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Primary and secondary vegetation patches as contributors to floristic diversity in a tropical deciduous forest landscape

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Abstract The floristic diversity of Mexican tropical deciduous forests (TDF) is of critical importance given the high species richness (alpha diversity), species turnover (beta diversity), and the intense deforestation rates. Currently, most TDF landscapes are mosaics of agricultural land, secondary vegetation, and patches of relatively undisturbed primary vegetation. Here we illustrate how both primary forest remnants and secondary vegetation patches contribute to the floristic diversity of TDF in a landscape of volcanic origin in central Veracruz, Mexico. Our objectives were to assess sampling efficiency and inventory completeness, to compare mean and cumulative species richness between primary forest and secondary vegetation sites, and to analyze beta diversity between vegetation types. In an area of 12,300 m² we recorded 105 families, 390 genera, and 682 species. Species inventories for both vegetation types were about 80% complete. Secondary vegetation is more alpha diverse than primary forest, both in terms of cumulative and mean species richness. We found a remarkably high beta diversity between vegetation types (75% of complementarity, 91.60% of mean dissimilarity). We also identified the species that contribute the most to similarity within vegetation types and to dissimilarity between vegetation types. Our results support the idea that assessing biodiversity on the landscape scale is an appropriate way to ascertain the impact of human activities. For this land mosaic, conservation of the flora would not be possible by focusing solely on primary forest remnants. We propose the implementation of a network of small conservation areas with a flexible structure, following the "archipelago reserve" model.

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Introduction

Tropical deciduous forest (TDF) (sensu Miranda and Hernández 1963; also known as seasonally dry tropical forest, in the broad sense of Mooney et al. 1995), in Mexico is notably rich in vascular flora; its richness is higher than that of other dry Neotropical forests with even better moisture conditions (Toledo 1982; Gentry 1982; Lott 1987; Sarukhán 1998; Trejo and Dirzo 2002). Furthermore, the plant species richness of some sites of TDF is comparable to or even greater than that of some moist forests (Gentry 1982; Janzen 1988). The floristic diversity of Mexican TDFs in terms of species richness is associated with an outstanding rate of species turnover among sites (high complementarity values) along with an elevated number of endemisms and rare species (Trejo and Dirzo 2002; Gordon et al. 2004; Trejo 2005). Thus, both the floristic richness at some localities (alpha diversity) and the species turnover (beta diversity) among localities are of critical importance to the remarkably high biodiversity of Mexican TDFs.

TDFs rank amongst the most endangered of terrestrial ecosystems (Murphy and Lugo 1986; Lerdau et al. 1991; Gerhardt 1993; Laurance 1999; Trejo and Dirzo 2000; Li et al. 2006). The endangerment of dry forests is disproportionate and is mainly a consequence of the extended dry season. The climate where TDF occurs naturally is considered to be particularly suitable for livestock and agriculture, and human population densities are also higher in dry forest regions than in any of the world's other major tropical ecosystems (Murphy and Lugo 1986). So, TDF is now frequently found in a mosaic of disturbed secondary vegetation, and patches of relatively undisturbed primary vegetation on several spatial scales (Trejo and Dirzo 2000; Steininger et al. 2001; Gordon et al. 2004; Gove et al. 2005) which constitute a marked heterogeneity in terms of solar radiation, temperature, moisture and the rate of nutrient release from decomposing litter (Khurana and Singh 2001). Although this is the vegetation type with the highest percentage of cover of the Mexican territory (Ricker et al 2007), in a recent assessment, Trejo and Dirzo (2000) calculated that by 1990 only 27% of the original area of Mexico's TDFs was in a relatively satisfactory condition with respect to forest structure and integrity. Their results clearly show that these forests have been severely affected by human activities; particularly agriculture, extensive cattle ranching and timber extraction. In addition, some specific localities have alarmingly high deforestation rates of up to 1.4% per year (Trejo and Dirzo 2000).

In spite of this, TDF is a well represented plant community on the Mexican Pacific slope, where it is distributed from southern Sonora and southwestern Chihuahua, with some inland penetration along the Santiago and Balsas Rivers, to the central Chiapas basin and Central America (Rzedowski 1978). In contrast, on the Atlantic slope the distribution of TDF originally covered less surface and the discontinuity was marked. Now, as a result of the intense deforestation caused by human activities, there are only three isolated patches remaining: the first in southern Tamaulipas, southeastern San Luis Potosí and the northern tip of Veracruz; the second in central Veracruz; and the third occupies almost the entire state of Yucatán and a small part of Campeche (Rzedowski 1978; Sarukhán 1998; Trejo and Dirzo 2000). The best conserved TDF remnants on the Atlantic slope are probably those found growing on basaltic rock of volcanic origin in the upper basin of the Actopan River in central Veracruz, Mexico. These fragments have been mainly preserved because they are difficult to use due to the kind of substrate in which they are growing. The flora

found in such areas is rich in endemic species (Medail and Verlaque 1997) and succulents belonging to the Cactaceae, Crassulaceae, Euphorbiaceae, Orchidaceae, and Bromeliaceae families. Given that these remnants are imbedded in land mosaics with significant anthropogenic pressure, we need to understand landscape patterns of diversity to promote adequate conservation practices.

