WOODY SPECIES STRUCTURE, DIVERSITY AND FLORISTIC AFFINITIES IN SEASONALLY DRY FOREST IN THE UXMAL ARCHAEOLOGICAL ZONE†

[ANÁLISIS DE LA ESTRUCTURA, DIVERSIDAD Y AFINIDADES FLORÍSTICAS DE ESPECIES LEÑOSAS EN LA SELVA ESTACIONAL SECA DE LA ZONA ARQUEOLÓGICA MAYA DE UXMAL]

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SUMMARY

Archaeological zones in Mexico effectively preserve the vegetal diversity within them. An analysis and description were done of woody vegetation structure, diversity and floristic affinity in the Uxmal Archaeological Zone, in the Puuc region of Yucatan, Mexico. Twenty quadrants measuring 10 x 10 m (100 m^2) were placed throughout the zone to sample its diverse substrates. Height and diameter at breast height (DBH) of woody species with DBH >1cm were measured in each quadrant. Floristic affinities were analyzed with a dendrogram generated using the Morisita-Horn index. A total of 1,622 individuals were recorded which belonged to 101 species and 76 genera from 31 families. The richest families were Fabaceae, Rubiaceae, Malvaceae, Polygonaceae and Euphorbiaceae. The species with the highest relative importance values were *Bursera simaruba*, *Piscidia piscipula*, *Diospyros anisandra*, *Thouinia paucidentata*, *Gymnopodium floribundum* and *Lonchocarpus xuul*. The most frequent species were *B. simaruba* and *D. anisandra*, those with the greatest density were *D. anisandra* and *L. xuul*, and the most dominant were *G. floribundum* and *P. piscipula*. Floristic affinity analysis identified three floristic groups: dry tropical forest; mixed seasonally flooded forest; and semi-evergreen tropical forest. Although relatively small in area, Uxmal has highly diverse microclimates and substrate types which support a diverse woody species composition, structure and physiognomy within the same seasonally dry tropical forest.

Keywords: Yucatan peninsula; Puuc region; floristic similarity; floristic diversity; vegetation.

RESUMEN

En el presente trabajo se presenta un análisis y descripción de la estructura, diversidad y las afinidades florísticas de la vegetación leñosa de la zona arqueológica de Uxmal, en la región Puuc de Yucatán. El muestreo consistió en establecer 20 parcelas de 10 m por 10 m tratando de abarcar la diversidad de sustratos de la zona arqueológica. En cada parcela se midieron las especies leñosas con un DAP mayor a 1 cm. Las afinidades florísticas se analizaron con un dendograma utilizando el índice de Morisita-Horn. Se registraron un total de 1,622 individuos leñosos pertenecientes a 31 familias, 76 géneros y 101 especies. Las familias más ricas son Fabaceae, Rubiaceae, Malvaceae, Polygonaceae y Euphorbiaceae. Las especies con mayor valor de importancia relativa son *Bursera simaruba, Piscidia piscipula, Diospyros anisandra, Thouinia paucidentata*, *Gymnopodium floribundum* y *Lonchocarpus xuul. B. simaruba* y *D. anisandra* son las más frecuente; *D. anisandra* y *L. xuul* con mayor densidad y *G. floribundum* y *P. piscipula* las especies más dominantes. El análisis de la similitud florística permite reconocer tres grupos florísticos. A pesar de su pequeña área, Uxmal presenta una alta heterogeneidad en cuestiones microclimaticas y tipos de sustratos, permitiendo que la composición, la estructura y la fisonomía de sus componentes arbóreos varíen dentro de la misma selva estacional. Se identificó que el sitio arqueológico Uxmal se encuentra cubierto por tres tipos de selvas: grupo florístico 1= selva baja caducifolia, grupo florístico 2= selva inundable mixta; grupo florístico 3= selva mediana subcaducifolia.

Palabras claves: península de Yucatán; región Puuc; similitud florística; diversidad florística; vegetación.

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INTRODUCTION

Dry seasonal forest is one of the most threatened vegetation types (*sensu* Pennington *et al.*, 2006) and is at risk of disappearing (Janzen, 1988). It is also one of the most affected by changes in human use and increases in human populations (Murphy and Lugo, 1986; Flores and Espejel, 1994; Maass, 1995; Fajardo *et al.*, 2005). Large areas of dry forest have been modified and continue disappearing as land use transitions to agriculture, animal production and urban development (Fajardo *et al.*, 2005). These changes in land use and cover are largely caused by humans and are driven by political, economic, cultural and biophysical factors, although deforestation and ecosystem disturbance are especially accelerated by political and economic factors (Sánchez-Azofeifa *et al.*, 2005).

Be they federal, state, municipal or private, natural protected areas (NPAs) are a way of directly conserving biological diversity. They fulfill multiple goals and functions at the regional, national and international levels, including 1) protection of wild flora and fauna; 2) safeguarding natural landscapes; 3) maintenance of ecological processes; 4) providing recreational opportunities; 5) resources for education; and 6) scientific research areas (CONANP, 2017). Other resource preservation instruments inadvertently protect the biological resources contained within them. In Mexico, archaeological zones are created with the principal objective of preserving and adequately managing the physical remains of pre-European contact cultures. However, they are also often extremely effective at conserving the biological diversity within them, in some cases more effectively than NPAs.

