1	87	13	23	16	4.23	1.54
2	79	18	27	23	6.65	2.19
3	91	10	30	29	2.87	1.32
4	62	18	29	23	8.51	2.18
5	62	21	58	48	11.18	2.62
6	65	13	21	15	4.89	1.78
7	60	19	48	34	9.58	2.23
8	47	20	40	43	13.16	2.72
9	44	21	36	31	15.75	2.81
10	37	21	45	37	20	2.89
Total	634	77	102	112	22.95	3.47
C						
1	107	8	11	9	2	1.69
2	123	10	19	23	2.57	1.72
3	98	8	27	21	2.06	1.54
4	143	15	27	23	4.22	2.19
5	111	19	58	39	6.6	2.63
6	140	11	21	18	2.8	1.74
7	134	10	11	10	2.5	2.07
8	93	15	36	25	5.06	2.41
9	97	11	13	12	3.19	2.22
10	108	15	18	16	4.73	2.28
Total	1,154	60	76	74	13.44	3.55

Variables are number of individuals (Ind), observed richness (S_{obs}), estimators ICE and Chao2, Fisher's alpha (α), Shannon's diversity index. The total is given for the regional dry forest of central Veracruz, Mexico.

A Canopy trees ≥ 5 cm dbh, B understory trees and saplings <5 cm dbh, C seedlings <2 m tall

atomaria, *Tabebuia chrysantha* and *Thouinidium decandrum* were strongly associated with sites 4–8. *Bursera simaruba*, *Cochlospermum vitifolium*, *Eugenia hypargyrea*, and *Savia sessiliflora* were strongly associated with sites 9 and 10 which, in turn, were associated with altitude and slope (Fig. 4).

For understory tree vegetation, axis 1 (eigenvalue = 0.684) and axis 2 (eigenvalue = 0.556) of the CCA described 17.1 and 13.9% of the variance in the species-environment relationship, respectively (Monte Carlo test of significance, first axis $F = 2.64$, $P = 0.005$; all canonical axes $F = 1.39$, $P = 0.005$). In this case, there were three groups of

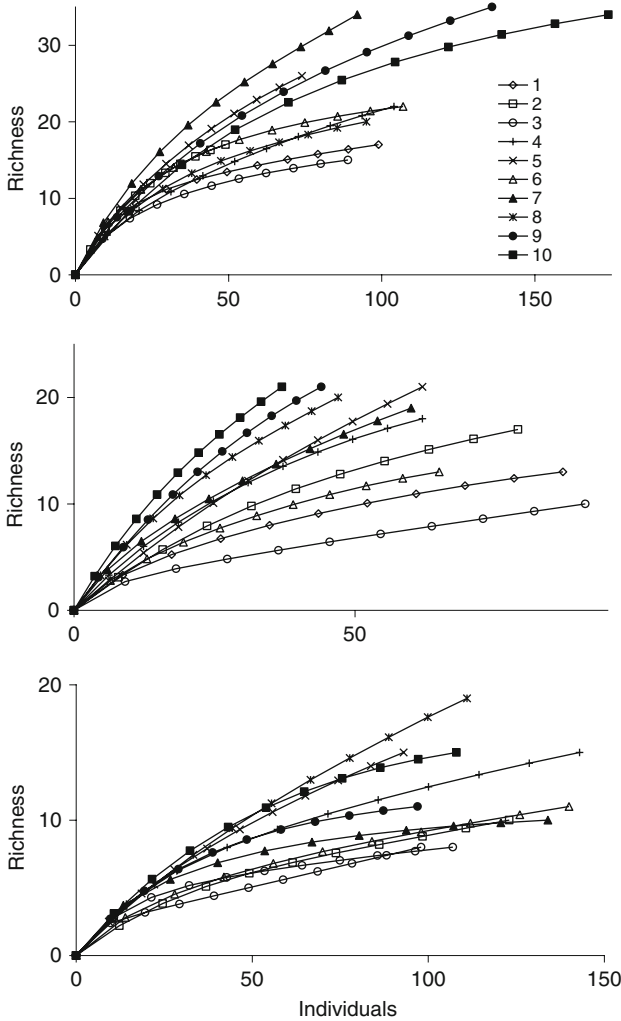


Fig. 3 Rarefaction curves for canopy, understory, and seedling tree species in ten dry forest fragments in central Veracruz, Mexico

sites: sites 1, 2 and 3 are located to the left of axis 1, whereas site 8 is on the right lower side of axis 1. The other sites are on the right upper part of axis 2. *Acalypha alopecuroides*, *Calyptranthes schiediana*, *Croton cortesianus* and *Luehea speciosa* were strongly associated with the 1-2-3 site group. *Achatocarpus nigricans*, *A. aff. villosa*, and *Eugenia mozombombensis* showed a strong association with the rather isolated site 8, while *Euphorbia schlechtendalii*, *Leucaena lanceolata*, *Luehea candida*, and *Trichilia trifolia* were strongly associated with the rest of the sites which constitute another group (Fig. 5).

