

Floristic diversity of sabal palmetto woodland: an endemic and endangered vegetation type from Mexico

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Abstract. The sabal palmetto woodland is a tropical plant formation dominated by *Sabal mexicana*, with restricted distribution to southeast Mexico. Sabal palms grow on poor soils but accumulate large quantities of organic substrate in their crowns, harboring a contingent of plants that use it as phorophyte. Although it is a threatened formation, basic information on its biodiversity is scant. We examined the floristic diversity of recruited (diameter at breast height, DBH, ≥ 1 cm) and understory (DBH ≤ 1 cm) plants, and its variation with anthropogenic disturbance. We also examined the floristic diversity of plants that use the sabal palms as phorophytes, and assessed its variation with human impact. All plants present in transects within a conserved and an adjacent perturbed area were sampled. The list of observed taxa shows that this vegetation has a clear affinity with tropical dry and wet forests of Mexico, with a small representation of taxa from desert ecosystems. The floristic contingent included a total of 81 species in 2000 m². Richness, composition and diversity were affected by disturbance. Recruited and understory vegetation in the disturbed site were 5- and 1.6-times less diverse than in the conserved site, and species of mature, conserved vegetation were substituted by heliophytes in the disturbed site. In contrast, abundance of palms and diversity and identity of epiphytic/hemiepiphytic plants were not affected by disturbance. We show that even monodominated tropical ecosystems growing on poor soils have a high floristic diversity and that current anthropogenic impact threatens not only species and populations but also entire plant formations.

Introduction

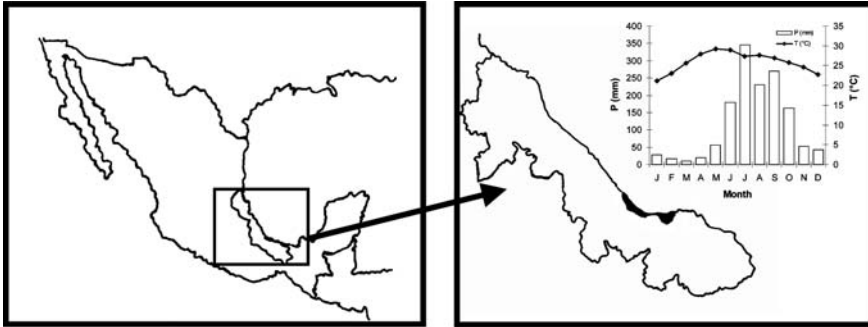
In their classic paper on the vegetation types of Mexico, Miranda and Hernández-X (1963) described 32 distinct vegetation units, defined largely on the basis of their structure, physiognomy and phenological patterns. In their anthology, 'palmares' (palmetto woodlands) are included as a distinct vegetation type. Palmetto woodlands constitute a group of communities, characterized by the predominance of plants of the family Arecaceae, which define the overall physiognomy of the vegetation (Rzedowski 1978). Within this general vegetation type, two variants can be distinguished: those dominated by palms of pinnate leaves, represented mainly by *Atalea* spp., and those dominated by

palms with fan-shaped leaves, with predominance of *Sabal mexicana* (Mart.) (Miranda and Hernández-X (1963)). The latter are known as sabal palmetto woodlands. This woodland is characterized by its association with soils which are frequently affected by flooding and, presumably, of low fertility (Gómez-Pompa 1980). This constrains the establishment and maintenance of plants, even under the relatively benign climatic conditions of the Mexican tropics (see Pennington and Sarukhán 1998). In contrast to these edaphic conditions, the palms of *S. mexicana* accumulate large quantities of matter (litter, scat and other animal debris, wind-blown materials of various kinds, etc.) on the axils of their huge petioles, producing an 'aerial' organic substrate which, given the predominance of the sabal palms, is abundant and potentially appropriate for the establishment and growth of numerous epiphytic and hemiepiphytic plants. The latter include fig trees (*Ficus* spp.) which provide an additional distinctive element to the physiognomy of this vegetation type (see Figure 1). Thus the floristic diversity of this palmetto woodland includes the terrestrial and the epi/hemiepiphytic community.

In their description of the sabal palmetto woodland, Pennington and Sarukhán (1998) mention that almost all of the current coverage of the sabal woodland in Mexico is the result of human-driven conversion of what used to be semi-evergreen tropical forest dominated by *Brosimum alicastrum* (see examples in Puig 1976), with one exception: that of the palmetto woodlands located between the Cities of Veracruz and Alvarado, where it is a primary formation (Figure 1).

This formation is highly threatened. Most of its original distribution, constituted by a coastal band in Veracruz, a small patch in Oaxaca (Pennington and Sarukhán 1998) and another small enclave in Guatemala (J. Rzedowski, com. pers.) has been largely eliminated. Moreover, the remaining vegetation, by growing on tropical lowlands of relatively smooth topography, is increasingly being cut and converted to grasslands for cattle ranching. The converted terrains are typically subjected to dry-season fires or are abandoned, forming vegetation mosaics under different degrees of regeneration. Furthermore, the sabal palms themselves seem to be resistant to, or even favored by such practices (see Pennington and Sarukhán 1998). As a result, what currently seem to be intact palmetto remnants are patches of secondary vegetation. Such a situation masks the real degree of endangerment this vegetation is subjected to nationally and (given its restricted distribution to southeast Mexico) globally. All of the above highlights the need to describe the biodiversity and the effects of human impact on the remaining patches of this endemic plant formation. By

Figure 1. Area of distribution and climate of the *Sabal mexicana* woodland in Mexico and view of the general physiognomy of this vegetation type in the study area, under two contrasting situations of human impact: perturbed (a) and conserved (b). Photographs also show the other predominant element of the physiognomy, the hemiepiphytic figs, *Ficus* spp. (F). Map of distribution range after Pennington and Sarukhán (1998).



centering on an endemic vegetation type from Mexico, we hoped to illustrate a global conservation problem: the risk of extinction of geographically restricted vegetation assemblages.