Approximately 2035 archaeological sites have been recorded in the state of Yucatan, of which sixteen are open to the public (Covarrubias-Reyna, 2003). As is to be expected, most of research done in these zones focuses on their archaeology, ethnography and anthropology, with very little attention given to their flora. Studies of biological diversity at the sites of Dzibilchaltún (Thien *et al.*, 1982), Sayil (Trejo and Dirzo, 2002) and Kabah (Palma, 2009) have produced descriptions of ecological parameters, and the structure and diversity of tree and bush species. In addition, studies have been done at Kabah, Dzibilchaltún and Uxmal on the richness, abundance, diversity and social aspects of bats (Ortega *et al.*, 2010; Estrella *et al.*, 2014).

Of the sixteen archaeological zones open to the public in Yucatan, eight (Chacmultun, Kabah, Labna, Loltun, Sayil, Oxkintok, Uxmal and Xlapak) are in the Puuc region. The Puuc region is a term used to designate the archaeological area delimited by a physiographic region integrated by the Sierrita de Ticul and the karstic formations of valleys and hills located on the southern border between the states of Campeche and Yucatán. The region known as Puuc covers a triangular portion of approximately 7,500 km2 of the states of Yucatán and Campeche; Among the outstanding topographic features of this region is the so-called Sierrita de Ticul, which starts from the south of the town of Maxcanú, following a northwest-southwest route to the outskirts of the community of Tzucacab (Arzápalo-Marín, 1995; Lugo-Hubp y García-Arizaga, 1999). Among the most important sites in this area are Uxmal, Kabah and Oxkintok (Covarrubias-Reyna, 2003). Archaeological site of the Uxmal was the largest and most important settlement among them when they were occupied and is currently one of the largest and most visited archaeological sites in the state. The area protected within the archaeological zone provides an excellent opportunity to study largely undisturbed vegetation. In addition, biological and cultural support is needed to help protect and conserve the existing biodiversity against threats such as growth in tourist infrastructure and deforestation for the building of new hotels and extraction of building materials. The present study objective was to analyze the diversity, structure and floristic affinities of the dry tropical forest inside the Uxmal Archaeological Zone.

MATERIALS AND METHODS

Study area

One of the principal archaeological sites in the state of Yucatan, Uxmal is located in the municipalities of Santa Elena and Muna in the region known as the Puuc. Of the zone's 283 hectares (ha), only 55 cover the area of restored structures open to the public (Figure 1). Vegetation in this area is managed and receives the heaviest anthropogenic impact. The remaining approximately 228 ha is covered with well-preserved vegetation that has been only minimally impacted over the least 70 years. The sampling quadrants were placed in this portion of the archaeological zone.

Uxmal has high topographic and soil type heterogeneity (Barrera-Vázquez *et al.*, 1981), it is located on a karstic plateau with variable altitude interspersed with intermontane valleys. The plateaus are interspersed with valleys of incipient development. On the hills, the soil is the Leptosol type, black soil with a high percentage of organic matter; on the slopes is the Cambisol, dark reddish-brown soil; in the plains Luvisols are red and Vertisols, very clayey soils that are periodically flooded (García-Gil *et al.*, 2013). In addition, the site is in a transition zone of vegetation between tropical dry forest and semi-perennial tropical forest (Flores and Espejel, 1994). It is also part of the Puuc Biocultural State Reserve (Reserva Estatal Biocultural del Puuc).

Vegetation data generated from the present study will therefore help to create a baseline for use in developing a reserve management plan to guide protection and conservation decisions.