For the seedlings, axis 1 (eigenvalue = 0.746) and axis 2 (eigenvalue = 0.602) represented 16.2 and 13.1% of the variance in the species-environment relationship (Monte Carlo test of significance, first axis $F = 3.10$, $P = 0.005$; all canonical axes $F = 1.81$, $P = 0.005$). Only two sets of sites were observed: sites 1, 2, and 3 on the right side of axis 1, and the other sites on the left side. Some of the species strongly associated with the 1-2-3

Table 3 Beta diversity according to the Chao Jaccard raw abundance-based estimator for tree species between pairs of tropical dry forest fragments in central Veracruz, Mexico

	1	2	3	4	5	6	7	8	9
A									
2	0.50								
3	0.62	0.30							
4	0.28	0.14	0.17						
5	0.17	0.23	0.08	0.31					
6	0.44	0.26	0.30	0.43	0.17				
7	0.35	0.17	0.17	0.50	0.22	0.31			
8	0.28	0.13	0.18	0.54	0.34	0.35	0.38		
9	0.42	0.24	0.31	0.27	0.32	0.17	0.45	0.35	
10	0.28	0.17	0.23	0.18	0.34	0.21	0.33	0.27	0.56
B									
2	0.18								
3	0.56	0.17							
4	0.08	0.07	0.03						
5	0.01	0.17	0.01	0.10					
6	0.36	0.18	0.33	0.15	0.04				
7	0.02	0.08	0.03	0.44	0.09	0.05			
8	0.04	0.08	0.01	0.28	0.18	0.05	0.30		
9	0.28	0.14	0.27	0.24	0.14	0.36	0.29	0.31	
10	0.10	0.04	0.12	0.10	0.06	0.28	0.26	0.19	0.39
C									
2	0.27								
3	0.50	0.13							
4	0.03	0.04	0.03						
5	0.09	0.02	0.13	0.11					
6	0.01	0.01	0.02	0.16	0.15				
7	0.01	0.00	0.03	0.19	0.08	0.05			
8	0.06	0.01	0.02	0.24	0.33	0.25	0.16		
9	0.15	0.05	0.32	0.24	0.28	0.03	0.17	0.40	
10	0.12	0.00	0.21	0.20	0.12	0.09	0.18	0.22	0.52

A Canopy trees, B understory trees, C seedlings

site group were *Astronium graveolens*, *Acalypha alopecuroides*, *Citharexylum berlandieri*, and *Senna atomaria*. Species strongly associated with the 4–10 site group were *Eugenia hypargyrea*, *Leucaena lanceolata*, *Randia monantha*, and *Luhea candida* (Fig. 6).

Correlations between variables

Correlations between species richness and structural variables suggest that in the PO TDF, canopy tree species richness increases with canopy tree basal area and density, and with height of the understory. On the other hand, understory tree richness was positively correlated with all understory structural variables. Seedling density was positively correlated with the maximum height of the understory vegetation (Table 5A).

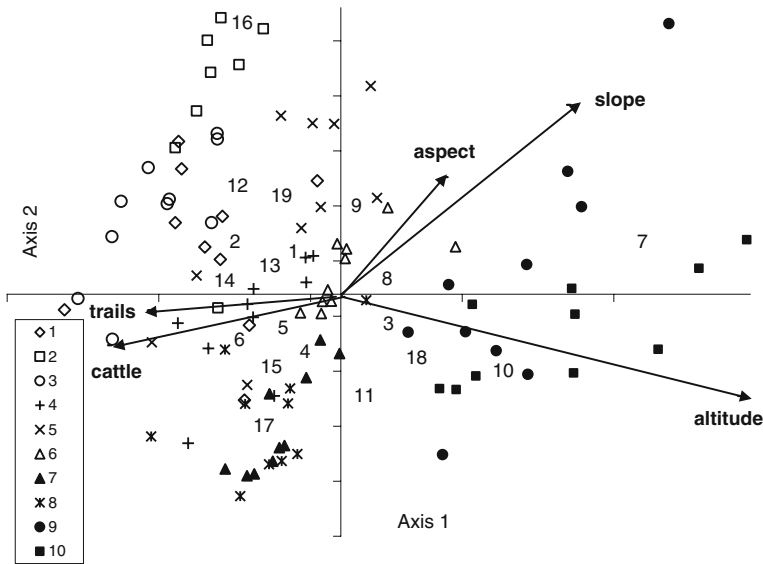


Fig. 4 CCA ordination of 100 plots and 98 canopy tree species in ten sites of TDF in central Veracruz, Mexico. *Triplot* vectors represent the significant explanatory variables: altitude, aspect, slope, trails and cattle. *Triplot* represent some of the canopy tree species with more weight in the ordination. 1, *Heliocarpus donnellsmithii*; 2, *Calyptanthes schiediana*; 3, *Bursera simaruba*; 4, *Luehea candida*; 5, *Ipomoea wolcottiana*; 6, *Tabebuia chrysantha*; 7, *Savia sessiliflora*; 8, *Bursera cinerea*; 9, *Comocladia engleriana*; 10, *Eugenia hypargyrea*; 11, *Lysiloma divaricatum*; 12, *Bursera fagaroides*; 13, *Guazuma ulmifolia*; 14, *Stemmadenia pubescens*; 15, *Senna atomaria*; 16, *Brosimum alicastrum*; 17, *Thouinidium decandrum*; 18, *Cochlospermum vitifolium*

Most of the environmental variables and those related to human activities were correlated among themselves. Sites at higher altitudes had lower percentages of canopy openness, exposed rock, bare soil, herb cover, trails and cattle presence. Radiation decreases with slope and water proximity, but increases in the presence of trails and dead trees. Stoniness was negatively correlated with herb cover and trails but positively correlated with water proximity. The presence of trails was positively correlated with canopy openness, cattle presence, bare soil, and herb cover, and the presence of cut trees was correlated with the presence of cattle (Table 5B).