The present study aims at providing the first quantitative floristic characterization of sabal palmetto woodland, addressing the impact of human activities on several facets of its floristic diversity. The specific questions we addressed were: (i) what is the floristic diversity of this vegetation type considering the established trees, shrubs and lianas and how does it vary with the anthropogenic impact typical of the area? (ii) what is the diversity of the understory vegetation, representing the potential for floristic regeneration, and how is it affected by human impact? and (iii) what is the floristic diversity of plants that use the sabal palms as a phorophyte and how does it vary with current human activity? To address these questions we surveyed an area in southern Veracruz, Mexico, including a patch representative of primary vegetation, amid the predominantly disturbed landscape.

Materials and methods

Study area

This study was carried out in the Gulf of Mexico's coastal plains in the municipality of Tlalixcoyan, Veracruz (18°49' N, 96°05' W), at an elevation of 10 m a.s.l. This region formerly supported an extensive tract of sabal palmetto woodland (Miranda and Hernández-X 1963), dominated by palms of *S. mexicana* growing on sandy soils subjected to periodical floods (Rzedowski 1978). The study area is a remnant of the palmetto woodland reported by (Pennington and Sarukhán 1998, p. 60) as primary vegetation, originally extending from close to the City of Veracruz, down to the area of Alvarado (Figure 1). Climate in the area is hot and humid (Figure 1), with a mean temperature of 25.9 °C. Mean rainfall is 1302.2 mm, 60% of which concentrates between the months of June–October. There is a relatively dry season extending from November to May (García 1988). Floods occur during the rainy season; typically they are of short duration, mainly affecting the riparian and the lowest-lying sites.

Soils of the area can be characterized as of low fertility (López 2005). Levels of organic matter, C, N, and P are low, with concentration values $\leq 1\%$ in the case of the former two, or of 2% in the case of the latter. In addition, its low pH gives these soils a relatively acidic character. In contrast, the abundant organic substrate that accumulates in the axils of the palms' leaves is of better quality, with significantly greater concentrations of C, N, P and less acidic than the soil. Moreover, the average volume of organic substrate accumulated per palm is considerable: 953 (± 546 SD) g dry weight. At an estimated density of 640 palms/ha, collectively this material provides an abundant substrate available to the plants that establish on this stratum.

Floristic diversity and regeneration potential

We chose two contrasting sites with regards to their conservation status: a conserved one (18°50'603" N and 96°04'702" W) and a perturbed one (18°50'589" N and 96°04'644" W). Within the currently restricted distribution of this vegetation type, the conserved site was the only one identified which satisfied two important criteria: (i) no evident human intervention (absence of cattle and dung piles, no evidence of burning, no tree stumps) and (ii) confirmation from long-established local informants that it was not known to have been altered by human activity. The perturbed site was chosen by being as close as possible to the conserved site and by reflecting the perturbation resulting from the typical management of the region: extensive cattle grazing and yearly application of fire during the dry season. Given the extent of human impact in the area, independent perturbed sites are easy to find, but we could not find several separate conserved sites that we could use as independent replicates within the region. This determines that our results will be, in principle, only applicable to the study area. However, this limitation is compatible with the extremely restricted nature of this vegetation type.

Following Gentry's methodology (Gentry 1982, 1988) with some modifications as described below, in each of the sites we randomly established ten 2 × 50 m transects, thus accumulating a total sampled area of 1000 m² at each site. To define the specific location of each transect we measured the longest dimension of the site, along which we chose 10 random positions. These were used as the point of origin of each of the ten transects. All plants with diameter at breast height (DBH) ≥ 1.0 cm rooted within each transect were identified and had their DBH measured. In the case of lianas rooted within the transect we measured their trunk diameter at the base of the plant. Voucher specimens of the plants were deposited at the Instituto de Ecología AC Herbarium (XAL). With these data we calculated, for each species, the following variables: density ($D = \text{no. individuals}/1000 \text{ m}^2$), dominance ($Do = \sum \text{basal area of all individuals}$) and frequency ($F = \text{no. transects in which the species was present}/10$). With the relative values (R) of the three parameters we calculated a Value of Importance (VI) as: $VI = DR + FR + DoR$. Thus, the cumulative value for all the species would be 300%.

To assess the intensity of our sampling effort we developed species cumulative curves for plants ≥ 1.0 cm DBH, applying a 50-times sorting of the order of the transects (Coldwell and Coddington 1994) and, subsequently, we adjusted Clench models (Soberón and Llorente 1993) in order to determine the number of species where the curves' asymptote would be reached in each of the two sites.

To estimate the regeneration potential of the two sites we registered and identified, on the same transects, all saplings with a DBH ≤ 1.0 cm but with a height ≥ 30 cm. This insured that the survey considered plants that were already fully established, instead of considering newly established seedlings, in which mortality is very high and recruitment probability is very low (R. Dirzo,

unpub. data). For the plants in this stratum we calculated a VI on the basis of the sum of their relative density and relative frequency. In this case, the VI of all species would sum 200%.