In this paper we show how both the remnants of primary forest and patches of secondary vegetation contribute to the floristic diversity of TDF in a landscape of volcanic origin in central Veracruz, Mexico. We apply a methodology that allows us to analyze the influence of alpha and beta diversities on the land mosaic diversity and assess the importance of the different aspects of biodiversity (Halffter 1998). Our objectives were: (1) to assess sampling efficiency and inventory completeness for each vegetation type, (2) to compare species richness between primary forest and secondary vegetation sites, examining mean and cumulative richness separately, and life forms composition, (3) to analyze beta diversity using the concepts of complementarity and similarity to get a broader view of species composition throughout the landscape, and (4) to identify the species that most contribute to the similarity within vegetation types and to dissimilarity between vegetation types. Analyzing biodiversity at the landscape scale and in terms of its alpha and beta components can aid in the development of management strategies for land mosaics that still conserve primary forests patches.

Materials and methods

Study area

The study area is located between 19°31′ and 19°37′ N, and between 96°41′ and 96°54′ W, in the Actopan River basin in central Veracruz, Mexico (Fig. 1). The landscape is 17 km long, with a variable width of 0.5–2.7 km, a surface area of 3,976 ha, and ranging from 400 to 900 m a.s.l. From a geological viewpoint, the zone is comprised of volcanic rock of chaotic basalt deposited during different periods. The largest lava flow was deposited during the most recent period (Holocene), approximately 10,000 years ago (Negendank et al. 1985).

Climate is type Aw_1, warm with summer rains and mean temperature is 24°C, with a minimum greater than 18°C and a maximum of 26°C. Mean annual precipitation is 893.8 mm. There are two quite distinct seasons: the dry season from October to May with a mean monthly rainfall of 17 mm and the rainy season from June to September, with a monthly mean of 180 mm (García 1981).

Floristic structure

The original vegetation in the area is TDF. Canopy height ranges from 3 to 8 m and is dominated by *Bursera cinerea*, *Cephalocereus palmeri* var. *sartorianus*, *Lysiloma microphyllum*, and *L. acapulcense*. The understory is characterized by *Bernardia interrupta*, *Casearia corymbosa*, *Comocladia engleriana*, *Cnidoscolus aconitifolius*, and *Croton ciliato-glandulosus*. The most common herbs are *Anthurium schlechtendalii* var. *schlechtendalii*, *Bidens reptans*, *Callisia fragrans*, *C. repens*, *Mammillaria eriacantha*, and *Micrograma nitida*.

The original plant cover has been fragmented along a substantial area of the volcanic rock. The present landscape is a mosaic that includes remnant patches of primary vegetation
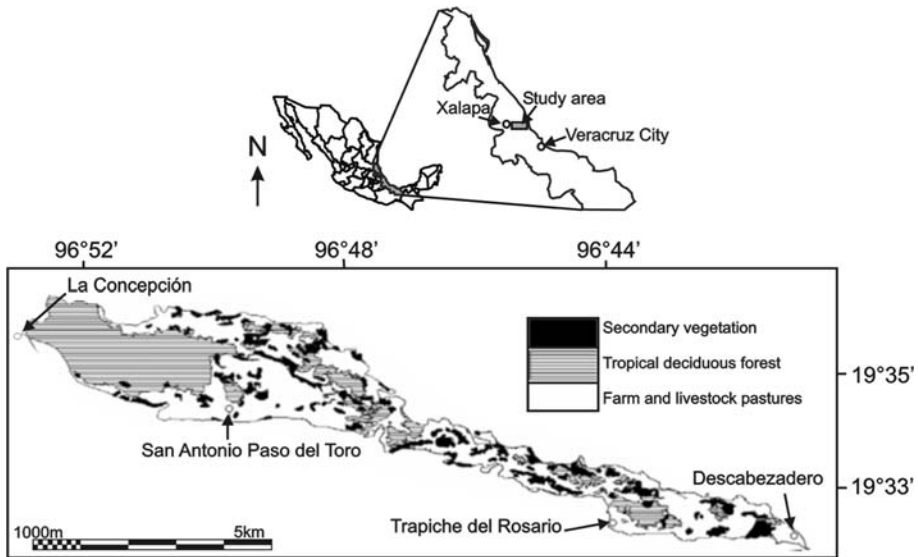
Fig. 1 Location of study area and vegetation types studied on a tropical deciduous forest landscape in central Veracruz, Mexico

(Ortega 1981), secondary vegetation (Fig. 1), induced or introduced pastureland, and crops such as sugar cane (*Saccharum officinarum*), chayote (*Sechium edule*), mango (*Mangifera indica*), and coffee (*Coffea arabica*).

Depending on when crop fields or pastures were abandoned (one to 12–20 years), secondary vegetation is observed at different regenerative stages. Despite this spatial heterogeneity, all the fragments are imbedded in the same landscape. The floristic structure of secondary vegetation that was abandoned over 10 years ago has from one to three strata. The arboreal layer is 3–7 m high, and the most characteristic species are *Acacia pennatula*, *Cochlospermum vitifolium*, *Guazuma ulmifolia*, *Heliocarpus americanus*, *H. pallidus*, and *Urera caracasana*. The shrub layer is 1–3 m high and is characterized by *Acacia cornigera*, *Calea urticifolia*, *Calliandra rubescens*, *Cracca caribaea*, *Croton ciliato-glandulosus*, *C. niveus*, and *Pisonia aculeata*. The herbaceous layer is 1–2 m high and is characterized by *Acalypha alopecuroides*, *Baltimora recta*, *Bidens pilosa*, *Desmodium tortuosum*, *Panicum maximum*, *Rhynchelytrum repens*, *Sida rhombifolia*, and *Wisadula amplissima*.