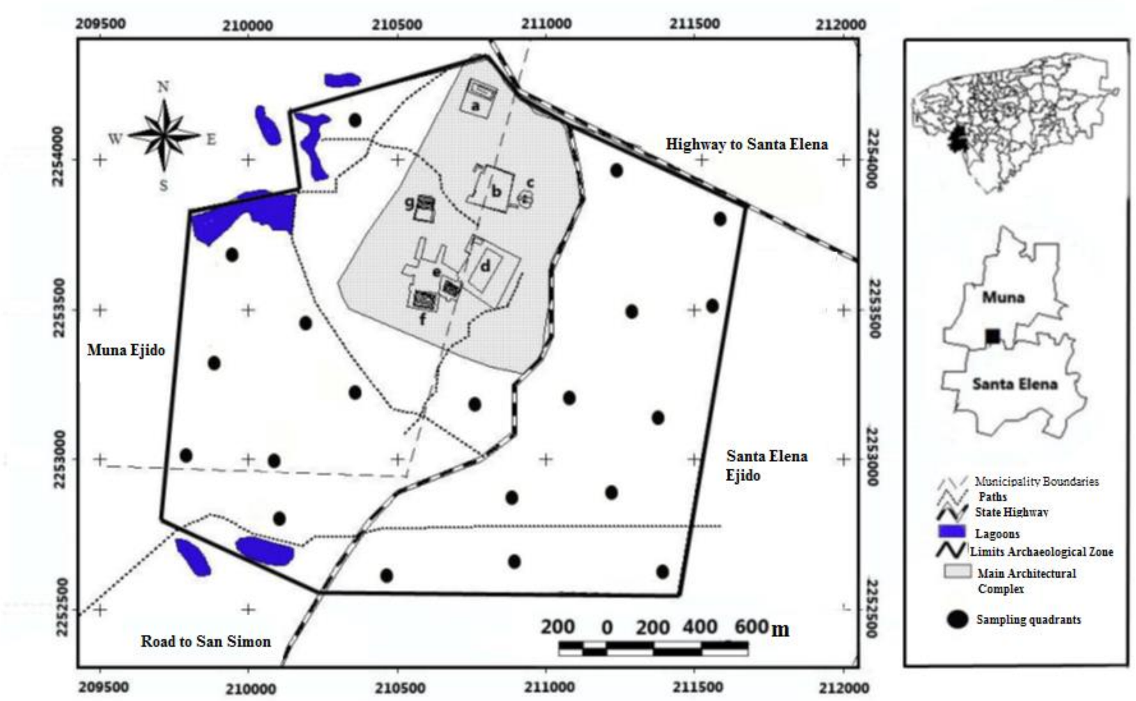

Figure 1. Location of Uxmal Archaeological Zone. Black dots indicate the twenty sampling quadrants. Letters (a to g) indicate structures in principal complex of monumental architecture.

Sampling and data analysis

In a preliminary reconnaissance, the entire area of the archaeological zone was examined. Soils were found to be highly heterogeneous (e.g. red clay soils without rock outcrops; seasonally flooded grey clayey soils without rock outcrops; flat, black soils with abundant loose rock and rock outcrops), and the area was confirmed as topographically uneven with natural and anthropogenic features (e.g. monumental platforms, pyramids, etc.). To adequately sample this substrate heterogeneity, twenty 10 x 10 m (100 m^2) quadrants were placed throughout the study area; total sampled area was therefore 2000 m^2 (0.2 ha) of conserved vegetation. Again, no samples were taken in the area open to the public since it experiences very heavy anthropogenic impacts (this area is not shown on the map: Figure 1). Inside each sampling quadrant all individual trees and bushes taller than 1.5 m and with a diameter at breast height (DBH) ≥ 1 cm were documented.

Quantitative structural analysis of the woody vegetation in each quadrant was calculated based on density, basal area and frequency. The relative importance value (RIV) for each species in each quadrant was determined by adding the relative values for density, frequency and basal area (Mueller-Dombois and Ellenberg, 2002). A species accumulation curve was built to evaluate if sampling effort (20 quadrants = 2000 m^2) was enough to record the largest possible number of species. This was done using the EstimateS ver. 9.1 program (Colwell, 2013) with the Chao1, Chao2, ACE, and Jacknife estimators. Species diversity was estimated with the PAST 3.19 program (Hammer, 2018) and the Shannon-Wiener diversity index, which reflects the relationship between richness and uniformity (Magurran, 1988). The same program was used to describe vegetation associations, or similar vegetation communities, or groups of quadrants with the same floristic affinity measurements. The Morisita-Horn index (Magurran, 1988) was applied because in addition to considering Shannon-Wiener diversity, it includes the abundance for each species in the two areas being compared. This makes it responsive to species richness and sample size, and highly sensitive to species abundance. The Morisita-Horn index measures the probability that two randomly selected individuals from two different sites or groups will be the same species and the results are presented as a similarity dendrogram.

RESULTS

Diversity

A total of 1,622 woody plants were recorded which represented 101 species and infraspecific taxa from 76 genera and 31 families (Appendix 1). Those families with the largest number of species in the samples were Fabaceae (24), Rubiaceae (10), Malvaceae (6), Polygonaceae (5) and Euphorbiaceae (4); the remaining families were represented by from three to one species. The genera *Trichilia* (4), *Randia* (4), *Coccoloba* (3), *Caesalpinia* (3), *Diospyros* (3) and *Guettarda* (3) had the highest number of species and the remaining genera were represented by two to one species. The species accumulation curve estimators confirmed sampling effort to be sufficient, with the representativity of each estimator being >90% (Figure 2); 101 species were recorded, and the estimated number of species ranged from 107 to 125. Shannon-Wiener diversity was 3.83 and estimated evenness was 0.46.

Structural parameters

Diameter at breast height (DBH) ranged from 1.0 to 117 cm. The largest number of individuals (47%) was in the 1 to 5 cm diameter class, and the lowest in the >16 cm class (Figure 3). Most individuals were in the 4 to 6 m height class, and the fewest were in the >10 m class (Figure 4). Six species had the highest RIV: *Bursera simaruba*, *Piscidia piscipula*, *Diospyros anisandra*, *Thouinia paucidentata*, *Gymnopodium floribundum* and *Lonchocarpus xuul* (Table 1; Appendix 1). All other species had a RIV of <15. Of the most important species, *B. simaruba* and *D. anisandra* were the most frequent (i.e. they were found in most of the quadrants); *D. anisandra* and *L. xuul* had the highest density; and *G. floribundum* and *P. piscipula* were the most dominant.