We used the data of presence/absence of all species from the two strata to assess the floristic similarity between the two conservation conditions by performing a principal component analysis (PCA) (Gauch 1982). This analysis was complemented with the calculation of Sorensen's similarity coefficient ($S = 2C/A + B$ where C is the number of species common to both sites, and A and B are the number of species in each of the sites).

We compared the number of species in each of the two conservation conditions with a bootstrap- t , using 10,000 iterations (Manly 1997) to generate hypothetic distributions for each of the two sites, based on the number of species in each transect. We also calculated Shannon's diversity index (H') for the plants of each stratum and compared it between the conserved and perturbed site using Hutchenson's t (Zar 1999).

Floristic diversity of the epiphytic and hemiepiphytic community

We used a separate set of 10 independent transects (50×2 m) in each of the two sites to estimate the number of sabal palms, as well as the diversity and abundance of the species that use them as phorophytes. Using a ladder we collected and identified all plants present on the palms of these transects. For these plants we calculated, for each species present, relative density (no. individuals/total individuals) and relative frequency (no. palms in which the species was present/total no. palms). Both variables were used to calculate a VI for the epiphytic/hemiepiphytic species.

Results

Floristic diversity and between-site differences

Remarkably, the relatively restrictive edaphic environment of the area sustains a rich community of 81 species of vascular plants (epi/hemiepiphytic and terrestrial) of 45 families in 2000 m², or 69 species of 41 families, disregarding the epi/hemiepiphytes (see Appendix 1A). Such terrestrial plants included 54% trees, 22% shrubs, 17% lianas and 7% herbaceous plants, while among epi/hemiepiphytes 53% corresponded to herbaceous plants. The application of Clench's model to the overall terrestrial community, that is, plants from both sites but considering only plants ≥ 1.0 cm DBH (i.e., disregarding the understory plants) suggests a species richness of 89 terrestrial species.

A total of 46 species of plants with DBH ≥ 1 cm were recorded, of which 42 corresponded to species from the conserved site and only eight were species from the perturbed site (Table 1). Such 5.2-fold difference is reflected in the

Table 1. Diversity and structural characteristics of the vegetation from each of the two conservation situations (conserved, perturbed), including data for plants with DBH ≥ 1 cm (A), the regeneration understory (B), and the epiphytic/hemiepiphytic plants (C) from the sabal woodland.

	Conserved	Perturbed
<i>(A) Plants ≥ 1.0 cm DBH</i>		
Number of individuals	288	23
Number of species	42	8
Shannon–Weiner (log 10)	1.293	0.75
<i>(B) Regeneration</i>		
Number of individuals	578	381
Number of species	43	26
Ratio individuals/species	13.44	14.65
Shannon–Weiner (log 10)	1.151	1.016
<i>(C) Epi/hemiepiphytic</i>		
Number of individuals	182	237
Number of species	13	14
Shannon–Weiner (log 10)	0.734	0.815

highly significant between-sites contrast ($t = 5.2$, $p < 0.001$) resulting from the Bootstrap. In addition, we found that the overall density of the plants with DBH ≥ 1 cm (Table 1) is 12.5-times greater in the conserved site. Finally, diversity, as reflected by Shannon's diversity index (Table 1), was also significantly greater in the conserved site ($t = 7.37$, $p < 0.001$).

The variation between sites was also evident in terms of species composition and ecological predominance. The species that showed the highest importance was *Sabal mexicana* (Figure 2), which had a VI of 92% in the conserved site and of 150% in the disturbed site. This is approximately three times greater than that of the species that follow it in importance: *Pithecellobium dulce* (VI = 30) and *Cocoloba barbadensis* (VI = 53), in the conserved and perturbed site, respectively. However, in the perturbed site only eight species accumulated the total VI of 300% while in the conserved site the eight most important species accumulated a total VI of 210% and the residual 90% corresponds to 33 additional species, with VIs that range from 1 to 7% (Figure 2). That is, a large contingent of relatively rare species becomes absent under anthropogenic impact.

Apart from *S. mexicana*, *Cocoloba barbadensis* was the only other species common to both sites among the eight that attained highest importance values. In contrast, *Acacia cornigera*, a light-demanding species, typical of naturally or anthropogenically disturbed tropical sites, was the third most important species in the perturbed site, while in the conserved site this species was rare (17th in ranking of importance). Likewise, *Randia xalapensis* was an important species in the perturbed site (6th position), while in the conserved site it occupied the last ranking. Such limited coincidence of arboreal species between sites is reflected in the low Sorensen's similarity coefficient, of only 16%. The number of shared species corresponds to 50% of the total number of species