Species inventory and botanical material collection

Sampling was carried out along transects located at six altitudinal levels, from 400 to 900 m a.s.l. (Table 1). For each altitudinal transect, 100 m² plots (10 × 10 m) were used for arboreal and shrub layer surveys. At each transect, plots were separated by 50 m intervals along the transect. For herbaceous vegetation inventory, we sampled three subplots of 4 m² inside each 100 m² plots. At each plot we collected specimens of the species present, recording its coverage as a percentage within the 100 m², although for this paper our analyses are based only on species presence–absence data.

The number of plots varied with the width of the study area and the size of the original and human induced plant cover fragments, but for each vegetation type (primary forest and

Table 1 Total number of plant species recorded and total area sampled on each altitudinal transect in primary forest remnants and secondary vegetation in the studied landscape

Transect	Altitude (m a.s.l.)	Primary forest		Secondary vegetation	
		Cumulative number of species	Area (m²)	Cumulative number of species	Area (m²)
1	400	123	1,000	229	1,100
2	500	121	900	164	1,000
3	600	140	1,500	171	1,100
4	700	156	1,100	176	1,000
5	800	168	800	152	1,000
6	900	202	1,000	151	800

secondary vegetation) we sampled around 1,000 m^2 at each altitudinal level (Table 1). Also, the biggest fragment of tropical deciduous forest is located at the Northwest of the landscape (Fig. 1), where the highest altitude occurs. Even though there were variations in the number of sampling plots, the number of plant species recorded is not significantly correlated with sample size (Spearman rank correlation r = 0.22; *P* = 0.466).

Sampling was carried out during the rainy season—when most species flower and bear fruit- and during consecutive 4-month periods over 2 years (August–November of 1999–2000). Botanical material was identified using dichotomous keys from the Flora de Veracruz (fascicles 1–141, 1978–2006) and by comparing with material identified by specialists. We collected voucher specimens of all the species recorded and they are deposited in the XAL herbarium of the Instituto de Ecología, A.C.

Data analysis

To assess the completeness of inventories we compared the observed species richness for each vegetation type with the expected maximum number of species predicted by applying two approaches: a nonlinear regression model and a non-parametric estimator. We decided to compare both methods because their predictions are calculated by giving weight to different aspects of an inventory: the first one is based on the shape of the species accumulation curve, while the second is based on the number of rare species detected (species encountered in only one and two samples). For the regression model we tested the three functions for non-linear regression adjustment described by Soberón and Llorente (1993), following the procedure of Díaz-Francés and Soberón (2005) and using the Species Accumulation Functions freeware developed by the Centro de Investigación en Matemáticas A.C. (available at www.cimat.mx). For the second approach, we computed the Incidence-based Coverage Estimator (ICE) after randomizing sample order 50 times using the EstimateS 7.5 software (Colwell 2005). The ICE estimator was chosen because it has been successfully used in vegetation studies (Chazdon et al. 1998; Williams-Linera 2002).

To test whether the cumulative richness between the two vegetation types was statistically different, we plotted Sample-based Rarefaction Curves (Mao-Tau functions, Gotelli and Colwell 2001; Colwell et al. 2004) with 95% confidence intervals. These functions were also computed using EstimateS 7.5. We then counted the species richness for each 100 m^2 sample, and tested if the mean richness per sample was statistically different between primary and secondary vegetation, using a t-test, after a square-root transformation of the data.

To assess beta diversity we plotted Venn diagrams with the number of species, genera and families in three groups: those present only in primary vegetation, those present only in secondary vegetation, and those shared by both vegetation types. Then, we calculated the complementarity value for primary and secondary vegetation, using the index described by Colwell and Coddington (1994). The value of this index, expressed as a percentage, ranges from 0% for identical species composition to 100% when species composition is completely different. This measure of complementarity is therefore a direct measure of beta diversity.

Also, we calculated the Bray-Curtis similarity index using presence–absence data. To compare the similarity in species composition among altitudinal transects we constructed a single linkage cluster dendrogram. Then, in order to test statistical differences in similarity between primary and secondary vegetation, and between transects nested within each vegetation type, we performed a non-parametric two-way analysis of similarity (ANOSIM) with a simple nested design (Clarke and Warwick 1994). ANOSIM is a permutation procedure applied to the (rank) similarity or dissimilarity (beta diversity) matrices. The ANOSIM was performed using the PRIMER program (Clarke and Gorley 2001).

Finally, we determined which species make a greater contribution to the similarity within each vegetation type, and which species make a greater contribution to the dissimilarity between primary and secondary vegetation. These contributions were calculated using the SIMPER algorithm of the PRIMER program (Clarke and Gorley 2001).

