Botanical Sciences 102 (2): 513-533. 2024
DOI: 10.17129/botsci.3388

Received: August 9, 2023, Accepted: January 19, 2024
On line first: March 21, 2024

Taxonomy and Floristics / Taxonomía y Florística

Seasonally flooded Coquinal: typifying a particular plant association in the northern Yucatan peninsula, Mexico

Rodrigo Duno de Stefano[1], Mayte Aguilar-Canché[1], Germán Carnevali Fernández-Concha[1], Ivón Ramírez-Morillo[1], José Luis Tapia-Muñoz[1], Gabriela Reyes-Palomeque[1], and Diego F. Angulo[1,2]*

[1] Herbarium, CICY, Centro de Investigación Científica de Yucatán A.C., Mérida, Yucatán, Mexico.
[2] Centro Interdisciplinario de Investigaciones Biológicas y Humanas. Facultad de Ciencias Químicas. Universidad Autónoma Benito Juárez de Oaxaca, Oaxaca, Mexico.
*Author for correspondence: diangulo@gmail.com

Abstract

Background: One of the most diverse and threatened plant associations in the Yucatan peninsula has not been characterized and therefore not included in any protection category in Mexico. We characterize and describe this plant association, which is rapidly disappearing or being irreversibly transformed as a result of anthropic activities. We propose a name and attempt a preliminary assessment of its taxonomic richness, and the identification of priority species to be preserved.
Questions: What is the species richness and plant endemism associated within this plant association? What are the ecologically important and high-priority species for conservation? How is it different from associated or similar plant associations?
Studied species: Vascular plants.
Study site and dates: Northern Yucatan peninsula; 2021-2023.
Methods: The plant association was characterized, and quantitative parameters were recorded. The Importance Value Index was estimated to assess its local ecological importance, and each species was assigned a conservation category in order to evaluate the conservation status in a global context.
Results: We propose Seasonally flooded Coquinal (SFC) as a name for this plant association based on geomorphological, physiognomic, and structural attributes. A total of 206 species were recorded, two of which are endemic to the SFC and 28 to the Yucatan Peninsula Biotic Province (YPBP). Twelve species are listed under a risk category.
Conclusions: The SFC harbors a high plant diversity of species endemic to the YPBP, 12 of which are included in the IUCN red list, for which its typification and conservation should be a high priority in Mexico.
Keywords: diversity, dry forest, endemic flora, flooded environments, Yucatan.

Resumen

Antecedentes: Una de las asociaciones vegetales más diversas y amenazadas de la península de Yucatán no ha sido reconocida, por tanto, no incluida en alguna categoría de protección en México. Se caracterizó y describió esta vegetación, la cual está desapareciendo o siendo transformada resultado de actividades antrópicas. Proponemos un nombre y realizamos una primera aproximación al conocimiento de su riqueza taxonómica y especies prioritarias a conservar.
Preguntas: ¿Cuántas especies de plantas hay y cuáles son los endemismos que contiene? ¿Cuáles son las especies con mayor importancia ecológica y prioritarias para conservar? ¿Cómo se puede diferenciar de vegetación asociada o similar?
Especies estudiadas: Plantas vasculares.
Sitio y fechas de estudio: Norte de la Península de Yucatán; 2021-2023.
Métodos: Se caracterizó la asociación vegetal y se registraron parámetros cuantitativos. El Índice de Valor de Importancia fue estimado para evaluar la importancia ecológica local y la categoría de conservación de las especies fue asignada evaluando el estatus de conservación en un contexto global.
Resultados: En función de sus características geomorfológicas, fisonómicas y estructurales, proponemos "Coquinal Estacionalmente Inundado" (CY) como un nombre para esta asociación vegetal. Un total de 206 especies fueron registradas, incluyendo dos especies endémicas al CY y 28 endémicas a la Provincia Biótica Península de Yucatán (PBPY). Doce especies están en alguna categoría de riesgo.
Conclusiones: El CY alberga una alta diversidad de especies endémicas a la PBPY, 12 de ellas incluidas en la lista roja de la IUCN, por lo que su tipificación y conservación es de alta prioridad en México.
Palabras clave: ambientes inundados, diversidad, flora endémica, selva seca decidua, Yucatán.