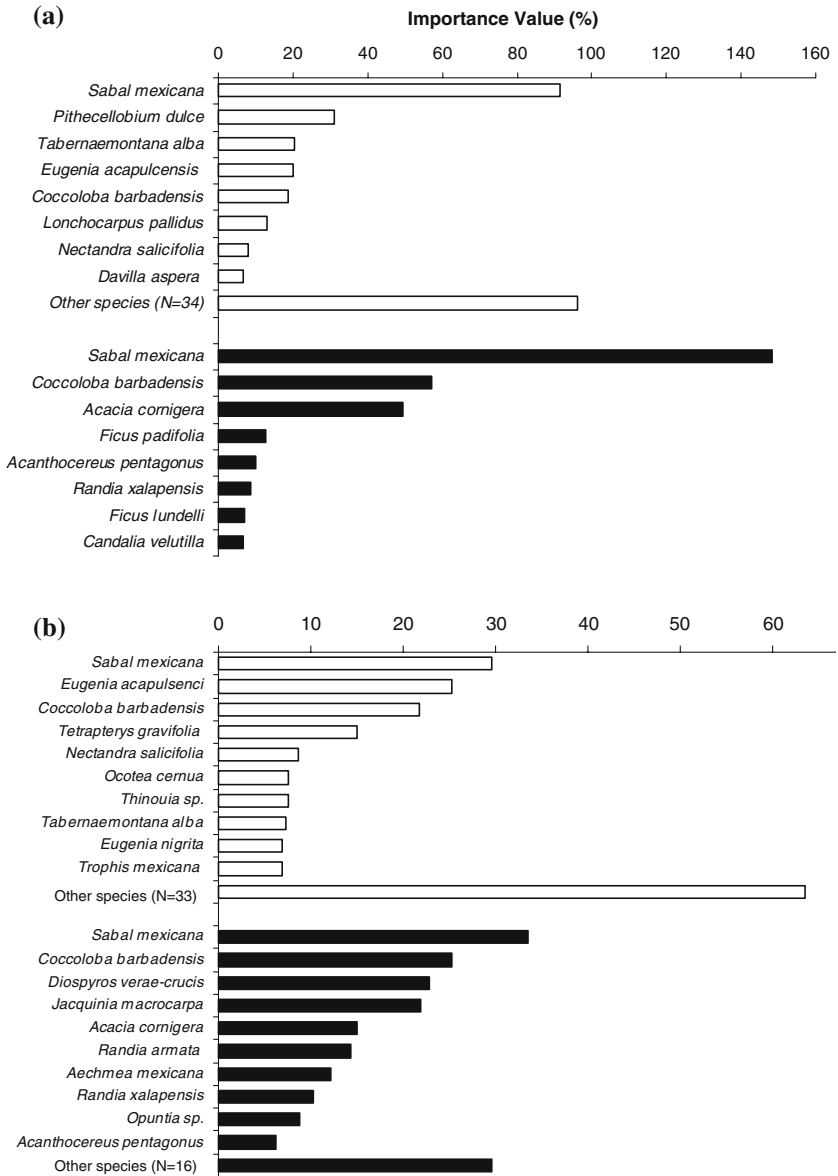


Figure 2. Values of Importance (VI) of the species with the 10 highest rankings, including plants with DBH ≥ 1 cm (a), and in the regeneration understory (≥ 30 cm height, but ≤ 1 cm DBH) (b), in the conserved (open bars) and perturbed (solid bars) site. See text for details.

present in the perturbed area but only to 9.5% of those present in the conserved area, which again underscores the marked floristic impoverishment, and the prevalence of a few secondary species under human impact.

Finally, accumulation curves (not shown) considering plants with DBH ≥ 1 cm showed a similar tendency to approach the asymptote in the two sites, although leveling of the curve was much more evident in the perturbed site. Clench's model predicted that for the conserved site the asymptote would be set at 60 species, while in the perturbed site this would take place at 13 species. Such predictions suggest a sampling deficit of 18 and five species, respectively, but the observed ratio of species conserved/perturbed site (5.2), is similar to that predicted by the model (4.6).

Regeneration potential

The understory plants (DBH ≤ 1 cm, ≥ 30 cm height), representing the regeneration potential, included a total of 56 species, most of them woody (59% trees, 24% shrubs, 13% lianas and 4% herbaceous), similar to the stratum of plants ≥ 1 cm DBH (Appendix 1A). Again, some differences between sites are evident (Table 1). While the perturbed site had 26 species, species richness of the conserved site was 1.6-times greater (43 species). In addition, the density of plants from this stratum was 1.5 greater in the conserved site. The ratio individuals/species was very similar between sites (Table 1), but Shannon's diversity index was significantly greater in the conserved site ($t = 4.32$, $p < 0.05$) and floristic similarity was low (34%). Despite these contrasts, a bootstrap- t test showed that species richness was only marginally different ($t = 1.96$, $p = 0.06$), indicating that the understory floristic diversity is reduced under human impact, but the effect is not as manifest as in the case of the plants ≥ 1 cm DBH (see Figure 2). This result may be due in part to the fact that species from more open, adjacent habitats invade the disturbed site (see below).

The distribution of the importance value among the species in this stratum shows a marked skew to the right in both sites (Figure 2), although the degree of skewness is greater in the conserved site, given the much larger tail accounted for by its additional 33 species (vs. 16 in the former). In addition, considering only the 10 most important species of the understory (Figure 2), the accumulated VI corresponded to 126 and 170% in the conserved and perturbed site, respectively. Species identity in the VI histograms shows that, again, in both sites *S. mexicana* and *C. barbadensis* are the most important, with the latter being the third and the second in ranking in the conserved and perturbed site, respectively. However, the set of additional most important species in the conserved site includes juvenile plants of species typical of mature tropical forest, several of them being taxa of importance as timbers (e.g., in the genera *Nectandra*, *Ocotea*, *Trophis*, *Brosimum*), or some species typical of the mature understory/low strata (e.g., *Eugenia* spp.), as well as some lianas (e.g., *Thinouia*, *Tetrapterys*) from mature forest. In contrast, the perturbed site lacks these species and instead has, as important elements, species typical of disturbed habitats (e.g., *Acacia cornigera*), or of open and insolated habitats such as the adjacent sand dunes, including some Cactaceae (e.g., *Opuntia* spp.,