Results

We recorded 105 families, 390 genera, and 682 species in a total survey area of 12,300 m². Only one species from primary forest and four species from secondary vegetation were exotic. For both vegetation types the minimum survey area per altitudinal sampling level was 800 m² (Table 1). Alpha diversity per altitudinal level transect varied from 121 to 202 species in tropical deciduous forest and from 151 to 229 species in secondary vegetation (Table 1). The higher richness of primary forest (202 species at 900 m a.s.l.) corresponds to the biggest continuous fragment, and thus such richness might be related with vegetation connectivity, which might favors species permanence. For both primary forest and secondary vegetation, our inventories are about 80% complete (Table 2). Following the procedure of Díaz-Francés and Soberón (2005), we found that for both vegetation types the best adjustment is attained with the logarithmic model. However, this model is non-asymptotic and thus it does not allow us to predict the total number of species. So, we used the prediction of the Clench model because it gave the second best fit for both vegetation types. The total number of species predicted by the Clench model was higher than the number predicted by the ICE estimator: three species more for primary forest, and 26 species more for secondary vegetation (Table 2).

Cumulative and mean alpha diversity

The total number of species was higher for secondary vegetation (462 species) than for primary forest (390), and these cumulative alpha diversity values were statistically different given that the 95% confidence intervals for the species accumulation curves do not overlap (Fig. 2). Secondary vegetation had also higher alpha diversity than primary forest when we calculated the mean species richness per sample (Fig. 3). The square-root transformed number of species was statistically different between vegetation types ($t = -2.48$,

Table 2 Inventory completeness and life forms in each vegetation type

	Observed richness	Clench model		ICE		Life forms			
		Expected richness	%	Expected richness	%	Trees	Shrubs	Lianas	Herbs
Primary forest	390	484	80.58	481	81.08	63, 16%	70, 18%	38, 10%	218, 56%
Secondary vegetation	462	584	79.11	558	82.80	54, 12%	80, 17%	52, 11%	276, 60%

Inventory completeness is assessed as a percentage of the expected maximum number of species (predicted using two methods) as represented by the observed species richness. For each life form we provide the number of species and the percentage they represent in each vegetation type
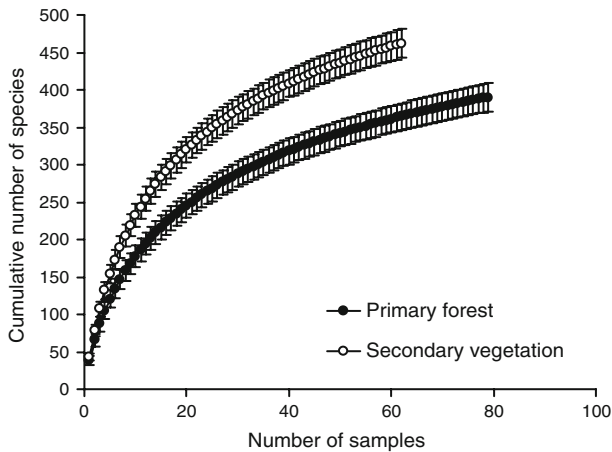

Fig. 2 Species accumulation curves for the primary forest remnants and the secondary vegetation on the studied landscape. Circles represent the Mao Tau function of observed richness and the bars are 95% confidence intervals, both calculated using EstimateS (Colwell 2005)

d.f. = 139, P = 0.0144). At both vegetation types herbs contribute the most to species composition, but at primary forest they represent 56% of the species, while for secondary vegetation they represent up to 60% (Table 2). Contrary, in primary forest trees represent a higher percentage of species composition (16%), while in secondary vegetation only 12% of the species are trees (Table 2).

Beta diversity, complementarity and similarity

Along the taxonomic hierarchy, as we increased in detail complementarity increased: 35% for families, 61% for genera and 75% for species (Fig. 4). For all three taxonomic levels the number of taxa that were exclusive to one vegetation type was greater for secondary vegetation than for primary forest. For families and genera the number of taxa shared between the primary and secondary vegetation was higher than the number of taxa exclusive to either vegetation type. However, we found the opposite trend at the species level, where the number of shared species was lower than the number of species exclusive to primary forest or to secondary vegetation (Fig. 4).
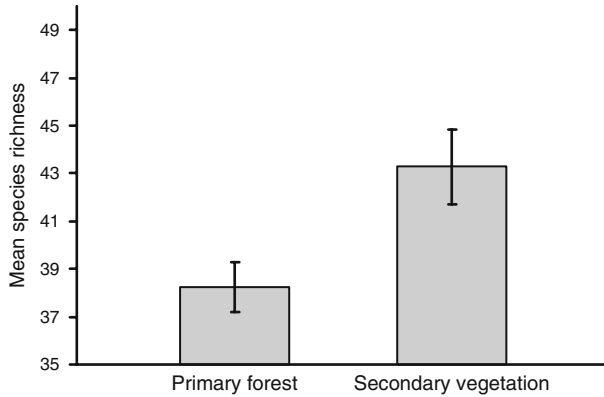
Fig. 3 Mean number of species per sample in primary forest remnants (n = 79) and secondary vegetation (n = 62). Values for square-root transformed species richness were statistically different between vegetation types (t = −2.48, d.f. = 139, P = 0.014)
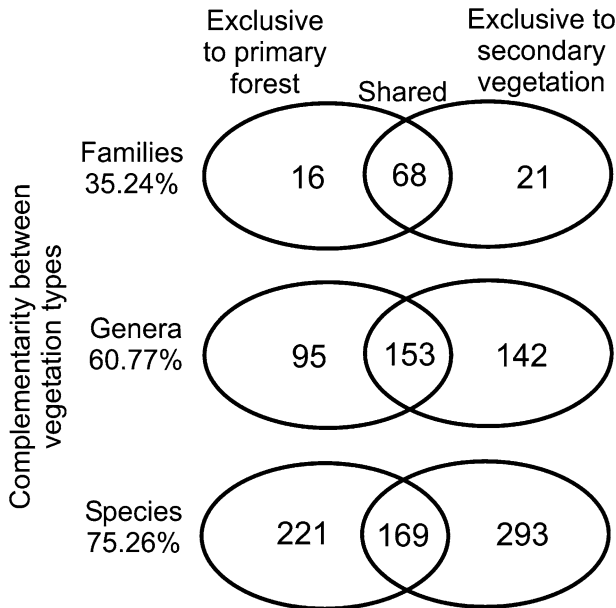