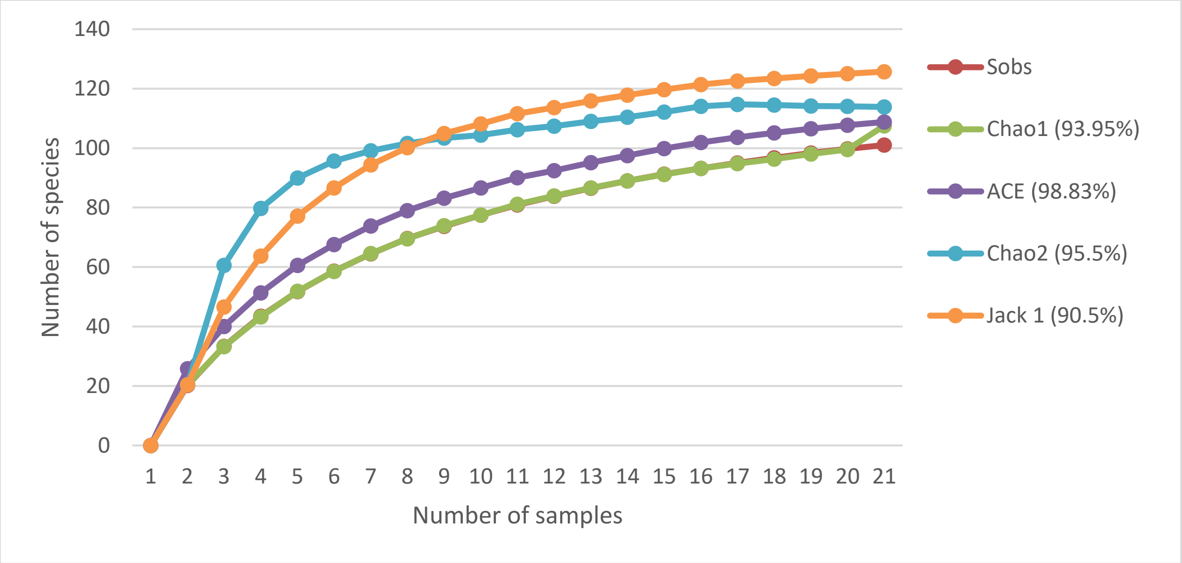

Figure 2. Species accumulation curve generated using Chao1, Chao2, ACE and Jacknife estimators; Sobs = observed species; each estimator's representativity is indicated in parenthesis.

Table I. Species with highest Relative Importance Values (RIV).

Species	Rel. Freq.	Rel. Dens.	Rel. Domin.	RIV
Bursera simaruba (L.) Sarg.	4.34	5.98	10.13	20.45
Piscidia piscipula (L.) Sarg	3.83	4.62	11.25	19.70
Diospyros anisandra S.F. Blake	4.34	10.36	2.97	17.66
Thouinia paucidentata Radlk	3.32	4.32	9.60	17.23
Gymnopodium floribundum Rolfe	1.53	3.64	12.05	17.22
Lonchocarpus xuul Lundell.	2.30	10.05	4.48	16.83

Rel Fre = relative frequency, Rel Den. = relative density, Rel Domin. = relative dominance

Floristic affinities

Floristic similarity analysis identified three floristic groups, indicating that certain species are characteristic to each of the sampling quadrants (Figure 5A). The richness of the shared species among floristic groups is represented (Figure 5B). In total the three floristic groups share nine species; the floristic group 3 has the highest number of non-shared species (51), it is also observed that group 3 shares a greater number of species with groups 1 and 2, while groups 1 and 2 share only 10 species.

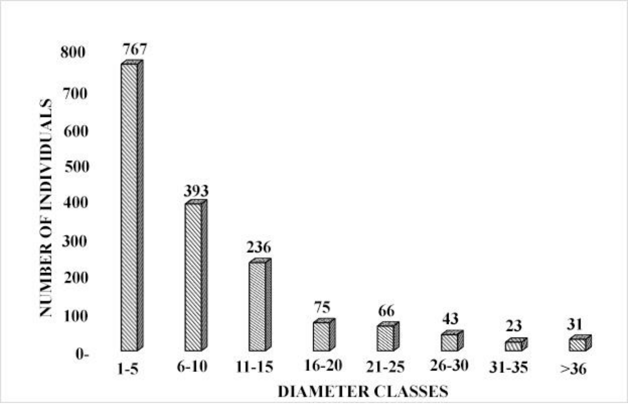

Figure 3. Individual distribution by diameter classes (centimeters).

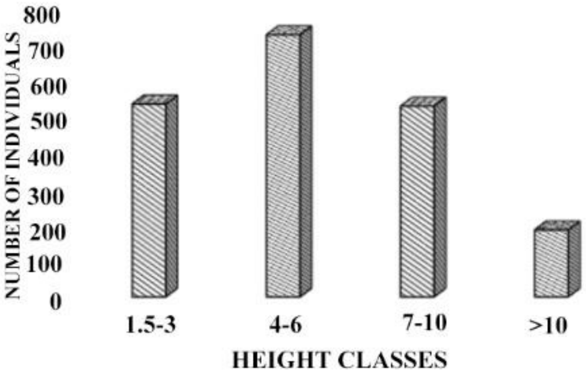

Figure 4. Individual distribution by height classes (meters).