Vegetation classification in Mexico has been a challenging and continuous task over time, in part due to the physiognomic-structural-floristic complexity of the plant communities, which is supported by processes determined mainly by climatic (ranging from arid ecosystems to temperate and even cold ecosystems), geomorphological (ranging from high mountains to wide plains), edaphic and ecological components, which interact, simultaneously, and continuously, for long periods of time (Rzedowski 1978, García 1998, Challenger & Soberón 2008, Velázquez *et al*. 2016). This complexity has led to different perceptions respect to number and circumscriptions of existing vegetation types. For example, Rzedowski (1978) has recognized ten types of vegetation, whereas Miranda & Hernández-X (1963) recognized 32 types and up to 53 by González-Medrano (2003).

Tropical dry forest represents one of the most distinctive vegetation types of Mexico and covers an important geographic area of the surface of the Yucatan peninsula, particularly in the state of Yucatan, and to a lesser extent those of Campeche and Quintana Roo (Rzedowski 1978, Becerra 2005, Reyes-Palomeque *et al*. 2021).

Faustino Miranda in his work "*Rasgos fisiográficos de interés para estudios botánicos*" (1958) carried out a study describing the vegetation and some plant associations in the Yucatan peninsula. His work included a general description of a variant of the tropical dry forest characterized by the abundance of columnar cacti, which he referred to as tropical dry forest with columnar cacti (TDFCC). He remarked "…height from 8 to 15 m., sometimes not reaching more than 6 m., and many of the elements that compose it are downright deciduous. It forms a belt of about 10 to 15 km wide at the southern edge of the "Cienega" (wetland) inland; … parallel to the coast … This type of forest was well distinguished by Lundell (1938)". Likewise, elsewhere on the text, he mentioned "...in open areas, the development of small grass meadows, where *Andropogon glomeratus* [*Andropogon gerardii* Vitman], *Eragrostis domingensis* [*E. prolifera* (Sw.) Steud.], and *Paspalum vaginatum* Sw. are common species". Flores & Espejel (1994) and Carnevali *et al*. (2021) described these "*open areas*" as part of the TDFCC (both naming it thorny deciduous forest but provided no further details on these plant associations). In the past few years, we have studied the TDFCC (Duno 2017, Duno *et al.* 2018, Carnevali *et al.* 2021, Aguilar-Canché *et al*. 2022), finding that what Miranda described as "*open areas*" requires more in-depth attention.

The TDFCC referred to by Miranda (1958) is located just south of the northern coastline of the Yucatan peninsula, where dry forest species such as *Havardia albicans* (Kunth) Britton & Rose, *Agave angustifolia* Haw. var. *angustifolia*, *Bursera simaruba* Sarg., *B. schlechtendalii* Engl., *Gymnopodium floribundum* Rolfe in Hook., *Pithecellobium unguis-cati* (L.) Benth., *Plumeria obtusa* L., and *Sphinga platyloba* (Bertero ex DC.) Barneby & J.W. Grimes are common, but cactus species such as *Acanthocereus tetragonus* (L.) Hummelinck, *Selenicereus grandiflorus* (L.) Britton & Rose subsp. *donkelaarii* (Salm-Dyck) Ralf Bauer, *Mammillaria gaumeri* (Britton & Rose) Orcutt, *Stenocereus laevigatus* (Salm-Dyck) Buxb., and *Pilosocereus gaumeri* (Britton & Rose) Backeb. are representative elements, conferring it a distinctive structure and physiognomy.

In the TDFCC there are also representative elements of the coastal plant communities such as mangroves (*Conocarpus erectus* L.), herbaceous marshes (dominated by such species as *Sporobolus spartinus* (Trin.) P.M.Peterson & Saarela and *Eleocharis elegans* (Kunth) Roem. & Schult., cattail (dominated by *Typha domingensis* Pers.), and reedbed (dominated by *Phragmites australis* (Cav.) Trin. ex Steud.). Then, the TDFCC comprises a heterogeneous plant matrix adapted to harsh environments because of the prevalent shallow, rocky soils, low annual precipitation, high salinity, and high temperatures (Miranda 1958, Flores & Espejel 1994).