Acanthocerus pentagonus) and other xerophytic plants (e.g., *Aechmea mexicana*). A common denominator to all but one of the additional eight most important species of this site is that, in addition to their heliophytic character, they are species with a certain capability to reduce browsing by ungulates (cattle in this case), with prime examples being *Randia armata* and *Acacia cornigera* (see Figure 2). Accordingly, the PCA using the presence/absence data from each of the 10 transects as data points clearly showed distinct clusters according to the conservation status (Figure 3), separating, along axis 1, the contingents of plants from the two conservation situations. Such separation is given by high, positive eigenvalues associated to heliophytic species such as *Opuntia* sp., *Randia armata*, *R. vazquezii*, *R. xalapensis* and *Achantocereus pentagonus* in the perturbed site, while negative values are associated to species typical of primary vegetation, including *Lonchocarpus pallidus*, *Eugenia acapulcensis*, *E. capuli*, and *Cordia* sp.

Sabal mexicana as a phorophyte and its associated flora

We detected a lower number of sabal palms in the conserved site as compared to the perturbed site (52 and 75, respectively). Using each transect as an independent sample to obtain measures of variation between sites, the difference in density of *S. mexicana* (at the scale of 100 m²) is not significant, or is just marginally so ($U = 26$, $p = 0.069$).

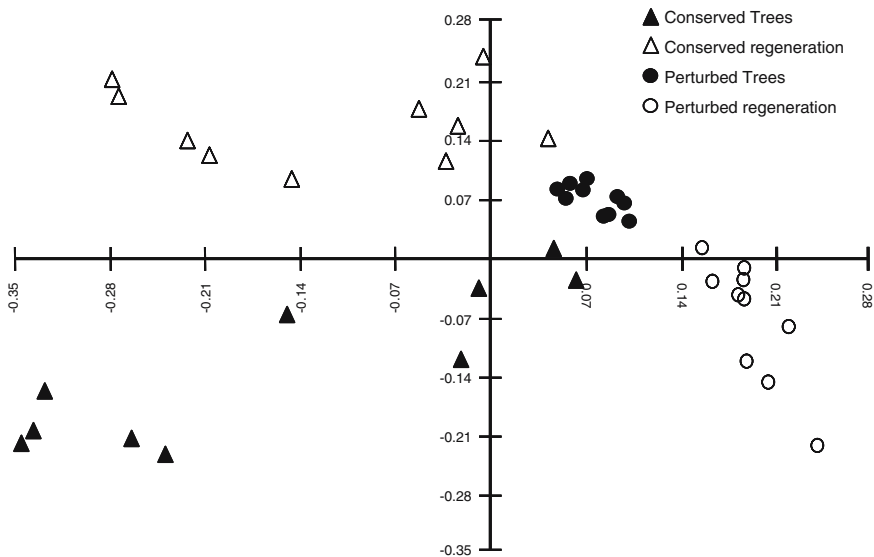


Figure 3. Results of a principal component analysis on presence-absence data of the species from the two sites (conserved, perturbed) and the two strata (trees, regeneration).

Such marginal difference was not reflected in the floristic contingent of plants that use the sabal palms as a phorophyte. The proportion of palms that were used by at least one epiphytic/hemiepiphytic species is essentially the same in both sites (94.3 and 94.6% in the conserved and perturbed site, respectively).

The total floristic contingent associated to sabal palms as epiphytic/hemiepiphytic plants was of 18 species in seven families and the distribution of VI among species yielded a similar histogram for both sites (Figure 4). Several elements attain a similar importance in both sites, with a particular prevalence of plants in the family Araceae, particularly *Anthurium schlechtendalii*. This species occupied the first and second position in the conserved and perturbed site, respectively. In addition, *Syngonium chiapense* (sixth and first position, respectively), and some epiphytic cacti such as *Selenicereus testudo* were also important elements.

The comparison of Shannon's diversity index for these plants (Table 1) did not show significant differences between sites ($t = 1.63, p > 0.05$). In addition, Sorensen's similarity index was relatively high (67%), with a total of 10 shared species. In sum, the epiphytic community remained essentially unaltered by human activities.