Fig. 4 Venn diagrams with a schematic representation of the beta diversity components: the total number of taxa (families, genera and species) found in only one of the two vegetation types (exclusive) and the number of species shared between primary forest and secondary vegetation. The percentage of complementarity in species composition between vegetation types was calculated using the index described by Colwell and Coddington (1994)

With the ANOSIM procedure we found significant statistical differences in similarity among the altitudinal transects nested within vegetation types (R = 0.515; P = 0.001). Also, there were statistically significant differences in the similarity between primary forest and secondary vegetation when transects were used as samples (R = 0.948, P = 0.002).
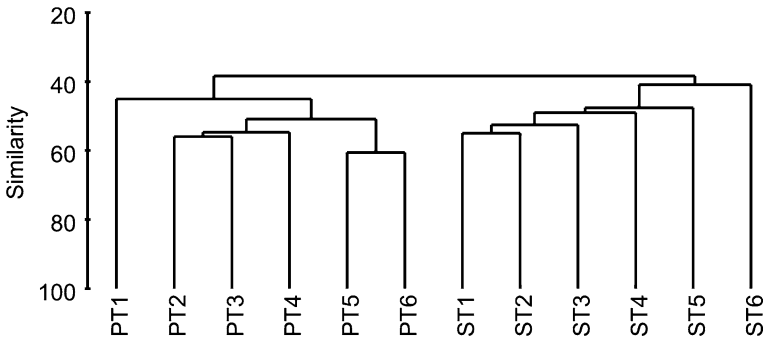
Fig. 5 Single linkage cluster dendrogram that groups the altitudinal transects according to their similarity in species composition (Bray-Curtis similarity index using presence–absence data). Transects marked with "P" were located in primary forest remnants and transects with "S" were in secondary vegetation. Transect numbers correspond to the numbers given in Table 1

Transects are well separated into two groups corresponding to primary and secondary vegetation (Fig. 5) using species presence–absence data. Within each major group, the grouping sequence reflects a gradient of species turnover along altitudinal transects (Fig. 5). According to the SIMPER analysis, mean dissimilarity between the vegetation types was 91.60%, while mean similarity among the six altitudinal transects of primary forest was 28.92, and 18.84% for the secondary vegetation transects.

In Table 3 we list the species that contribute the most to within sample similarity of primary forest, and of secondary vegetation. For primary forest the 20 species that made the greatest contribution to similarity accounted for more than 60% of the cumulative percentage of contribution, while for secondary vegetation the first 20 species accounted for <50%. *Cnidoscolus aconitifolius*, *Comocladia engleriana*, *Chamaesyce hirta*, *Astrolepis sinuata*, *Tillandsia schiedeana*, *Casearia corymbosa*, *Callisia repens*, *Callisia fragrans* and *Mammillaria eriacantha* are some of the species that most contributed to the dissimilarity between primary forest and secondary vegetation samples (Table 3).

Discussion

The floristic conservation of this land mosaic, originally covered by tropical deciduous forest, would not be possible by focusing only on primary forest remnants. The secondary vegetation we studied is even more alpha diverse than the primary forest, both in terms of the cumulative number of species and mean species richness. On one hand, the cumulative alpha value is the sum of all the species found in all the sampling plots of a vegetation type during the study. On the other hand, mean alpha diversity reflects a general tendency in sample richness values within a community, and should be interpreted with caution given that this mean value simplifies the information by ignoring local influences on diversity (Halffter and Moreno 2005).

Such higher species richness at secondary vegetation was recorded in spite of a more intense sampling effort in the primary forest (300 m^2 more sampled than in secondary vegetation, Table 1). Thus, the species–area relationship cannot explain the differences in species richness between vegetation types (although it could certainly influence species richness per altitudinal level, an issue not assessed in this paper). With a total sampling

Table 3 Species making the greatest contribution to intra-group similarity, and between group dissimilarity