Within this heterogeneous plant matrix, a vegetational variant develops on the shallow soils associated with the limestone outcroppings, which Miranda (1958) called *open areas,* which are locally known as *calichal or blanquizal* (Bautista-Zúñiga 2010, Duno 2017, Pérez-Sarabia *et al*. 2017, Carnevali & Tapia-Muñoz 2017, Ramírez-Morillo 2019, Aguilar-Canché *et al*. 2022), referring to the type of substrate rather than to the associated vegetation.

Several studies have highlighted the different attributes of tropical vegetation on limestone outcroppings pinpointing their differences with communities typical of other substrates (Ibarra-Manríquez & Martínez-Ramos 2002, Pérez-García & Meave 2005, Pérez-García *et al*. 2009, Ibarra-Manríquez *et al.* 2022). In these particular communi-

ties the role of smaller-scale environmental factors (microclimatic, topographic, and edaphic), as well as a large array of natural and anthropic disturbances determine the variable composition and structure of plant communities influencing the variability of the vegetation (Ibarra-Manríquez & Martínez-Ramos 2002, Do *et al*. 2015, Méndez-Toribio *et al*. 2016, Sánchez-Reyes *et al.* 2021, Ibarra-Manríquez *et al*. 2022).

Some authors have used the concept of biogeomorphic ecosystems to refer to the interaction between plant communities and their physical landscape. That is, the ability of plants to adjust their genotypic and phenotypic adaptations to the geomorphologically dynamic environment, thus enhancing connectedness (*i.e*., the degree to which the integrity of an ecosystem is controlled through internal feedback between small- and large-scale processes) and resistance and resilience (*i.e*., the ability of the system to recover from physical disturbances) (Balke *et al*. 2014, Corenblit *et al*. 2015, Viles & Coombes 2022). Like many biogeomorphic ecosystems, the *open areas* are dynamic ecosystems, which are unstable and subject to frequent and regular physical disturbance due to tropical storms and hurricanes (Boose *et al*. 2003, Islebe *et al*. 2015).

Despite its biological and ecological importance and being under great anthropic pressure due to its strategic geographic location (between Mérida city and the extensive Gulf coast from Celestún to Ría Lagartos, Yucatán), the TDFCC, and particularly the *open areas* recognized by Miranda (1958), has been poorly studied. Consequently, this plant association should be explored in detail to understand and better act toward its preservation.

The objectives of this research are the following: a) perform a floristic characterization identifying and quantifying diagnostic species, b) conduct a conservation assessment identifying the species included in any IUCN risk category, and c) propose a formal name for this plant association based on plant and geomorphological information for ease of communication, as well as provide information that allows to differentiate it from other similar or associate vegetation types.

Materials and methods

Study area. The study was conducted in the Yucatan dry forest and dry forest with columnar cacti near the coastal region, particularly in areas with rock outcrops in the north of the Yucatan peninsula, Mexico (Figure 1). The region is characterized by a strip of arid, warm climate (BS), which includes some climatic subtypes (for details, see Orellana *et al*. 1999). Three seasons are characteristic in the region: i) dry, ii) summer rains, and iii) winter rains or "nortes". The dry season extends from March to May, with an average precipitation up to 30 mm and a maximum temperature of 35.7 ºC. The summer rainy season spans from June to October, with an average precipitation of 141.2 mm, while the winter rainy season ranges from November to early February and is characterized by cooler winds accompanied by low atmospheric pressure, average temperatures of 24.6 ºC, and an average precipitation of 63 mm (SMN-CONAGUA 2022). The geological surface of the Yucatan peninsula is represented by extensive shell-rich deposits of the Quaternary, mainly from the Holocene, that form sandy beaches and marshy sedimentation basins in marshes and estuaries (Duch-Gary 1991). In contrast, the northern Yucatan peninsula, very close to the coastline, is characterized by the exposure of an early Miocene-Pliocene carbonate rock recognized as "coquina", which is associated with the Carrillo Puerto geological formation. The coquina is characterized by its conspicuous mollusk macrofossils (which lends it the name) and a cracked surface with irregular cavities of different sizes (Miranda-Huerta 2005, Shen *et al.* 2013).

Vegetation classification. The characteristics and criteria for an appropriate classification of this plant association were determined following the system of classification of the vegetation of Mexico SECLAVEMEX (Standardized Hierarchical Mexican Vegetation Classification System) (Velázquez *et al.* 2016).