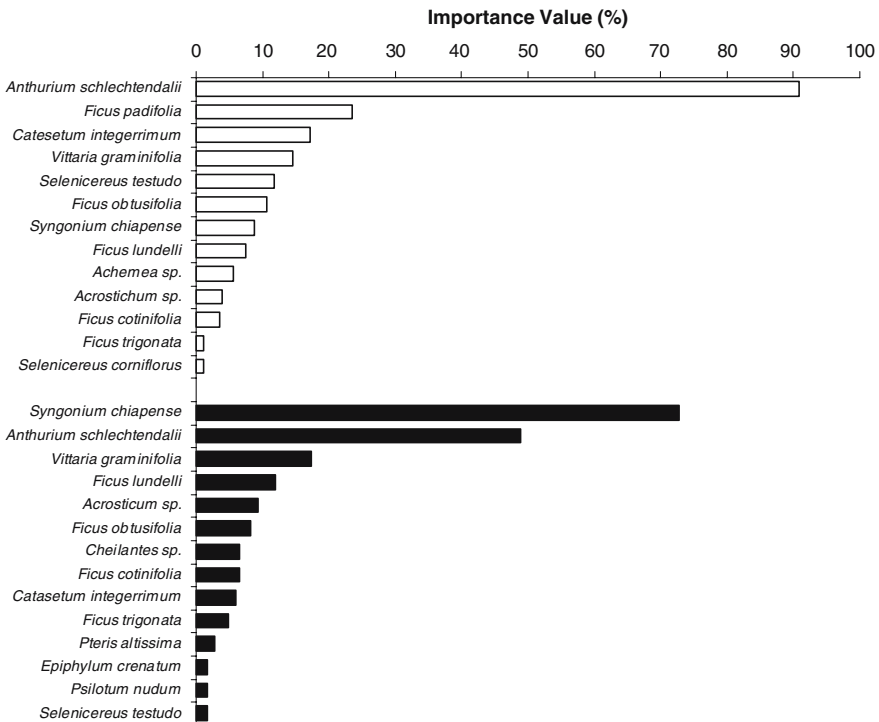


Figure 4. Values of Importance (VI) of the species that utilize sabal palms as phorophyte in the conserved (open bars) and perturbed (solid bars) site. See text for details.

Even though we did not estimate dominance of these plants on the basis of parameters such as basal area or biomass, it is evident that the most prominent element that uses *S. mexicana* as a phorophyte is a guild of strangler figs (*Ficus* spp.). These corpulent plants had a representation of four and five species in the conserved and perturbed site, respectively, and with a considerable abundance, in particular of *Ficus lundelli* in the conserved site, *F. pertusa* in the perturbed site, and *F. obtusifolia* in both sites (Figure 4). In addition, of the total of 127 sabal palms we sampled, 46% bore at least one strangler figure (cf. Figure 1), providing the typical physiognomy of this formation.

Discussion

Floristic diversity and affinity with other plant formations

Although the geographic distribution of the sabal palmetto woodland is very restricted and its physiognomy is very particular (cf. Figure 1), the biogeographic affinity of its elements is clearly tropical, although with a few elements of dry forest ecosystems from Mexico. By comparing with checklists of other tropical forests of Mesoamerica, we found that the floristic contingent present in the sabal palmetto woodland has a clear affinity with other tropical forests of that region: 66% of the genera/species are also present in tropical dry and wet forests, while 23% are taxa of distribution exclusive of tropical wet forest and 3% are taxa only represented in tropical dry forests. An additional 8% of the taxa found in the sabal palmetto are typical of arid or semi-arid vegetation from Mexico (see Appendix). Pennington and Sarukhán (1998) had already insinuated the affinity of this formation with semi-evergreen, semi-deciduous, and deciduous tropical forests of Mexico. Our results quantitatively confirm such affinities and make evident the presence of a few elements from arid and semi-arid regions. Another formation that presents a somewhat similar physiognomy is that of the subtropical palmetto woodland, 'dominated or co-dominated by *Sabal mexicana*' on flooded soils in Texas (Allard 1990). However, this isolated tract presents a clear association with temperate vegetation (including co-dominant species such as *Fraxinus berlandieriana* and *Ulmus crassifolia*), which makes it biogeographically, ecologically, and floristically different from the tropical sabal woodlands of Mexico. This underscores the uniqueness of this Mexican endemic plant formation.

Despite the relatively restrictive soil conditions where this woodland grows, floristic diversity was considerable (69 terrestrial plant species and 18 epiphytic/hemiepiphytic species). To place our findings of floristic diversity in perspective, we can compare with data from a detailed study of 20 sites of seasonally dry tropical forests of Mexico reported by Trejo and Dirzo (2002), using the same sampling protocol as that of the present study. The disturbed sabal palmetto site has a considerably lower diversity (eight

species) than even the least diverse site of Trejo and Dirzo (29 species). Our conserved site, with 42 species, is more diverse than three of the 20 dry forest sites, but it is 56% less diverse than the average reported by Trejo and Dirzo (2002). In addition, a site studied by Trejo and Dirzo, with a precipitation comparable to that of our palmetto is 2.5 times more diverse. Therefore, although the species richness of our site falls within the range of data reported in Trejo and Dirzo (2002), species richness of this type of woodland is located closer to the lower values of diversity present in Mexican tropical dry forest sites.

Changes in diversity and composition with human impact

Our study provides evidence of a significant anthropogenic impact on this endemic plant formation. In addition to the drastic reduction of the original coverage of the sabal woodland, we found that human activities can bring about an important negative effect on the diversity and floristic composition of the terrestrial plants of the sabal woodlands. We found, for example, that in addition to the 5- and 1.6-fold reduction in species richness of the perturbed site (large and understory plants, respectively), only three species (*Sabal mexicana*, *Coccoloba barbadensis* and *Acacia cornigera*) accounted for 85% of the total importance value of the species; in contrast, in the conserved zone, more than 13 species are necessary to reach such value and many rare species were absent from the perturbed site. In addition, in the two sites only two species, *S. mexicana* and *C. barbadensis*, coincided among the most important species in the vegetation.