Discussion

Only by sampling more than one site within a locality such as Paso de Ovejas can a full assessment of diversity at that locality be achieved (Gordon and Newton 2006). Variations recorded at the local scale in Mexican TDF strongly suggest that a significant part of regional scale variation may be an artifact of undersampling sites within locations (Gordon and Newton 2006). Given the importance of representing a locality such as PO with more than one sampled site, and in an effort to assess environmental heterogeneity, we used ten sites to characterize the TDF in this relatively small area. The forest fragments selected to characterize the TDF of PO were structurally and floristically diverse, but grow on sites that are topographically similar to those of other TDF fragments studied in Mexico, and Central America (e.g., Bullock et al. 1995; Trejo and Dirzo 2002; Balvanera et al. 2002;

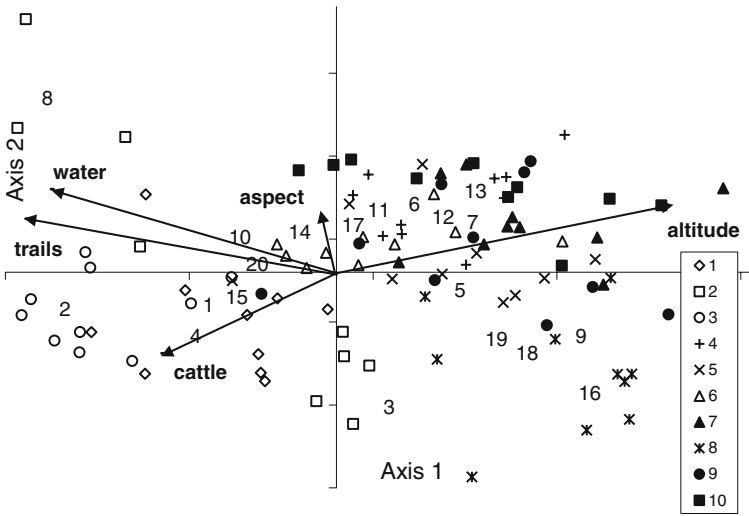


Fig. 5 CCA ordination of 100 plots and 77 understory tree and juvenile species in ten sites of TDF in central Veracruz, Mexico. *Triplot* vectors represent the significant explanatory variables: altitude, aspect, water proximity, trails and cattle. *Numbers* represent some of the understory tree species with more weight in the ordination. 1, *Croton cortesianus*; 2, *Luehea speciosa*; 3, *Astronium graveolens*; 4, *Citharexylum berlandieri*; 5, *Acalypha adenostachya*; 6, *Trichilia trifolia*; 7, *Leucaena lanceolata*; 8, *Acalypha alopecuroides*; 9, *Acalypha* aff. *villosa*; 10, *Stemmadenia pubescens*; 11, *Heliocarpus donnellsmithii*; 12, *Luehea candida*; 13, *Randia aculeata*; 14, *Tabebuia chrysantha*; 15, *Calypttranthes schiediana*; 16, *Eugenia mozomboensis*; 17, *Euphorbia schlehtendalii*; 18, *Achatocarpus nigricans*; 19, *Guazuma ulmifolia*; 20, *Senna atomaria*

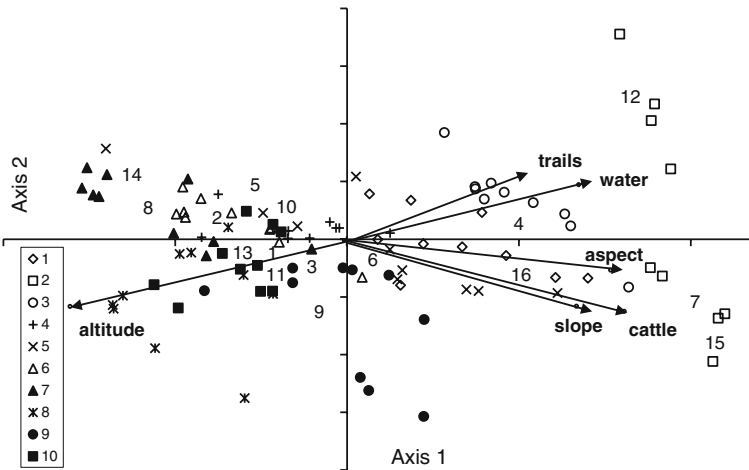


Fig. 6 CCA ordination of 100 plots and 60 seedling species for ten sites of TDF in central Veracruz, Mexico. *Triplot* vectors represent the significant explanatory variables: altitude, aspect, slope, water proximity, trails and cattle. *Numbers* represent some of the seedling species with more weight in the ordination. 1, *Leucaena lanceolata*; 2, *Thouinidium decandrum*; 3, *Randia aculeata*; 4, *Senna atomaria*; 5, *Trichilia trifolia*; 6, *Croton cortesianus*; 7, *Brosimum alicastrum*; 8, *Eugenia hypargyrea*; 9, *Bauhinia* sp.; 10, *Croton reflexifolius*; 11, *Acalypha adenostachya*; 12, *Acalypha alopecuroides*; 13, *Luehea candida*; 14, *Randia monantha*; 15, *Astronium graveolens*; 16, *Citharexylum berlandieri*