Vegetation sampling. We identified areas with exposed coquina-type rock outcrops where vegetation sampling was carried out. Six sites without apparent anthropogenic disturbance were selected covering the entire area where coquina outcrops exist (about 230 km). The average distance between sites was 46 km (range 8-125 km; Figure 1). Although we observed that in the sampled sites the richness and diversity of species are different, the comparison

between them was not the objective of this work. We established two linear 50 m transects at each site and perpendicular sub-transects of 10 × 2 m at 10 m intervals on alternate sides of the main transect (six in all, as the first was laid out at 0 m). The identity and quantitative parameters (species richness, abundance, and plant coverage) within each sub-transect were recorded. The two main transects of each site were separated by 50 m. This sampling effort has been previously shown to capture plant species richness and abundance in these sites accurately (Espejel 1984, Torres *et al*. 2010, Angulo *et al*. 2018). We recorded trees, shrubs, and due to the nature of the site, we were able to discern individuals in clump of grasses. Vines and epiphytes were recorded for richness, but not included in the analysis of abundance and plant coverage.

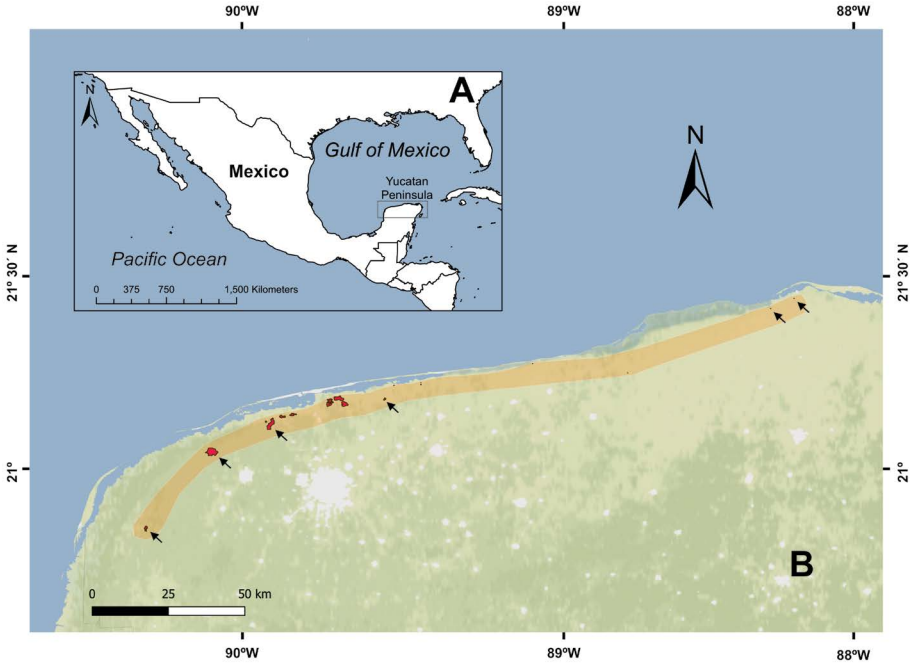

Figure 1. Map of Mexico and the Northern Yucatan peninsula. A) Study area located to the north of the Yucatan peninsula (delimited by a rectangle). B) showing the approximate distribution of the Seasonally flooded Coquinal (SFC) (orange shaded area). Red polygons represent selected Coquinal areas, but with improved characterization based on multitemporal LANDSAT remote sensing images. Arrows indicate sites sampled in this study.

Taxonomic identification, classification, and species dominance. We used The World Flora Online (www.worldfloraonline.org) and Carnevali *et al*. (2010) as a base for correct taxonomic nomenclature. Some scientific names have been updated, such as those related to *Caesalpinia* Plum. ex L. and *Prosopis* L. (Gagnon *et al.* 2016, Hughes *et al*. 2022). Plant samples not recognized in the field were identified using specialized literature and/or morphologically comparing them with those housed at herbarium CICY. The first set of vouchers were later deposited at CICY whereas duplicates were sent to GH, MEXU, MO, SEL, UADY, and XAL (acronyms according to Thiers 2023 [continuously updated]). The recorded species were arranged alphabetically; classification and nomenclature closely follow the Angiosperm Phylogeny Group (APG IV 2016). The quantitative parameters previously mentioned were used to estimate the Importance Value Index (IVI; Curtis & McIntosh 1950) to understand the local ecological value of each species recorded. The IVI was calculated as the sum of the relative values of frequency, density, and coverage (Curtis & McIntosh 1951), where the relative frequency is the number of occurrences of one species as a percentage of the total number of occurrences of all species, whereas the relative density is the number of individuals of one species as a percentage of the total number of individuals of all species and finally the relative dominance is the total area coverage of one species as a percentage of the total area coverage of all species. Coverage was estimated using the formula for the area of an ellipse.