In the case of the regeneration potential we found that, apart from the reduced diversity and plant abundance in the disturbed area, in both the disturbed and intact sites there was a predominance of *S. mexicana* and *C. barbadensis*. These species are resistant to perturbation (fire resistance of both species and re-sprouting of *C. barbadensis*). Therefore, under disturbance such species remain and may even become more abundant than in intact sites, as we found in this study. However, the floristic contingent in the disturbed understory included heliophytic species that are typical of disturbed conditions, or of adjacent open habitats such as the sand dunes, as well as species that resist grazing. In this zone the typical disturbances to the vegetation consists of clearing and burning to facilitate cattle grazing, apparently without a significant impact on established saplings and juvenile plants of the sabal palms, reported to be fire-resistant (McPherson and Williams 1998). This type of activity however, reduces the overall diversity and abundance of species and promotes the presence of heliophytic species and of species tolerant to grazing. The gross, 'macroscopic' physiognomy of the disturbed sites, when observed superficially, seems to be affected only slightly, given that *S. mexicana* and its epiphytic community remain as important components. This contributes to the under-appreciation of human impact on this plant formation. We conclude,

therefore, that the regeneration potential of the predominant species may persist, but the overall diversity and composition of the understory is affected by human disturbance, with potential to affect floristic and structural attributes of the vegetation over the long term.

The epiphytic and hemiepiphytic community

The great dominance of adult and juvenile plants of *S. mexicana* in this community may be explained by this species' ability to grow in poor soils and withstand the seasonal floods, as well as the protection afforded by the local inhabitants due to its multiple local uses (shading for cattle, thatch, posts for fencing and house construction, use of fruit as supplementary food for cattle). Its predominance and the rich organic substrate they provide in their crowns facilitate the establishment and maintenance of an epi/hemiepiphytic community in which the strangler figs become an important element that contributes to the physiognomy of the palm woodland. In accordance to our finding that human impact does not affect the density of sabal palms, we found no differences in the diversity and species richness of the plants that use sabal palms as phorophyte. This suggests that the community of epiphytic/hemiepiphytic plants is not affected by the local anthropogenic disturbance, as long as this does not negatively impact on the palms that, given their size, architecture and a voluminous accumulation of good-quality substrate, function as phorophytes (López 2005).

One of the most important aspects of the sabal palms is their role as phorophytes of hemiepiphytic trees in the genus *Ficus*, frequently regarded as keystone species for animals in tropical forests (Terborgh 1986), as well as important facilitators for forest regeneration (Guevara and Laborde 1993; Galindo-González et al. 2000). Therefore, their persistence as young hemiepiphytic plants (growing on the rich organic substrate of the palms) and mature individuals (growing on the poor soils as independent trees) (see Putz and Holbrook 1989; Putz et al. 1995; Holbrook and Putz 1996) can be of great importance for the dynamics and maintenance of the biodiversity of the sabal woodlands.

Implications for conservation

The present study indicates that remnant sabal palmetto woodlands need to be immediately protected and be used as inocula for the restoration of adjacent areas. The fact that disturbed remnants maintain some of the important elements of the palmetto woodland, particularly the sabal palms and the epi/hemiepiphytic flora provides an opportunity to develop relatively inexpensive restoration programs directed to increase its limited extent. A mosaic of patches currently under human use, together with conserved remnants and adjacent areas under restoration with connecting corridors (e.g., along the riparian

areas present in the zone) among them, can form the basis for the establishment of a natural protected area aimed to insure the long-term persistence of this endangered plant formation.

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Appendix

Appendix 1. Check list of the species present in two sites of contrasting conservation status (conserved, perturbed), including plants from two strata (plants with DBH ≥ 1 cm and understory regeneration) (A), and plants that use *S. mexicana* as a phorophyte (B). Data for (A) and (B) corresponds to a 2000 m² sampled area of sabal palm woodland in southern Veracruz, Mexico.

	Conserved		Perturbed	
	Trees	Understory	Trees	Understory
(A)				
Achatocarpaceae				
<i>Achatocarpus nigricans</i> Triana	x			
Apocynaceae				
<i>Forsteronia viridescens</i> Blake	x			
<i>Tabernamontana alba</i> Mill.	x	x		
Araceae				
<i>Monstera acuminata</i> K. Koch	x			
<i>Syngonium chiapense</i> Matuda	x			
Asclepiadaceae				
<i>Matelea pilosa</i> Benth.				x
Bignoniaceae				
<i>Arrabidaea</i> sp.	x			
<i>Cydista heterophylla</i> Seibert	x			
<i>Maefadyena uncatata</i> (Andrews) Sprague & Sandwith	x			x
<i>Tabebuia rosea</i> (Bertol.) DC.	x	x		x
Boraginaceae				
<i>Cordia</i> sp.		x		
<i>Cordia stellifera</i> I.M. Johnston.		x		
<i>Rochefortia lundellii</i> Camp		x		
Bromeliaceae				
<i>Aechmea mexicana</i> Baker				x
Cactaceae				
<i>Acanthocereus pentagonus</i> (L.) Britton & Rose			x	x
<i>Opuntia</i> sp.				x