Table 4 Environmental variables selected using the forward selection procedure (CCA) to determine their importance in explaining the ordination of plots and species for the canopy, understory and seedling species in the tropical dry forest of central Veracruz, Mexico

Significant effect variables						
Variables	Canopy trees		Understory trees		Seedlings	
	λA	<i>P</i>	λA	<i>P</i>	λA	<i>P</i>
Altitude	0.47	0.005	0.53	0.005	0.53	0.005
Slope	0.34	0.005	–	NS	0.46	0.005
Aspect	0.23	0.005	0.36	0.005	0.33	0.005
Trail	0.28	0.005	0.35	0.005	0.42	0.005
Cattle	0.28	0.005	0.30	0.005	0.46	0.005
Water	–	NS	0.45	0.005	0.54	0.00

λA is the eigenvalue, *P* is the significance level of the effect obtained with a Monte Carlo permutation test under the null model with 199 random permutations

Gallardo-Cruz et al. 2005; Gillespie et al. 2000). Mexican TDF grows predominantly on moderate to steep slopes, with shallow soils and rocky or limestone outcrops (Trejo and Dirzo 2002; Gallardo-Cruz et al. 2005; Vargas-Rodríguez et al. 2005; Durán et al. 2006), but exceptionally TDF can grow on different substrates such as on volcanic rock formations (Castillo-Campos et al. 2007).

Overall, the TDF of PO has structural values, tree species richness and Shannon Index well into the range of those reported for Mexican TDF (Lott et al. 1987; Rico-Gray et al. 1988; Trejo and Dirzo 2002; Durán et al. 2006) and other Neotropical TDFs (Gentry 1995; Murphy and Lugo 1995; Gillespie et al. 2000; Gordon and Newton 2006). Western Mexican dry forest is generally more diverse than other closed-canopy neotropical dry forests (Gentry 1995), and our eastern Mexican dry forest may be as diverse as those forests. Our tree sizes and sample area (1 ha) are not directly comparable with available data, but 40% of the sites had 40–45 tree species in 0.1 ha when the average for 20 locations in Mexico was 58 with a range of 22–97 species for trees with dbh >2.5 cm (Trejo and Dirzo 2002). If we consider that representing TDF for a location such as PO requires the inclusion of several sites, we find that tree species richness is relatively high with 122 woody species sampled over 10 sites, but still in the range of values reported for other sites in Mexico and Central America. In Huatulco, Oaxaca, Mexico, Gordon and Newton (2006) found 111 species in eight 0.1 ha samples, and 132 species in 0.45 ha. In Nizanda, Oaxaca, Mexico, Gallardo-Cruz et al. (2005), reported 145 species ≥ 1 cm dbh sampled in 0.3 ha, but they included woody and non-woody plants. In central Veracruz, Mexico, Castillo-Campos et al. (2007) reported 61 woody species in a TDF growing on volcanic rock. In the more extensive region of Nicaragua and Costa Rica, Gillespie et al. (2000) found 204 species ≥ 2.5 cm dbh in 0.7 ha sampled area. However, Murphy and Lugo (1995) reported a range of only 33–90 tree species on 1–3 ha.

The value of the Shannon Index obtained in PO is high (3.76) but in the range of values reported for other Mexican forests (2.84–4.17, Trejo and Dirzo 2002). In general, the value of the Shannon Index obtained from empirical data falls between 1.5 and 3.5 and rarely surpasses 4 (Magurran 2004).

A positive relationship between species diversity and basal area may be an important characteristic of the dry forest. In the PO forest, tree species diversity (alpha) increases with structural forest characteristics such as basal area, density, canopy height and

Table 5 Nonparametric measures of association Spearman rho between pairs of values