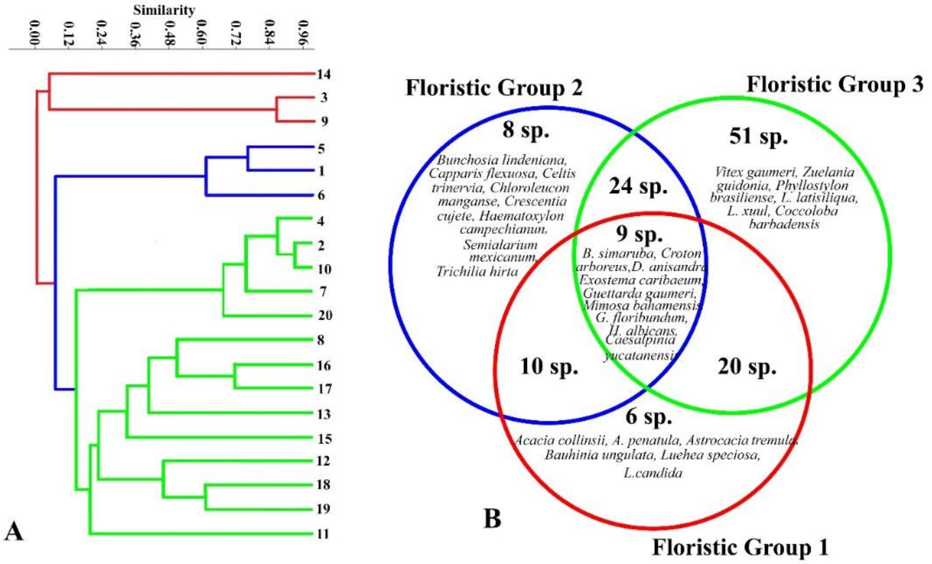

Figure 5. A) Similarity dendrogram comparing twenty sampling quadrants based on the Morisita-Horn similarity index. B) representation of the Venn diagram, the number of shared and unique species of each floristic group is mentioned and the species shared by the three floristic groups and the most representative species of each group are written. For more detail of the scientific names see Appendix 1.

DISCUSSION

Richness and floristic diversity

The species accumulation analysis confirmed that sampling effort was enough. Increased sampling effort away from the central archaeological zone increased tree species composition. Sampling using 10 x 10 m quadrants was apparently more efficient than using larger quadrants (e.g. 20 x 50 m). For example, a total of 101 species were recorded in the twenty quadrants (2000 m^2) applied in the present study, and 130 species were recorded in another study using the same methodology in an area at the state's southern extreme (Gutiérrez-Báez *et al.*, 2012). In contrast, 128 species were recorded in a series of nine, 20 x 50 m quadrants (9,000 m^2) used in another study in the southern portion of the state (Zamora *et al.*, 2008). Apparently, the use of smaller, widely dispersed quadrants (10 x 10 m) allows coverage of more substrate, topography and microclimate heterogeneity, allowing the documentation of more species.

The number of species registered in Uxmal is in the average range compared to other studies conducted in the south of the state of Yucatán (Palma, 2009; Escarraga, 2009; Peraza, 2008; Gutierrez-Baez *et al.*, 2012). However, if we compare Uxmal with other sites studied in northern Yucatan, we observe that in these sites the values of diversity and floristic richness is much lower (Thien *et al.*, 1982; Rico-Gray *et al.*, 1988; White and Darwin, 1995; Marín-Chávez, 1997; Mizrahi *et al.*, 1997; González-Iturbe *et al.*, 2002, Peraza, 2008; Escárraga, 2009. This phenomenon of diversity has been documented by several studies concluding that the richness and diversity of arboreal species in the Yucatan Peninsula increases in northwest-southeast direction (White and Hood, 2004).Neotropical dry forests is one of the most threatened tropical forests in the world, with less than 10% of its original extent remaining in many countries (DRYFLOR, 2016). It is can vary internally, with differences in the proportions of evergreen vs. deciduous species, height and diameter (DBH) structure, and composition at the genus and species (but not family) levels. The number of families in Neotropical dry forests can differ, but Fabaceae, Euphorbiaceae, Rubiaceae, Malvaceae, Polygonaceae and Bignoniaceae are the families richest in species, accounting for 45-70% of the total species recorded in various samples (Marcelo-Peña *et al.*, 2007; Fajardo, 2005; Guillespie *et al.*, 2000; Gallardo-Cruz *et al.*, 2005, Sánchez-Mejía *et al.*, 2007; Maass *et al.*, 2002; Zamora *et al.*, 2008; Palma, 2009). These families' adaptations to long drought periods have promoted species presence, prevalence and high richness in these forests (Lott *et al.*, 1987; Trejo and Dirzo, 2002). For example, in the present results 24% of all the recorded species were Fabaceae, making it the best represented in terms of number of species and genera. Species of this family have adapted to resist dry conditions and disturbances such as fire, and especially to symbiosis with nitrifying bacteria, which have allowed them to grow in scarce, rocky soils, and poor or infertile soils (Miller and Kauffman, 1998).

The most common tree genera in Neotropical dry forest are *Bauhinia, Casearia, Croton, Erytroxylon, Hippocratea, Randia, Serjania, Trichilia* and *Zanthoxylum* (Gentry, 1988, 1995). This differs notably from the predominant genera at Uxmal, save for the *Croton* and *Randia* genera. However, the most common genera at Uxmal (*Randia, Diospyros, Croton, Acacia, Lonchocarpus, Buchonsia, Guettarda, Pithecellobiun* and *Coccoloba*) exhibit a pattern similar to that of other tropical dry forests in Yucatan, sharing genera such as *Croton, Randia, Bunchosia, Guettarda, Lonchocarpus* and *Acacia*.

Structural parameters

Six species exhibited the highest abundance, dominance, basal area and RIV values at Uxmal: *Diospyros anisandra*, *Lonchocarpus xuul*, *Bursera simaruba*, *Havardia albicans*, *Piscidia piscipula* and *Thouinia paucidentata*. Resource availability may cause some species to be dominant over others in a community (Hubbell, 1979; Xing-Bing *et al.*, 2010). However, studies have not yet been done in the forests of the Yucatan Peninsula on the preferences of these species for particular resources that would allow them to dominate the region's forests. Diameter at breast height data in the Uxmal forest have an inverted "J" distribution similar to that of other sites studied in the dry forest of Yucatan; this distribution indicates that most individuals have a small diameter and very few are of large diameter (Trejo and Dirzo, 2002).