	Primary forest	Secondary vegetation	Dissimilarity between vegetation types
Cnidoscolus aconitifolius	7.41		1.06
Callisia repens	6.04	1.44	0.84
Comocladia engleriana	4.92		0.91
Astrolepis sinuata	4.19		0.9
Tillandsia schiedeana	4		0.89
Casearia corymbosa	3.98		0.84
Callisia fragrans	3.3		0.83
Mammillaria eriacantha	3.14		0.8
Plumeria rubra	2.82		0.77
Cephalocereus palmeri var. *palmeri*	2.64		0.74
Lysiloma acapulcense	2.49		0.72
Cephalocereus palmeri var. *sartorianus*	2.42		0.71
Euphorbia schlechtendalii	2.41		0.71
Agave angustifolia	2.13		0.67
Rhynchelytrum repens	2.11		0.68
Dodonaea viscosa	2.1		0.67
Diospyros verae-crusis	2.02	1.31	0.68
Tonduzia longifolia	1.99		
Bidens squarrosa	1.83	1.4	0.67
Croton ciliato-glandulosus	1.81		0.66
Pilea microphylla	1.79		
Psychotria erythrocarpa	1.69		
Panicum maximum	1.66	6.13	0.74
Hechtia stenopetala	1.56		
Chamaesyce hirta		5.28	0.9
Acalypha alopecuroides		3.73	0.76
Acacia pennatula		3.28	0.7
Spermacoce laevis		2.73	
Portulaca pilosa		2.66	0.66
Sida rhombifolia		2.42	
Acacia cornigera		2.34	
Evolvulus alsinoides		2.08	
Commelina erecta		1.99	
Desmodium tortuosum		1.9	
Sida ulmifolia		1.9	
Zinnia americana		1.7	
Bidens pilosa		1.64	
Sida acuta		1.49	
Wissadula amplissima		1.45	
Desmodium incanum		1.35	
Digitaria bicornis		1.09	
Solanum adscendens		1.07	
Chamaesyce ammannioides		1.04	
Indigofera mucronata		0.97	

effort of 6,300 m^2 at primary forest and 6,000 m^2 at secondary vegetation we recorded ca. 80% of the expected richness at each vegetation type, and the two estimators used yielded similar results (Table 2). This level of completeness might be considered high for a floristic inventory. For example, in a tropical montane cloud forest Williams-Linera (2002) recorded the 100% of expected tree richness in only one of her seven sampling sites, while for others the completeness was as low as 67%. For shrubs the inventories at the seven

sampling sites was only 60–92% complete (Williams-Linera 2002). Underestimation of total plant species richness seems to be common when sample-based estimators are compared with reference values obtained by traditional floristic and vegetation sampling (Chiarucci et al. 2001).

In our study, local influences are conspicuous, especially for secondary vegetation given that it includes different regenerative stages depending on the particular time since field abandonment, even when all the fragments are imbedded within a single landscape and share the same geological, climate and biogeographical history. Spatial heterogeneity is one of the main processes that allows for numerous plant species to persist given that it increases available resources (Tilman and Pacala 1993). Thus, the spatial heterogeneity in the study area may be the main factor increasing plant diversity in secondary vegetation. If a dynamic view of ecosystems is assumed, the different regenerative stages represent distinct phases in the succession cycle (Holling 1986). From another point of view, these successional stages may be viewed as a moderately disturbed scenario (Connell 1978), where disturbances occur with moderate frequency, intensity and duration, thus allowing resident species to cohabit with pioneer species, and resulting in greater species richness than in communities that have not been greatly affected by disturbances (primary forest remnants). Although we did not sample in pastures, corn or cane sugar plantations, according to the intermediate disturbance hypothesis we predict that these types of land use would also have lower richness than secondary vegetation because they are subject to quite large and frequent disturbance (Connell 1978). This dominance-controlled mechanism, as well as other founder-controlled models, where a competitive lottery may occur instead of a predictable succession, should be studied further in order to understand species richness dynamics (Begon et al. 2006).

The high spatial heterogeneity in the secondary vegetation may explain not only the high mean and cumulative alpha diversity, but also the presence of a greater number of exclusive species (perhaps pioneer or tolerant species), which results in a very low (<20%) similarity in species composition among the samples of secondary vegetation. However, this within-habitat species turnover is lower than the between-habitat beta diversity. The clear difference in composition between vegetation types (75% complementarity, 91.60% mean dissimilarity) is shaped by the species characteristic of primary forest such as *Cnidoscolus aconitifolius*, *Comocladia engleriana*, *Astrolepis sinuata*, *Tillandsia schiedeana*, *Casearia corymbosa*, *Callisia repens*, *Mammillaria eriacantha*, *Plumeria rubra*, *Cephalocereus palmeri* var. *palmeri* and *Lysiloma acapulcense*.

Our results reflect an outstanding floristic beta diversity on the landscape scale in the study area, and this is of critical importance to conservation management because policies must make the remnants of primary forest and highly diverse sites a priority, while keeping in mind that these sites can host a considerable number of exclusive species. On a broader scale, Trejo and Dirzo (2002) also highlighted the very low floristic similarities they found among 20 sites of well conserved seasonally dry tropical forest in Mexico, and proposed that protecting this type of forest would require a network of many reserves distributed throughout the country. This proposal coincides with the recently described scheme of "archipelago reserves" (Halffter 2005), in which the highest possible connectivity is maintained among a collection of small protected areas so that the greatest possible representation of species richness on the landscape is achieved through complementarity of the local diversity among areas. Such archipelago reserves would be especially appropriate in regions with high beta diversity, and constitute a complement to the current types of protected areas because they are characterized by a much more flexible administrative structure (Halffter 2005). In a beta-diverse region, such a network would be more effective

than other protected areas such as biosphere reserves or national parks, which were conceived to protect biodiversity in terms of high alpha diversity but usually without consideration of species turnover rates.