	S_{und}	BA	DEN	H_{mean}	H_{max}	ba	den	h_{mean}	h_{max}				
<i>A</i>													
S_{can}	0.086	0.247	0.714	-0.173	0.065	0.145	-0.162	0.324	0.237				
S_{und}		-0.093	0.101	-0.085	-0.007	0.507	0.456	0.247	0.460				
BA			0.355	0.406	0.575	-0.017	-0.24	0.267	0.136				
DEN				-0.188	0.137	0.071	-0.168	0.190	0.052				
H_{mean}					0.723	-0.001	-0.004	0.283	0.161				
H_{max}						0.098	-0.081	0.337	0.181				
ba							0.545	0.407	0.502				
den								-0.029	0.216				
h_{mean}									0.849				
	Radiation	Canopy	Slope	Aspect	Rock	Stone	Soil	Herb	Water	Trails	Cattle	Cut	Dead
<i>B</i>													
Altitude	-0.162	-0.306	0.094	-0.207	-0.284	0.109	-0.609	-0.392	0.010	-0.421	-0.250	0.029	0.076
Radiation		0.100	-0.226	0.061	-0.017	-0.194	-0.048	0.136	-0.262	0.198	-0.017	0.106	0.210
Canopy			0.145	0.053	0.212	-0.117	0.196	0.180	0.124	0.390	0.015	-0.015	-0.046
Slope				0.070	0.072	0.121	0.083	-0.031	0.573	-0.092	0.002	0.029	0.039
Aspect					0.142	0.006	0.218	0.052	0.134	0.204	-0.132	-0.022	-0.046
Rock						0.390	0.190	-0.156	0.293	-0.024	-0.169	-0.032	0.113
Stone							0.167	-0.292	0.387	-0.332	-0.003	0.051	-0.084
Soil								0.192	0.232	0.335	0.295	0.021	-0.273
Herb									-0.212	0.401	0.331	-0.055	-0.030
Water										0.054	0.029	0.111	0.008
Trails											0.271	0.137	-0.065

Table 5 continued

	Radiation	Canopy	Slope	Aspect	Rock	Stone	Soil	Herb	Water	Trails	Cattle	Cut	Dead
Cattle												<i>0.247</i>	0.030
Cut													0.159

A Richness and basal area (BA, ba), density (DEN, den), mean height (H_{mean} , h_{mean}) and maximum height (H_{max} , h_{max}), S_{can} is observed richness for canopy trees, S_{und} is observed richness for understory trees and saplings, BA, DEN, H_{mean} and H_{max} are structural variables for canopy trees; ba, den, h_{mean} and h_{max} are structural variables for understory vegetation, *B* explanatory variables: altitude, radiation, canopy openness, slope, aspect, rockiness, stoniness, bare soil, herbaceous cover, water proximity, trails, cattle presence, and natural and cut dead trees

Significant correlations are highlighted, $P < 0.001$ by bold-italic type, $P < 0.01$ by bold, and $P < 0.05$ by italic type

understory vegetation. Similarly, Sagar and Singh (2006) reported this relationship in the Vindhyan TDF of India. In addition, if we take basal area as a surrogate of biomass and net productivity, diversity may be positively associated with productivity.

Beta diversity was very high in the PO TDF region. Only a few species were widely distributed and prevalent as canopy, understory or seedlings, and found at several sites; most species (~ 50%) were found at just one of the ten sites (see Appendix). Differences in tree dominance between sites related to environmental variables in one locality have been reported by several authors. Lott et al. (1987) found these differences between arroyos and upland sites in Chamela, Mexico. Also in Chamela, Durán et al. (2006) described tree community patterns in six different morphopedological land units, and found that canopy structure and diversity are not related, but dominant tree species segregated parcels in two groups with granitic versus non-granitic lithology.

The PO TDF sites differed in their environmental and anthropogenic variables, and this variation is reflected in the plant communities and tree species assemblages of each study site. The altitudinal range is clearly a proxy for other variables. Elevation within a range of 97–420 m was important for explaining species diversity patterns, and since elevation was correlated with several variables, it may be used as a surrogate for other factors related to the growth of plants (Pausas and Austin 2001). Elevation has been identified in several studies of tropical and temperate forest communities as the most important environmental feature influencing woody plant composition and structure. For instance, for the Chiricahua National Monument, Sierra Madre Occidental, in Arizona, elevation was the single most important factor, though the independent effects of heat load, soil moisture, and soil type also play important roles in species' sorting patterns (Poulos et al. 2007). In a chaparral, Santa Ynez, California, shrub species diversity increased at higher elevations, on steep slopes, in rocky conditions, where potential soil moisture was low, where local topographic variability was high, and where total canopy cover was low (Moody and Meentemeyer 2001). In Chamela, Mexico, elevation is leading the differentiation in forest structure and floristic composition between arroyos and uplands, but those differences are undoubtedly due to different hydrological conditions (Lott et al. 1987). Segura et al. (2003) found that small-scale environmental gradients in topographically irregular areas promoted the occurrence of different habitats where species segregate or where the same species perform differentially. Other authors have reported different patterns or no species richness pattern along small scale altitudinal gradients within dryland regions. In lowland dryland in Kenya, Mwaura and Kaburu (2009) found that woody species richness and altitudinal gradient showed a dual peak pattern with the main richness peak in low lying areas which were mainly close to a riparian environment, while the minor peak was identified in higher areas. In the TDF of Manantlán, Jalisco, Mexico, Vargas-Rodríguez et al. (2005) reported that the effects of short elevation gradients may not be an overriding factor however, they found that the presence or absence of adult trees might be determined by slope and disturbance. White and Hood (2004) found that topographic and substrate attributes clearly affect the distribution and abundance of woody species in the forests of the Yucatan Peninsula. Their results identified slope as an important factor correlated with the patterns of the vegetation in that region. Plots with higher slopes had soils that were shallow, more rocky and with higher pH.