Floristic affinities

Variation in species dominance in each sampling quadrant can be attributed to microclimate conditions, soil type, soil moisture content and anthropogenic effects. These can produce structural, physical and floristic variations (Rico-Gray and García-Franco, 1991).

In floristic group 1, species establish themselves on flat surfaces with deep red soils (Luvisoles and Cambisoles), abundant leaf-litter and no rock outcrops. All the species except *P. sartorianum* are characteristic and common in the tropical dry forests of the Yucatan Peninsula (Flores and Espejel, 1994; Olmsted *et al.*, 1999). Although the potential distribution of dry tropical forest has been reported as the north of the states of Yucatan and Campeche, other reports exist of small fragments of this vegetation type in the south-central Yucatan Peninsula in regions such as Calakmul, Campeche (Martínez and Galindo Leal, 2002); Tzucacab, Yucatan (Zamora, 2008); and in the present results.

Floristic group 2 is characterized for its seasonally flooded soils. Three vegetation associations, defined by their dominant plant species, have been reported for this soil type: the tintal, dominated by *Haematoxylon campechianum*; the pucteal, dominated by *Bucida buseras*; and the mucal, dominated by *Dalbergia glabra* (Miranda, 1958; Flores and Espejel, 1994; Olmsted *et al*., 1999; Carnevali *et al*., 2003; Pennington and Sarukhan, 2005). However, none of the sampled seasonally flooded forest at Uxmal is dominated by any of these species, and it is therefore referred to as “mixed flooded forest” (*sensu* Martínez and Galindo-Leal, 2002). The presence of patches of this flooded vegetation community in Uxmal may be principally due to two factors. First, the deliberate filling in of shallow lagoons for agricultural use for thousands of years created conditions favorable to this community (Miranda, 1958a; Harrison, 1990). Second, rain could have washed soils from upslope into closed lagoons and basins, which would explain why fragments of flooded forest can be found in different progression stages.

The structure and dominant species in floristic group 3 correspond to semi-evergreen tropical forest (Flores and Espejel, 1994; Miranda and Hernández-X, 1963). One of the subgroups was identified in quadrants on archaeological remains and the other in quadrants without remains. Differences in tree species composition and diversity between areas with and without archaeological remains like those observed in the present results have been reported previously (Rico-Gray *et al.*, 1985; Lambert and Arnason, 1978; White and Darwin, 1994). However, *Brosimum alicastrum* is cited as the dominant and most important species in these studies, which does not correspond to the present results. This inconsistency precludes any generalization about differences in vegetation communities on archaeological remains being the result of ancient Maya silvicultural practices. Before any kind of conclusions can be made regarding this phenomenon, extensive additional multidisciplinary research will be needed involving the likes of ethnobiology, archaeobotany and paleoecology, among others.

Uxmal in the conservation of floristic diversity

Even with a small surface, the archaeological site of Uxmal has a high floristic diversity. However, the deforestation of the surrounding forest for the construction of hotel zones, monoculture areas of citrus plants and banks of materials, threat this site in the conservation of local floristic diversity. During the deforestation, many species along with their and local use value and their cultural knowledge, are lost (Trejo and Dirzo, 2000). In the case of Uxmal, the site is surrounded by Mayan communities (Muna, Santa Elena and San Simón) that still preserve a tradition in the use of traditional medicine and many of the plants they use are obtained from the forest that surround the archeological site. The conservation of local vegetation also involves the conservation of various animal species, for example Sauzo-Ordoñez *et al.* (2008) have emphasized that with the reduction in canopy cover, woody stems, roots and litter from tropical dry forests negatively affect the abundance of lizard, turtle and amphibian species.

In conclusion richness and diversity in the dry tropical forest in the Uxmal Archaeological Zone are average for seasonally dry tropical forests in southeast Mexico and Central America. Although relatively small in area, Uxmal contains a highly heterogeneous vegetation due to its many microclimates and substrate types. These generate variability in the composition, structure and physiognomy of this forest’s arboreal component. Three forest types were identified at Uxmal: floristic group 1= dry tropical forest; floristic group 2= mixed seasonally flooded forest; and floristic group 3= semi-evergreen tropical forest.

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Appendix 1. Floristic list of the 101 tree species registered in the 20 sampling plots. Rel Fre = relative frequency, Rel Den = relative density, Rel Dom = relative dominance, RIV = value of relative importance, GF1 = floristic group 1, GF2 = floristic group 2, GF3 = floristic group 3, 0 = species absent in the group floristic, 1 = species present in the floristic group.