Appendix 1. Continued

	Conserved		Perturbed	
	Trees	Understory	Trees	Understory
Celastraceae				
<i>Rhacoma eucymosa</i> (Loes. & Pittier) Standl.	x	x		
Combretaceae				
<i>Combretum</i> sp.		x		
Connaraceae				
<i>Rourea schippii</i> Standl.	x	x		
Cycadaceae				
<i>Zamia furfuracea</i> Aiton				x
Dilleniaceae				
<i>Davilla aspera</i> (Aubl.) Benoist	x	x		
<i>Tetracera volubilis</i> L.	x			
Ebenaceae				
<i>Diospyros verae-crucis</i> (Standl.) Standl.	x			x
Euphorbiaceae				
<i>Adelia barbinervis</i> Schltdl. & Cham.		x		
<i>Euphorbia schlechtendalii</i> var. <i>Websteri</i> McVaugh				x
Fabaceae				
<i>Acacia cornigera</i> (L.) Willd.	x	x	x	x
<i>Lonchocarpus pallidus</i> Killip	x			x
<i>Lonchocarpus rugosus</i> Benth.		x		
<i>Machaerium lunatum</i> (L. f.) Ducke				x
<i>Pithecellobium dulce</i> (Rolb.) Benth	x	x		x
<i>Pterocarpus</i> sp.		x		
<i>Senna</i> sp.				x
Flacourtiaceae				
<i>Xylosma panamense</i> Turcz		x		
Lacistemataceae				
<i>Lacistema aggregatum</i> (P.J. Bergius) Rusby	x	x		x
Lauraceae				
<i>Nectandra salicifolia</i> (Kunth) Nees	x	x		
<i>Ocotea cernua</i> (Nees) Mez	x	x		x
Malpighiaceae				
<i>Tetrapteris glabrifolia</i> Small	x	x		x
Malvaceae				
<i>Malvaviscus arboreus</i> Cav.	x	x		
Marantaceae				
<i>Calathea</i> sp.		x		x
Moraceae				
<i>Brosimum alicastrum</i> Sw.	x	x		
<i>Ficus cotinifolia</i> Kunth	x			
<i>Ficus lundellii</i> Standl.			x	
<i>Ficus padifolia</i> Kunth			x	
<i>Ficus trigonata</i> L.	x			
<i>Trophis mexicana</i> (Liebm.)	x	x		
Myrsinaceae				
<i>Parathesis</i> sp.		x		
Myrtaceae				
<i>Eugenia acapulcensis</i> Steud.	x	x		

Appendix 1. Continued

	Conserved		Perturbed	
	Trees	Understory	Trees	Understory
<i>Eugenia capuli</i> (Schltdl. & Cham.) Berg	x	x		
<i>Eugenia nigrata</i> Lundell	x	x		
Nyctaginaceae				
<i>Pisonia</i> sp.	x			
Ochnaceae				
<i>Ouratea lucens</i> (Kunth) Engl.	x	x		
Palmae				
<i>Sabal mexicana</i> Mart.	x	x	x	x
Piperaceae				
<i>Piper aduncum</i> L.		x		
Poaceae				
<i>Lasiacis procerrima</i> (Hack.) Hitch.		x		
Polygonaceae				
<i>Coccoloba barbadensis</i> Jacq.	x	x	x	x
Pontederiaceae				
<i>Bunchosia</i> Sp		x		
Rhamnaceae				
<i>Condalia velutina</i> I.M. Johnst.			x	x
Rubiaceae				
<i>Alibertia edulis</i> (Rich.) A. Rich. et DC	x			
<i>Randia armata</i> (Sw.) DC.	x	x		x
<i>Randia vazquezii</i> Lorence & Dwyer		x		x
<i>Randia xalapensis</i> M. Martens & Galeotti	x	x	x	x
Rutaceae				
<i>Eisenbeckia</i> sp.	x	x		
Sapindaceae				
<i>Paullinia fuscescens</i> (Kunth)	x			
<i>Thinouia</i> sp		x		
Sapotaceae				
<i>Pouteria</i> sp.	x			
Solanaceae				
<i>Solanum nigrum</i> L.	x	x		
Theaceae				
<i>Ternstroemia seemanii</i> Triana & Planch.	x	x		
Theophrastaceae				
<i>Jacquinia macrocarpa</i> Cav.	x	x		x
Verbenaceae				
<i>Citharexylum hexangulare</i> Greenm.				x
(B)				
	Conserved		Perturbed	
Bromeliaceae				
<i>Aechmea mexicana</i> Baker	x			
Araceae				
<i>Anthurium schlehtendalii</i> Kunth	x		x	
<i>Syngonium chiapense</i> Matuda	x		x	
Orchidaceae				
<i>Catesetum integerrimum</i> Hook	x		x	

Appendix 1. Continued

	Conserved		Perturbed	
	Trees	Understory	Trees	Understory
Pteridaceae				
<i>Cheilantes</i> sp.			x	
<i>Pteris altissima</i> Poir			x	
<i>Acrostichum</i> sp.	x		x	
Moraceae				
<i>Ficus cotinifolia</i> Kunth	x		x	
<i>Ficus lundelli</i> Standl.	x		x	
<i>Ficus obtusifolia</i> Mart.	x		x	
<i>Ficus padifolia</i> Kunth	x			
<i>Ficus trigonata</i> L.	x		x	
Psilotaceae				
<i>Psilotum nudum</i> (L.) P.Beauv			x	
Cactaceae				
<i>Epiphyllum crenatum</i> (Lemb.) H.P:Kelsey & Dayton			x	
<i>Selenicereus corniflorus</i> (Weing.) Britton & Rose	x			
<i>Selenicereus testudo</i> (Karw. E Zucc.) Bulb	x		x	
Vittariaceae				
<i>Vittaria graminifolia</i> Kaulf	x		x	

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