Water availability was more important for understory trees and seedlings than for canopy trees in the PO forest, indicating that adult trees and young plants may have different strengths of association with this resource. Similarly, water proximity seems to be an important variable in Chamela, Mexico, although it was only significant for understory vegetation—not for mature canopy trees (Segura et al. 2003), and to differentiate woody

species composition between sites located in upland or stream conditions (Lott et al. 1987). Different variables have been used as a surrogate for water availability (e.g., rainfall, topography, evapotranspiration, soil drainage index; Pausas and Austin 2001), but it has been demonstrated that not all of them are useful. Apparently, proximity to small permanent or intermittent streams, or water bodies in dry areas may be an appropriate surrogate for water availability.

The richest sites were strongly associated with altitude, aspect and slope whereas sites with lower richness were associated with trails and cattle. Anthropogenic disturbance variables appear to be negatively correlated with altitude because low altitude sites are more accessible since they are closer to the Municipality seat and tend to be located on less steep slopes (Fig. 1; Table 1). Sites and assemblages of canopy, understory and seedling tree species were significantly related to anthropogenic disturbance in the form of trails in the forests. Furthermore, trails are good indicators of human disturbance since they indirectly reveal the extraction of forest products. Therefore, the observed presence of trails indirectly indicated that wood and other forest products were being collected inside forest fragments.

The presence of cattle was significant for the ordination of canopy and understory trees, and seedlings. Grazing by livestock together with induced fire and wood collection are considered the most important types of anthropogenic disturbance in TDF (Murphy and Lugo 1995; Gillespie et al. 2000). Although agricultural practices in the study area include burning during the dry season, we did not record signs of recent fires in the plots sampled in the forest interior. Apparently, the use of firebreaks around the fields contained prescribed fires and only pastures were burned. However, past fires may have been important in producing current patterns in species distribution and species diversity in dry land communities (Moody and Meentemeyer 2001). Gillespie et al. (2000) propose that further research in forest fragments that examines individual and combinations of disturbance agents would help clarify the importance of anthropogenic disturbances on species richness and abundance.

Conclusions

Vegetation structure, tree species richness and species dominance varied within the PO TDF, therefore it is advisable to use as many fragments as possible to define a regional reference system for conservation or ecological restoration projects. The results of this study will be used to identify priority areas for conservation and forest restoration. It is worthwhile noting that in most of the ten fragments we found species such as *Bursera cinerea*, *Calyptanthes schiediana*, *Comocladia engleriana*, and *Leucaena lanceolata*, which are endemic to Mexico (the first is endemic to Veracruz). We also found *Ipomoea wolcottiana*, *Diospyros salicifolia*, *Savia sessiliflora*, and *Thouinidium decandrum*, which have a disjunct distribution between western and eastern Mexico (Rzedowski 1978). Additionally, *Tabebuia chrysantha* and *Astronium graveolens* are on the Mexican red list as endangered species (SEMARNAT 2002), and other species are important for timber, food or medicinal purposes (*Luehea candida*, *Spondias purpurea*, *Brosimum alicastrum*).

In this paper, we have explored the impact of environmental and human disturbance variables on tree diversity patterns of TDF in central Veracruz, Mexico. Each forest fragment has intermediate alpha diversity, but the great regional beta diversity is related to the heterogeneity of the landscape. We conclude that tree species diversity is not completely dependent on topographic variables. However, species diversity may be affected by

environmental filters that act during different stages of the tree's life cycle. This way, some environmental variables are more important for adult trees and others for earlier stages. For example, water proximity is important for saplings and seedlings but not for adult trees. Additionally, anthropogenic disturbances act in a synergistic way, modifying plant communities even more. An important aspect is that disturbance by humans diminishes species diversity in the TDF of central Veracruz. Disturbances, such as the presence of trails, play a key role in determining the vegetation structure and tree biodiversity patterns. Since sites at lower elevations have more anthropogenic disturbance and lower diversity, we need to study further how environmental factors would affect TDF if there were no disturbance.

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Appendix

Species composition of the tropical dry forest in Paso de Ovejas, Veracruz, Mexico

	Species	Family	<i>T</i>	<i>t</i>	<i>s</i>
1	<i>Acacia cochliacantha</i> Humb. & Bonpl. ex Willd.	Fabaceae	1	1	–
2	<i>Acacia cornigera</i> (L.) Willd.	Fabaceae	4	6	4
3	<i>Acalypha adenostachya</i> Müll. Arg.	Euphorbiaceae	11	22	31
4	<i>Acalypha alopecuroides</i> Jacq.	Euphorbiaceae	–	18	30
5	<i>Acalypha arvensis</i> Poepp. & Endl.	Euphorbiaceae	–	21	–
6	<i>Acalypha</i> aff. <i>villosa</i> Jacq.	Euphorbiaceae	–	15	3
7	<i>Achatocarpus nigricans</i> Triana	Achatocarpaceae	–	7	4
8	<i>Amyris</i> sp.	Rutaceae	1	–	–
9	<i>Annona reticulata</i> L.	Annonaceae	–	1	–
10	Asteraceae 1	Asteraceae	–	3	3
11	Asteraceae 2	Asteraceae	6	–	–
12	Asteraceae 3	Asteraceae	–	2	–
13	<i>Astronium graveolens</i> Jacq.	Anacardiaceae	2	24	22
14	<i>Ayenia magna</i> L.	Malvaceae	–	1	–
15	<i>Bauhinia</i> sp.	Fabaceae	13	11	33
16	<i>Beaucarnea recurvata</i> Lem.	Ruscaceae	3	–	–
17	<i>Bernardia interrupta</i> (Schltdl.) Müll. Arg.	Euphorbiaceae	1	3	–
18	<i>Brosimum alicastrum</i> Sw.	Moraceae	16	5	40
19	<i>Bucida buceras</i> L.	Combretaceae	–	–	1
20	<i>Bunchosia biocellata</i> Schltdl.	Malpighiaceae	1	–	–
21	<i>Bursera cinerea</i> Engl.	Burseraceae	35	6	1
22	<i>Bursera fagaroides</i> (Kunth) Engl.	Burseraceae	24	–	–
23	<i>Bursera graveolens</i> (Kunth) Triana & Planch	Burseraceae	15	2	–