Family	**Species**	**Rel Fre**	**Rel Den**	**Rel Dom**	**RIV**	**GF 1**	**GF 2**	**GF 3**
Annonaceae	*Sapranthus campechianus* (Kunth) Standl.	1.02	0.80	0.03	1.86	0	0	1
Apocynaceae	*Plumeria obtusa* L.	0.51	0.12	0.10	0.73	1	0	1
	Plumeria rubra L.	0.51	0.18	0.12	0.82	1	0	1
	Thevetia gaumeri Hemsley	0.51	0.12	0.07	0.70	0	0	1
Arecaceae	*Chamaedorea seifrizii* Burret	0.26	0.86	0.04	1.16	0	0	1
	Sabal mexicana Mart.	0.51	0.12	0.12	0.76	0	0	1
Bignoniaceae	*Crescentia cujete* L.	0.26	0.06	0.01	0.33	0	1	0
	Tecoma stans (L.) Juss. ex HBK.	0.26	0.12	0.06	0.43	0	0	1
Boraginaceae	*Bourreria pulchra* (Millsp.) Millsp.	1.28	1.05	0.27	2.60	0	0	1
	Ehretia tinifolia A. DC	1.53	1.29	0.98	3.80	0	0	1
Burseraceae	*Bursera simaruba* (L.) Sarg.	4.34	5.98	10.13	20.45	1	1	1
Capparaceae	*Capparis flexuosa* (L.) L.	0.26	0.25	0.03	0.53	0	1	0
	Capparis incana Kunth	0.26	0.06	0.03	0.35	0	0	1
	Forchammeria trifoliata Radlk	0.77	0.18	0.03	0.98	0	0	1
Caricaceae	*Carica papaya* L.	0.26	0.06	0.02	0.34	0	0	1
Celastraceae	*Hippocratea volubilis* L.	1.28	0.62	0.10	1.99	0	0	1
	Semialarium mexicanum (Miers) Mennega	0.26	0.12	0.06	0.43	0	1	0
Cochlospermaceae	*Cochlospermum vitifolium* Willd. Ex Spreng.	0.51	0.80	0.72	2.03	1	1	
Ebenaceae	*Diospyros anisandra* S.F. Blake	4.34	10.36	2.97	17.66	1	1	1
	Diospyros cuneata Standley	1.53	1.29	0.79	3.62	0	0	1
	Diospyros yatesiana Standley	1.02	0.43	0.06	1.51	0	1	1
Erythroxylaceae	*Erythroxylon rotundifolium* Lunan	1.53	1.05	0.24	2.82	0	0	1
Euphorbiaceae	*Cnidoscolus aconitifolius* (Mill.) I. M. Johnston	0.26	0.06	0.00	0.32	0	0	1
	Croton arboreus Millsp.	1.53	1.79	0.43	3.75	1	1	1
	Croton reflexifolius Kunth	2.30	1.66	1.07	5.03	0	1	1
	Jatropha gaumeri Greenm.	1.53	0.55	0.26	2.34	0	1	1
Fabaceae	*Acacia collinsii* Safford	0.26	0.06	0.00	0.32	1	0	0
	Acacia pennatula (Schlecht. & Cham.) Benth	0.26	0.06	0.01	0.33	1	0	0
	Apoplanesia paniculata C. Presl	0.51	0.37	0.17	1.05	0	0	1
	Bauhinia divaricata L.	1.28	1.29	0.08	2.65	0	0	1
	Bauhinia ungulata L.	3.32	2.53	0.28	6.12	1	0	0
	Caesalpinia gaumeri Greenm.	1.53	1.91	0.59	4.03	0	1	1
	Caesalpinia mollis (Kunth) Spreng.	0.77	0.49	0.61	1.86	0	1	1
	Caesalpinia vesicaria L.	0.77	0.62	1.65	3.03	0	1	1
	Caesalpinia yucatanensis Greenm.	1.28	0.86	0.26	2.40	1	1	1
	Chloroleucon manganse (Jacq.) Britton & Rose	0.26	0.12	0.02	0.40	0	1	0