There are still several lines of research we need to pursue in order to develop a comprehensive strategy for tropical deciduous forest conservation in central Veracruz. We need to study more than just the species richness patterns, and must include a deep analysis of the community structure both in primary forest and anthropogenic ecosystems. Species abundances, coverage patterns, altitudinal variations and life forms should all be taken into account. For example, the primary forest in our study area has a high diversity of trees and shrubs but low diversity in the herbaceous layer. This contrasts with the secondary vegetation, which has a wide diversity of herbaceous species (Table 2). Also, analysis of ecological structure could be relevant for selecting priority areas for conservation or, in other cases, developing restoration or regeneration plans, given that the remaining forests are a rich source of locally adapted plant species (Murphy and Lugo 1986; Vieira and Scariot 2006). Also, more concrete conservation proposals should be based on a serious economic assessment to identify the external pressures that are imposed on forest remnants and current types of land use (Edwards and Abivardi 1998). Such valuation would also be useful to detect and manage species of ethnobotanical importance (Hernandez-Stefanoni et al. 2006) and to identify the ecosystem services that are regulated by biodiversity (Chee 2004; Brooks et al. 2006). This information could also be used to increase the level of interest that decision makers and the general public have in biological conservation.

Finally, our results support the idea that assessing components of biodiversity on the landscape scale is an appropriate way to evaluate the impact of farming activities on original forest (Halffter 1998). Thus, our analysis of the alpha and beta components of plant biodiversity in a landscape greatly affected by human activities highlights the importance of including secondary vegetation patches in conservation management strategies. Ecological studies with conservation goals should not only focus on well conserved or mature forests (Gordon et al. 2004), but should rather consider the entire landscape that includes a successional mosaic of conditions in order to allow the spatiotemporal analysis of diversity from a patch dynamics perspective (DeAngelis and Waterhouse 1987; Begon et al. 2006; Hernandez-Stefanoni 2006). Our proposal for this area is to manage a network of conservation areas using a flexible structure and taking into account the whole landscape matrix, with not only species-rich sites or primary forest remnants, but also species turnover rates between small forest patches and habitats that have been modified by people.

References

Begon M, Townsend CR, Harper JL (2006) Ecology: from individuals to ecosystems, 4th edn. Blackwell Publishing, London

Brooks TM, Mittermeier RA, da Fonseca GAB, Gerlach J, Hoffmann M, Lamoreux JF, Mittermeier CG, Pilgrim JD, Rodrigues ASL (2006) Global biodiversity conservation priorities. Science 313:58–61

Chazdon RL, Colwell RK, Denslow JS, Guariguata MR (1998) Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of northeastern Costa Rica.

In: Dallmeier F, Comiskey JA (eds) Forest biodiversity research, monitoring and modelling: conceptual background and old world case studies. The Parthenon Publishing Group, Paris, pp 285–309

Chee YE (2004) An ecological perspective on the valuation of ecosystem services. Biol Conserv 120:549–565

Chiarucci A, Maccherini S, De Dominicis V (2001) Evaluation and monitoring of the flora in a nature reserve by estimation methods. Biol Conserv 101:305–314

Clarke KR, Warwick M (1994) Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth

Clarke KR, Gorley RN (2001) PRIMER v5: user manual/tutorial. Plymouth Marine Laboratory, Plymouth

Colwell RK (2005) EstimateS: statistical estimation of species richness and shared species from samples. Version 7.5. Available on line at: http://viceroy.eeb.uconn.edu/estimates. University of Connecticut, Storrs

Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. Phil Trans R Soc B 345:101–118

Colwell RK, Mao CX, Chang J (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 85:2717–2727

Connell JH (1978) Diversity in tropical rainforests and coral reefs. Science 199:1302–1310

DeAngelis DL, Waterhouse JC (1987) Equilibrium and non-equilibrium concepts in ecological models. Ecol Monogr 57:1–21

Díaz-Francés E, Soberón J (2005) Statistical estimation and model selection of species-accumulation functions. Conserv Biol 19:569–573

Edwards PJ, Abivardi C (1998) The value of biodiversity: where ecology and economy blend. Biol Conserv 83:239–246

García E (1981) Modificaciones al sistema de clasificación climática de Köppen. Indianápolis 30, México

Gentry AH (1982) Neotropical floristic diversity. Ann Mo Bot Gard 69:557–593

Gerhardt K (1993) Tree seedling development in tropical dry abandoned pasture and secondary forest in Costa Rica. J Veg Sci 4:95–102

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett 4:397–391

Gordon JE, Hawthorne WD, Reyes-García A, Sandoval G, Barrance AJ (2004) Assessing landscapes: a case study of tree and shrub diversity in the seasonally dry tropical forests of Oaxaca, Mexico and southern Honduras. Biol Conserv 117:429–442

Gove AD, Majer JD, Rico-Gray V (2005) Methods for conservation outside of formal reserve systems: the case of ants in the seasonally dry tropics of Veracruz, Mexico. Biol Conserv 126:328–338

Halffter G (1998) A strategy for measuring landscape biodiversity. Biol Int 36:3–17

Halffter G (2005) Towards a culture of biodiversity conservation. Acta Zool Mex (n.s.) 21:133–153