Appendix continued

	Species	Family	<i>T</i>	<i>t</i>	<i>s</i>
24	<i>Bursera simaruba</i> (L.) Sarg.	Burseraceae	61	3	–
25	<i>Caesalpinia pulcherrima</i> (L.) Sw.	Fabaceae	4	2	–
26	<i>Caesalpinia cacalaco</i> Bonpl.	Fabaceae	1	2	9
27	<i>Calliandra rubescens</i> (M. Martens & Galeotti) Standl.	Fabaceae	1	–	–
28	<i>Calyptanthes schiedeana</i> O. Berg	Myrtaceae	77	8	–
29	<i>Capparis frondosa</i> Jacq.	Brassicaceae	–	–	4
30	<i>Casearia aculeata</i> Jacq.	Salicaceae	1	1	3
31	<i>Casearia nitida</i> (L.) Jacq.	Salicaceae	1	–	–
32	<i>Ceiba aesculifolia</i> (Kunth) Britton & Baker f.	Malvaceae	11	1	3
33	<i>Celtis caudata</i> Planch.	Celtidaceae	12	6	3
34	<i>Chamaecrista nictitans</i> (L.) Moench	Fabaceae	–	–	20
35	<i>Chloroleucon mangense</i> (Jacq.) Britton & Rose	Fabaceae	1	–	3
36	<i>Citharexylum berlandieri</i> B. L. Rob.	Verbenaceae	3	2	22
37	<i>Cnidocolus</i> sp.	Euphorbiaceae	2	1	–
38	<i>Cochlospermum vitifolium</i> Willd. ex Spreng.	Cochlospermaceae	13	–	–
39	Combretaceae	Combretaceae	1	3	–
40	<i>Comocladia engleriana</i> Loes.	Anacardiaceae	28	4	2
41	<i>Cordia megalantha</i> S. F. Blake	Boraginaceae	4	–	–
42	<i>Cordia</i> sp.	Boraginaceae	2	–	–
43	<i>Coursetia caribaea</i> (Jacq.) Lavin	Fabaceae	–	–	93
44	<i>Croton cortesianus</i> Kunth	Euphorbiaceae	8	134	71
45	<i>Croton</i> sp.	Euphorbiaceae	–	1	–
46	<i>Croton reflexifolius</i> Kunth	Euphorbiaceae	7	53	36
47	<i>Diospyros salicifolia</i> Humb. & Bonpl. ex Willd.	Ebenaceae	1	–	8
48	<i>Diphysa cartagenensis</i> Jacq.	Fabaceae	1	1	–
49	<i>Enterolobium cyclocarpum</i> (Jacq.) Griseb.	Fabaceae	1	–	–
50	<i>Erythrina americana</i> Mill.	Fabaceae	2	–	–
51	<i>Erythrina</i> sp.	Fabaceae	1	–	–
52	<i>Erythroxylum mexicanum</i> Kunth	Erythroxylaceae	2	–	–
53	<i>Esenbeckia macrantha</i> Rose	Rutaceae	4	1	–
54	<i>Eugenia hypargyrea</i> Standl.	Myrtaceae	27	13	37
55	<i>Eugenia mozomboensis</i> P. E. Sánchez	Myrtaceae	–	8	17
56	<i>Euphorbia calcarata</i> (Schltdl.) V. W. Steinm.	Euphorbiaceae	3	5	10
57	<i>Euphorbia schlechtendalii</i> Boiss.	Euphorbiaceae	13	8	–
58	<i>Euphorbia tithymaloides</i> L.	Euphorbiaceae	–	1	14
59	Euphorbiaceae	Euphorbiaceae	1	1	3
60	Fabaceae 1	Fabaceae	–	1	–
61	Fabaceae 2	Fabaceae	–	–	10
62	<i>Ficus cotinifolia</i> Kunth	Moraceae	–	1	–
63	<i>Ficus</i> sp.	Moraceae	1	–	–
64	<i>Gliricidia sepium</i> (Jacq.) Kunth ex Walp.	Fabaceae	9	–	–
65	<i>Guazuma ulmifolia</i> Lam.	Malvaceae	23	7	9
66	<i>Guettarda elliptica</i> Sw.	Rubiaceae	6	–	–