	Enterolobium cyclocarpum (Jacq.) Griseb.	0.26	0.06	0.55	0.86	0	0	1
	Erythrina standleyana Krukoff	0.51	0.18	0.13	0.82	0	0	1
	Dalbergia glabra (Mill.) Standl.	0.51	0.18	0.01	0.70	0	1	0
	Havardia albicans (Kunth) Britton & Rose	1.53	2.10	3.50	7.13	1	1	1
	Lonchocarpus rugosus Benth.	1.79	2.47	0.97	5.22	1	0	1
	Lonchocarpus xuul Lundell.	2.30	10.05	4.48	16.83	0	0	1
	Lysiloma latisiliqua A. Gray ex Sauvalle	2.04	1.60	4.67	8.31	0	0	1
	Mimosa bahamensis Benth.	1.79	0.92	0.31	3.03	1	1	1
	Piscidia piscipula (L.) Sarg	3.83	4.62	11.25	19.70	1	0	1
	Pithecellobium dulce (Roxb.) Benth.	0.77	0.80	1.14	2.71	0	1	1
	Platymiscium yucatanum Standl	0.77	0.86	0.82	2.45	0	1	1
	Senegalia gaumeri (S.F. Blake) Britton & Rose	1.53	1.05	1.66	4.23	0	0	1
	Senna atomaria (L.) H.S. Irwin & Barneby	0.51	0.12	0.03	0.66	0	0	1
	Senna racemosa (Mill.) H.S. Irwin & Barneby	0.51	0.18	0.02	0.72	0	0	1
Lamiaceae	*Vitex gaumeri* Greenm	1.79	1.23	6.17	9.18	0	0	1
Malpighiaceae	*Bunchosia lindeniana* A. Juss.	0.26	0.18	0.01	0.45	0	1	0
	Bunchosia swartziana Griseb.var. *yucatanensis* Nied.	3.06	2.84	0.39	6.29	1	0	1
	Malpighia glabra L.	0.77	0.18	0.71	1.66	1	0	1
Malvaceae	*Ceiba aesculifolia* (Kunth) Britt. & Baker f.	0.77	0.37	0.45	1.59	0	0	1
	Hampea trilobata Standl.	0.26	0.06	0.00	0.32	0	0	1
	Helicteres baruensis Jacq	0.26	0.06	0.00	0.32	0	0	1
	Luehea candida (DC.) Mart.	0.51	0.49	0.53	1.54	1	0	0
	Luehea speciosa Willd.	0.51	0.62	0.53	1.65	1	0	0
	Tabernaemontana amygdalifolia Jacq	0.26	0.18	0.03	0.47	0	0	1
Meliaceae	*Trichilia americana* (Sesse & Moc.) T. D. Penn	1.02	0.37	0.14	1.53	0	0	1
	Trichilia hirta L.	0.26	0.18	0.01	0.45	0	1	0
	Trichilia trifoliata L.	0.77	0.43	0.13	1.33	0	1	1
Moraceae	*Brosimum alicastrum* Sw.	0.51	0.12	0.03	0.66	0	0	1
	Ficus cotinifolia Kunth	0.26	0.25	0.58	1.09	0	0	1
	Maclura tinctoria (L.) D. Don ex Steud.	0.26	0.06	0.02	0.33	0	0	1
Myrtaceae	*Eugenia foetida* Pers.	1.28	0.68	0.10	2.05	0	0	1
	Eugenia rhombea (O. Berg) Krug & Urb.	0.51	0.31	0.13	0.95	0	0	1
	Psidium sartorianum (O. Berg) Nied.	1.02	3.33	1.94	6.29	1	0	1
Phyllanthaceae	*Astrocasia tremula* (Griseb.) G.L. Webster	0.51	0.18	0.06	0.75	1	0	0
Polygonaceae	*Coccoloba acapulcensis* Standl.	0.26	0.18	0.03	0.47	0	0	1
	Coccoloba barbadensis Jacq.	0.51	0.18	0.02	0.71	0	0	1
	Coccoloba spicata Lundell	0.51	0.49	0.18	1.19	0	1	1
	Gymnopodium floribundum Rolfe	1.53	3.64	12.05	17.22	1	1	1
	Neomillspaughia emarginata (H. Gross) S.F. Blake	1.02	1.11	0.88	3.01	1	0	1
Primulaceae	*Ardisia escallonioides* Schlecht. & Cham.	0.26	0.12	0.00	0.38	0	0	1

Rhamnaceae	*Colubrina greggii* Watson var. yucatanensis	1.02	0.37	0.05	1.44	0	0	1
	Karwinskia humboldtiana (Schult.) Zucc.	0.51	0.31	1.20	2.02	0	0	1
	Krugiodendron ferreum (Vahl) Urb.	1.02	1.11	1.13	3.26	1	0	1
Rubiaceae	*Chiococca alba* (L.) Hitchc	0.26	0.25	0.01	0.51	0	0	1
	Exostema caribaeum (Jacq.) Schult.	3.06	1.73	0.88	5.67	1	1	1
	Guettarda combsii Urb.	1.28	0.74	0.22	2.23	0	1	1
	Guettarda elliptica Sw.	1.28	0.99	0.32	2.58	1	0	1
	Guettarda gaumeri Standl.	1.28	0.55	0.95	2.78	1	1	1
	Machaonia lindeniana Baill.	0.51	0.43	0.13	1.07	0	0	1
	Randia aculeata L.	1.28	0.92	0.18	2.38	0	1	1
	Randia longiloba Hemsley	0.51	1.11	0.55	2.17	0	1	1
	Randia obcordata S. Watson.	1.02	0.37	0.22	1.61	0	0	1
	Randia truncata Greenm. & C.H. Thomps.	1.02	0.74	0.08	1.84	0	1	1
Salicaceae	*Samyda yucatanensis* Standl.	1.02	0.49	0.05	1.56	0	0	1
	Zuelania guidonia (Sw.) Britton & Millsp.	0.77	0.68	0.34	1.78	0	0	1
Sapindaceae	*Meliccocus oliviformis* Kunthssp. Oliviformis	0.51	0.31	1.97	2.78	0	0	1
	Thouinia paucidentata Radlk	3.32	4.32	9.60	17.23	1	0	1
Sapotaceae	*Pouteria glomerata* (Miq.) Radlk.	0.26	0.06	0.04	0.35	0	0	1
	Sideroxylon americanum (Mill.) T.D. Penn.	0.77	0.68	0.67	2.12	0	0	1
	Sideroxylon obtusifolium (Humb. Ex Roemer & Schul) T.D. Pen	0.77	0.37	0.06	1.20	0	0	1
Simaroubaceae	*Alvaradoa amorphoides* Liebm.	0.51	0.12	0.18	0.82	0	0	1
Ulmaceae	*Celtis trinervia* Lam.	0.51	0.31	0.03	0.85	0	1	0
	Phyllostylon brasiliense Capp. ex Benth. & Hook. f	0.51	1.29	4.04	5.84	0	0	1
Urticaceae	*Cecropia peltata* L.	0.26	0.06	0.03	0.35	0	0	1
	Urera caracasana (Jacq.) Gaudich. ex Griseb	0.51	0.25	0.01	0.77	0	1	1