Conservation status. The conservation status of the species recorded in the study was estimated based on information about each species from the IUCN Red List database (IUCN 2021) and Carnevali *et al.* (2021). Species were assigned to the IUCN categories, depending on their estimated threat level following the IUCN criteria. Species without available information were treated as Not Evaluated (NE) (Table 1)

Table 1. Plant species recorded in the Seasonally flooded Coquinal (SFC). Plant habit (Simpson 2006), Importance value index and IUCN status are featured. Endemic species of the Yucatan Peninsula Biotic Province (YPBP) are shown in bold. Quasi-endemic species (with populations outside but near the border of the YPBP) are shown with an asterisk. IUCN status based on Carnevali *et al*. (2021) are indicated with two asterisks. Species not recorded in the field transects, but their presence was observed during field work are indicated by three asterisks. Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), and Not Evaluated (NE). Vines, parasitic and epiphytic herbs were not considered for the IVI estimation.

Species	Plant habit	IVI	IUCN status
ACANTHACEAE			
Aphelandra scabra (Vahl) Sm.	Subshrub	0.233	
Bravaisia berlandieriana (Nees) T.F.Daniel	Subshrub	0.310	LC
Dicliptera sexangularis (L.) Juss.	Herb	0.282	
***Justicia* sp. nov.** (in process of publication)	Subshrub	0.971	
Ruellia ciliatiflora Hook.	Herb	1.349	
Ruellia paniculata L.	Herb	1.736	
Tetramerium nervosum Nees	Herb	0.508	
AGAVACEAE			
Agave angustifolia Haw. var. *angustifolia*	Herb	7.422	LC
AIZOACEAE			
Trianthema portulacastrum L.	Herb	0.425	
AMARANTHACEAE			
Alternanthera flavescens Kunth	Herb	1.361	
Alternanthera obovata Millsp.	Herb	0.472	
Blutaparon vermiculare (L.) Mears var. *vermiculare*	Herb	1.820	
Iresine diffusa Humb. & Bonpl. ex Willd.	Herb	0.592	
AMARYLLIDACEAE			
Zephyranthes orellanae Carnevali, Duno & J.L.Tapia	Herb	0.621	EN**
ANACARDIACEAE			
Metopium brownei (Jacq.) Urb.	Tree	0.369	LC
APOCYNACEAE			
Asclepias curassavica L.	Herb	1.256	
Cascabela gaumeri (Hemsl.) Lippold	Tree	0.236	LC
Dictyanthus aeneus Woodson	Vine	-	LC**
Dictyanthus yucatanensis Standl.	Vine	-	LC**
Plumeria obtusa L.	Tree	1.871	LC
ARACEAE			
Anthurium schlechtendalii Kunth	Herb	0.958	