Appendix continued

	Species	Family	<i>T</i>	<i>t</i>	<i>s</i>
67	<i>Gyrocarpus jatrophifolius</i> Domin	Hernandiaceae	6	–	2
68	<i>Heliocarpus donnellsmithii</i> Rose	Malvaceae	80	13	12
69	<i>Hippocratea celastroides</i> Kunth	Celastraceae	–	1	6
70	<i>Hyperbaena mexicana</i> Miers	Menispermaceae	5	–	2
71	<i>Ipomoea wolcottiana</i> Rose	Convolvulaceae	52	4	8
72	<i>Jacaratia mexicana</i> A. DC.	Caricaceae	13	–	3
73	<i>Jatropha curcas</i> L.	Euphorbiaceae	1	–	–
74	<i>Karwinskia humboldtiana</i> (Roem. & Schult.) Zucc.	Rhamnaceae	1	4	8
75	<i>Leucaena lanceolata</i> S. Watson	Fabaceae	37	19	76
76	<i>Leucaena leucocephala</i> (Lam.) de Wit	Fabaceae	5	5	6
77	<i>Luehea candida</i> (Moc. & Sessé ex DC.) Mart.	Malvaceae	60	12	28
78	<i>Luehea speciosa</i> Willd.	Malvaceae	2	37	4
79	<i>Lysiloma acapulcense</i> (Kunth) Benth.	Fabaceae	1	–	–
80	<i>Lysiloma microphyllum</i> Benth.	Fabaceae	26	4	6
81	<i>Maclura tinctoria</i> (L.) D. Don ex Steud.	Moraceae	3	2	–
82	<i>Malpighia glabra</i> L.	Malpighiaceae	1	5	–
83	Malpighiaceae	Malpighiaceae	4	1	4
84	<i>Malvaviscus arboreus</i> Cav.	Malvaceae	–	1	–
85	<i>Matayba</i> sp.	Sapindaceae	8	–	–
86	<i>Melochia lupulina</i> Sw.	Malvaceae	1	–	–
87	<i>Morisonia americana</i> L.	Brassicaceae	3	6	–
88	Morphospecies 1	Unknown	1	–	–
89	Morphospecies 2	Unknown	1	–	–
90	Morphospecies 3	Unknown	–	1	–
91	<i>Neea tenuis</i> Standl.	Nyctaginaceae	6	5	3
92	<i>Petrea volubilis</i> L.	Verbenaceae	2	1	15
93	<i>Phyllanthus</i> sp.	Phyllantaceae	3	5	–
94	<i>Piper hispidum</i> Sw.	Piperaceae	–	–	11
95	<i>Piper</i> sp.	Piperaceae	–	1	–
96	<i>Pisonia aculeata</i> L.	Nyctaginaceae	1	5	22
97	<i>Pisonia</i> sp.	Nyctaginaceae	1	–	–
98	<i>Plumeria rubra</i> L.	Apocynaceae	5	1	–
99	<i>Podopterus mexicanus</i> Bonpl.	Polygonaceae	1	3	8
100	<i>Randia aculeata</i> L.	Rubiaceae	9	11	57
101	<i>Randia laetevirens</i> Standl.	Rubiaceae	–	5	–
102	<i>Randia monantha</i> Benth.	Rubiaceae	1	3	23
103	<i>Ruprechtia</i> sp.	Polygonaceae	4	–	–
104	Rutaceae	Rutaceae	2	–	–
105	<i>Sapindus saponaria</i> L.	Sapindaceae	4	–	2
106	<i>Sapranthus microcarpus</i> (Donn. Sm.) R. E. Fr.	Annonaceae	2	4	–
107	<i>Savia sessiliflora</i> (Sw.) Willd.	Phyllantaceae	46	2	21
108	<i>Schoepfia schreberi</i> J. F. Gmel.	Schoepfiaceae	1	–	–
109	<i>Senna atomaria</i> (L.) H. S. Irwin & Barneby	Fabaceae	19	7	114

Appendix continued

	Species	Family	<i>T</i>	<i>t</i>	<i>s</i>
110	<i>Senna</i> sp.	Fabaceae	8	3	20
111	<i>Spondias mombin</i> L.	Anacardiaceae	2	–	–
112	<i>Spondias purpurea</i> L.	Anacardiaceae	1	1	–
113	<i>Spondias</i> sp.	Anacardiaceae	2	–	–
114	<i>Stemmadenia pubescens</i> Benth.	Apocynaceae	22	14	13
115	<i>Tabebuia chrysantha</i> (Jacq.) G. Nicholson	Bignoniaceae	51	9	9
116	<i>Tabebuia rosea</i> (Bertol.) A. DC.	Bignoniaceae	3	1	–
117	<i>Thouinidium decandrum</i> (Bonpl.) Radlk.	Sapindaceae	15	1	73
118	<i>Trichilia trifolia</i> L.	Meliaceae	11	21	44
119	<i>Verbesina persicifolia</i> Dc.	Asteraceae	1	–	–
120	<i>Wimmeria pubescens</i> Radlk.	Celastraceae	11	–	5
121	<i>Yucca periculosa</i> Baker	Agavaceae	3	–	–
122	<i>Zuelania guidonia</i> (Sw.) Britton & Millsp.	Salicaceae	5	–	–

Values are number of canopy trees over 1 ha (*T*), understory trees and saplings in 250 m² (*t*), and seedlings in 40 m² (*s*)

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