Halffter G, Moreno CE (2005) Significado biológico de las diversidades alfa, beta y gamma. In: Halffter G, Soberón J, Koleff P, Melic A (eds) Sobre Diversidad Biológica: el Significado de las Diversidades Alfa, Beta y Gamma. M3M: Monografías Tercer Milenio, vol 4. Sociedad Entomológica Aragonesa, Zaragoza, pp 5–18

Hernandez-Stefanoni JL (2006) The role of landscape patterns of habitat types on plant species diversity of a tropical forest in Mexico. Biodivers Conserv 15:1441–1457

Hernandez-Stefanoni JL, Bello-Pineda J, Valdes-Valadez G (2006) Comparing the use of indigenous knowledge with classification and ordination techniques for assessing the species composition and structure of vegetation in a tropical forest. Environ Manage 37:686–702

Holling CS (1986) The resilience of terrestrial ecosystems: local surprise and global change. In: Williams CC, Munn RE (eds) Sustainable development of the biosphere. IISASA. Cambridge University Press, Cambridge, pp 289–317

Janzen D (1988) Tropical dry forest: the most endangered major tropical ecosystems. In: Wilson EO (ed) Biodiversity. National Academy Press, Washington DC, pp 130–137

Khurana E, Singh JS (2001) Ecology of seed and seedling growth for conservation and restoration of tropical dry forest: a review. Environ Conserv 28:39–52

Laurance WF (1999) Reflections on the tropical deforestation crisis. Biol Conserv 91:109–117

Lerdau M, Whitbeck J, Holbrook NM (1991) Tropical deciduous forest: death of a biome. Trends Ecol Evol 6:201–202

Li J, Ren Z, Zhou Z (2006) Ecosystem services and their values: a case study in the Qinba mountains of China. Ecol Res 21:597–604

Lott EJ (1987) Floristic diversity and structure of upland and arroyo forest of coastal Jalisco. Biotropica 19:228–235

Medail F, Verlaque R (1997) Ecological characteristics and rarity of endemic plants from southeast France and Corsica: implications for biodiversity conservation. Biol Conserv 80:269–281

Miranda F, Hernández XE (1963) Los tipos de vegetación de México y su clasificación. Bol Soc Bot Méx 28:29–179

Mooney HA, Bullock SH, Medina E (1995) Introduction. In: Bullock SH, Mooney HA, Medina E (eds) Seasonally dry tropical forests. Cambridge University Press, Cambridge, pp 1–7

Murphy PG, Lugo AE (1986) Ecology of tropical dry forest. Ann Rev Ecol Syst 17:67–88

Negendank JFW, Emmermann R, Krawczyk R, Mooser F, Tobschall H, Werle D (1985) Geological and geochemical investigations on the eastern trans Mexican volcanic belt. Geofísica Internacional 24:477–575

Ortega OR (1981) Vegetación y flora de una corriente de lava (malpaís) al noreste del Cofre de Perote, Ver. Biotica 6:57–97

Ricker M, Ramírez-Krauss I, Ibarra-Manríquez G, Martínez E, Ramos CH, González-Medellín G, Gómez-Rodríguez G, Palacio-Prieto JL, Hernández HM (2007) Optimizing conservation of forest diversity: a country-wide approach in Mexico. Biodivers Conserv 16:1927–1957

Rzedowski J (1978) Vegetación de México. Limusa, México

Sarukhán J (1998) Los tipos de vegetación arbórea de la zona cálido húmeda de México. In: Pennington TD, Sarukhán J (eds) Árboles Tropicales de México. Universidad Nacional Autónoma de México and Fondo de Cultura Económica, México D.F., pp 13–65

Soberón J, Llorente J (1993) The use of species accumulation functions for the prediction of species richness. Conserv Biol 7:480–488

Steininger MK, Tucker CJ, Ersts P, Killeen TJ, Villegas Z, Hecht SB (2001) Clearance and fragmentation of tropical deciduous forest in the Tierras Bajas, Santa Cruz, Bolivia. Conserv Biol 15:856–866

Tilman D, Pacala S (1993) The maintenance of species richness in plant communities. In: Ricklefs R, Schluter D (eds) Species diversity in ecological communities: historical and geographical perspectives. The University of Chicago Press, Chicago, pp 13–25

Toledo VM (1982) Pleistocene changes of vegetation in tropical Mexico. In: Prance GT (ed) Biological diversification in the tropics. Columbia University Press, New York, USA, pp 93–111

Trejo I (2005) Análisis de la diversidad de la selva baja caducifolia en México. In: Halffter G, Soberón J, Koleff P, Melic A (eds) Sobre Diversidad Biológica: el Significado de las Diversidades Alfa, Beta y Gamma. M3M: Monografías Tercer Milenio, vol 4. Sociedad Entomológica Aragonesa, Zaragoza, pp 111–122

Trejo I, Dirzo R (2000) Deforestation of seasonally dry tropical forest: a national and local analysis in Mexico. Biol Conserv 94:133–142

Trejo I, Dirzo R (2002) Floristic diversity of Mexican seasonally dry tropical forests. Biodivers Conserv 11:2063–2048

Vieira DLM, Scariot A (2006) Principles of natural regeneration of tropical dry forests for restoration. Restor Ecol 14:11–20

Williams-Linera G (2002) Tree species richness complementarity, disturbance and fragmentation in a Mexican tropical montane cloud forest. Biodivers Conserv 11:1825–1843