Species	Plant habit	IVI	IUCN status
ARECACEAE			
Sabal mexicana Mart.	Tree	0.329	LC
ASTERACEAE			
Acmella filipes (Greenm.) R.K.Jansen	Herb	0.279	
Ageratum gaumeri B.L.Rob.	Herb	0.496	
Aldama dentata La Llave	Herb	0.783	
Eclipta prostrata (L.) L.	Herb	0.239	LC
Melanthera nivea (L.) Small	Herb	0.368	
Pectis linearis La Llave	Herb	0.233	
Pluchea odorata (L.) Cass.	Herb	0.237	
Porophyllum punctatum (Mill.) S.F.Blake	Shrub	0.236	
Wedelia acapulcensis Kunth	Herb	0.685	
BASELLACEAE			
Anredera vesicaria (Lam.) C.F.Gaertn.	Vine	-	
BIGNONIACEAE			
Crescentia cujete L.	Tree	0.914	LC
Parmentiera millspaughiana L.O.Williams	Shrub	2.220	LC
BIXACEAE			
Cochlospermum vitifolium (Willd.) Spreng.	Tree	0.865	LC
Cochlospermum wrightii (A.Gray) Byng & Christenh.	Herb	0.480	
BORAGINACEAE			
Cordia sebestena L.	Tree	0.275	LC
Heliotropium angiospermum Murray	Herb	0.524	
Varronia bullata L. *subsp. humilis* (Jacq.) Feuillet	Shrub	0.858	
Varronia curassavica Jacq.	Shrub	1.273	
BROMELIACEAE			
Bromelia karatas L.	Herb	-	
Tillandsia dasyliriifolia Baker	Herb (epiphyte)	-	LC**
Tillandsia recurvata (L.) L.	Herb (epiphyte)	-	
Tillandsia yucatana Baker	Herb (epiphyte)	-	NT**
BURSERACEAE			
Bursera schlechtendalii Engl.	Tree	2.602	LC
Bursera simaruba Sarg.	Tree	1.424	LC
CACTACEAE			
Acanthocereus tetragonus (L.) Hummelinck	Herb (succulent)	3.734	LC
Mammillaria gaumeri (Britton & Rose) Orcutt	Herb (succulent)	0.715	NT**
Opuntia inaperta (A.Schott ex Griffiths) D.R.Hunt	Herb (succulent)	1.537	LC**
Opuntia stricta (Haw.) Haw.	Herb (succulent)	3.901	LC

Species	Plant habit	IVI	IUCN status
Pilosocereus gaumeri (Britton & Rose) Backeb.	Shrub (succulent)	0.710	LC**
Selenicereus grandiflorus subsp. ***donkelaarii*** (Salm-Dyck) Ralf Bauer	Herb (succulent)	1.004	LC
Stenocereus laevigatus (Salm-Dyck) Buxb.	Tree (succulent)	0.244	LC
CAMPANULACEAE			
Lobelia yucatana E. Wimm.	Herb	0.236	EN**
CAPPARACEAE			
Crateva tapia L.	Tree	0.241	LC
Morisonia incana (Kunth) Christenh. & Byng	Tree	0.243	LC
COMBRETACEAE			
Conocarpus erectus L.	Tree	1.772	LC
COMMELINACEAE			
Callisia repens (Jacq.) L.	Herb	1.523	
Commelina diffusa Burm.f.	Herb	1.003	LC
Commelina erecta L.	Herb	2.277	LC
CONVOLVULACEAE			
Evolvulus convolvuloides (Willd.) Stearn	Herb	4.104	
Evolvulus sericeus Sw.	Herb	0.240	
Ipomoea carnea Jacq. subsp. *carnea*	Vine	7.013	
Ipomoea pes-caprae (L.) R. Br.	Vine	1.918	
Ipomoea sororia D.F.Austin & J.L.Tapia	Vine	-	VU**
Ipomoea trifida (Kunth) G.Don	Vine	-	LC
Ipomoea triloba L.	Vine	-	LC
Jacquemontia nodiflora G.Don	Vine	-	
Jacquemontia sp.	Vine	-	
Jacquemontia pentanthos (Jacq.) G.Don	Vine	-	LC
CUCURBITACEAE			
Cucurbita moschata Duchesne	Vine	0.238	
Ibervillea aff. *lindheimerii* (A.Gray) Greene	Vine	-	
Melothria pendula L.	Vine	0.234	
CYPERACEAE			
Cyperus elegans L.	Herb	1.950	
Cyperus squarrosus L.	Herb	1.801	LC
Eleocharis atropurpurea (Retz.) J.Presl & C.Presl	Herb	0.769	LC
Fimbristylis cymosa R.Br.	Herb	1.315	LC
Rhynchospora corymbosa (L.) Britton	Herb	0.377	LC
Rhynchospora scutellata Griseb.	Herb	0.253	
Rhynchospora tracyi Britton	Herb	0.534	

Species	Plant habit	IVI	IUCN status
DIOSCOREACEAE			
Dioscorea sp.	Vine	-	
ERYTHROXYLACEAE			
Erythroxylum rotundifolium Lunan	Herb	0.297	
EUPHORBIACEAE			
Acalypha alopecuroidea Jacq.	Herb	0.231	LC
Acalypha gaumeri Pax & K.Hoffm.	Subshrub	0.366	NT**
Caperonia palustris (L.) A.St.-Hil.	Herb	0.514	
Cnidoscolus souzae McVaugh	Shrub	0.293	LC**
Croton sp.	Subshrub	1.743	
Croton arboreus Millsp.	Tree	1.247	LC
Croton humilis L.	Subshrub	0.303	
Croton punctatus Jacq.	Subshrub	0.251	LC
Enriquebeltrania crenatifolia (Miranda) Rzed.	Shrub	0.558	LC**
Euphorbia adenoptera Bertol.	Herb	2.728	
Euphorbia dioeca Kunth	Herb	0.233	
Euphorbia mesembryanthemifolia Jacq.	Herb	0.682	LC
Euphorbia personata (Croizat) V.W.Steinm.	Succulent	1.205	
Euphorbia prostrata Aiton	Herb	0.346	
Euphorbia schlechtendalii Boiss.	Tree	1.068	
Euphorbia sp.	Herb	0.234	
Jatropha gaumeri Greenm.	Tree	5.369	LC**
Tragia glanduligera Pax & K.Hoffm.	Vine	0.235	
FABACEAE			
Cenostigma gaumeri (Greenm.) Gagnon & G.P.Lewis	Tree	1.290	LC**
Centrosema virginianum (L.) Benth.	Vine	-	
Chamaecrista chamaecristoides (Collad.) Greene var. *chamaecristoides*	Herb	1.096	
Chamaecrista flexuosa var. *texana* (Buckley) H.S.Irwin & Barneby	Herb	0.577	
Chloroleucon mangense (Jacq.) Britton & Rose	Tree	0.632	LC
Coulteria cubensis (Greenm.) Sotuyo & G.P.Lewis	Tree	1.324	
Coursetia caribaea (Jacq.) Lavin	Herb	0.476	LC
Ctenodon fascicularis (Schltdl. & Cham.) A.Delgado	Subshrub	0.830	
Dalbergia glabra (Mill.) Standl.	Tree	0.590	LC
Desmanthus virgatus (L.) Willd.	Herb	2.239	LC
Desmodium sp.	Herb	0.600	
Desmodium affine Schltdl.	Herb	0.348	
****Diphysa yucatanensis*** Hanan-Alipi & M.Sousa	Tree	1.436	

Species	Plant habit	IVI	IUCN status
Galactia striata (Jacq.) Urb.	Vine	-	
Gliricidia maculata (Kunth) Steud.	Tree	0.680	LC**
Haematoxylum campechianum L.	Tree	16.04	LC
Havardia albicans (Kunth) Britton & Rose	Tree	2.874	LC**
Indigofera subulata var. *scabra* (Roth) Meikle	Shrub	0.938	LC
Leucaena leucocephala (Lam.) de Wit	Tree	0.237	
Macroptilium lathyroides (L.) Urb.	Herb	0.401	
Marina scopa Barneby	Shrub	0.324	
Mimosa bahamensis Benth.	Tree	0.849	LC
Mimosa distachya Cav. var. *oligacantha* (DC.) Barneby	Shrub	2.205	
Neltuma juliflora (Sw.) Raf. var. *juliflora*	Tree	3.031	
Neptunia sp.	Herb	0.257	
Piscidia piscipula (L.) Sarg.	Tree	0.234	LC
Pithecellobium unguis-cati (L.) Benth.	Tree	3.361	LC
Rhynchosia minima (L.) DC.	Vine	-	LC
Senegalia gaumeri (S.F.Blake) Britton & Rose	Tree	1.064	LC**
Senna pallida (Vahl) H.S.Irwin & Barneby var. ***gaumeri*** (Britton & Rose) H.S.Irwin & Barneby	Tree	0.236	EN**
Senna racemosa (Mill.) H.S.Irwin & Barneby var. *racemosa*	Tree	0.557	LC
Sesbania herbacea (Mill.) McVaugh	Herb	1.991	
Sigmoidotropis elegans (Piper) A.Delgado	Vine	-	
*Sphinga platyloba (*Bertero ex DC.) Barneby & J.W.Grimes	Tree	2.288	
Stylosanthes humilis Kunth	Herb	1.249	
Tara vesicaria (L.) Molinari, Sánchez Och. & Mayta	Tree	1.043	LC
Tephrosia cinerea (L.) Pers.	Herb	1.018	NE
Vachellia collinsii (Saff.) Seigler & Ebinger	Tree	1.391	LC
Vachellia cornigera (L.) Seigler & Ebinger	Tree	0.267	
Vachellia farnesiana (L.) Wight & Arn.	Tree	0.894	LC
HYDROLEACEAE			
Hydrolea spinosa L.	Herb	0.466	
LAMIACEAE			
Cantinoa mutabilis (Rich.) Harley & J.F.B.Pastore	Herb	0.233	
Ocimum campechianum Mill.	Herb	1.824	
LOASACEAE			
Mentzelia aspera L.	Herb	0.234	
LOGANIACEAE			
Spigelia anthelmia L.	Herb	0.236	

Species	Plant habit	IVI	IUCN status
LORANTHACEAE			
Psittacanthus mayanus Standl. & Steyerm.	Herb (parasite)	-	
LYTHRACEAE			
Cuphea gaumeri Koehne	Herb	2.170	LC**
MALPIGHIACEAE			
Malpighia spathulifolia F.K.Mey.	Tree	1.806	LC
MALVACEAE			
Abutilon viscosum (L.) Dorr	Subshrub	0.252	
Bakeridesia gaumeri (Standl.) D.M.Bates	Shrub	0.331	LC
Cienfuegosia yucatanensis Millsp.	Herb	7.361	
Corchorus siliquosus L.	Herb	0.251	
Gossypium hirsutum Cav.	Shrub	0.233	VU
Guazuma ulmifolia Lam.	Tree	0.233	LC
Herissantia crispa (L.) Brizicky	Herb	0.244	
Hibiscus poeppigii (Spreng.) Garcke	Herb	0.474	
Malachra capitata (L.) L.	Herb	2.441	
Malvaviscus arboreus Dill. ex Cav.	Shrub	0.257	LC
Melochia tomentosa L.	Subshrub	2.849	
Sida ciliaris L.	Herb	55.57	
Waltheria rotundifolia Schrank	Herb	1.701	
MARSILEACEAE			
Marsilea vestita Hook & Grev. var. *vestita*	Herb	0.529	
NOLINACEAE			
******Beaucarnea pliabilis*** (Baker) Rose	Tree	-	NT
ORCHIDACEAE			
Cyrtopodium macrobulbon (Lex.) G.A.Romero & Carnevali	Herb	0.539	
Myrmecophila christinae Carnevali & Gómez-Juárez var. *christinae*	Herb (epiphyte)	-	LC**
PASSIFLORACEAE			
Passiflora bicornis Mill.	Vine	-	
Passiflora foetida L.	Vine	-	
PHYTOLACCACEAE			
Rivina humilis L.	Herb	0.308	
PLANTAGINACEAE			
Angelonia parviflora Barringer	Herb	1.056	LC**
Mecardonia procumbens (Mill.) Small	Herb	1.895	

Species	Plant habit	IVI	IUCN status
POACEAE			
Anthephora hermaphrodita (L.) Kuntze	Herb	1.394	LC
Aristida adscensionis L.	Herb	0.428	
Bouteloua repens (Kunth) Scribn. & Merr.	Herb	1.173	
Chloris barbata Sw.	Herb	0.805	
Dactyloctenium aegyptium (L.) Willd.	Herb	5.741	
Diplachne fusca (L.) P.Beauv. ex Roem. & Schult.	Herb	0.284	
Eragrostis amabilis (L.) Wight & Arn.	Herb	1.241	
Eragrostis ciliaris (L.) R. Br. var. *ciliaris*	Herb	3.640	
Eragrostis prolifera (Sw.) Steud.	Herb	1.329	LC
Eragrostis secundiflora J.Presl	Herb	0.618	
Panicum trichanthum Nees	Herb	0.925	
Setaria geminata (Forssk.) Veldkamp	Herb	1.747	LC
Sporobolus pyramidatus (Lam.) Hitchc.	Herb	1.383	
POLYGONACEAE			
Coccoloba uvifera L.	Tree	0.249	LC
Gymnopodium floribundum Rolfe in Hook.	Tree	2.996	LC
Neomillspaughia emarginata S.F.Blake	Tree	0.256	LC**
PONTEDERIACEAE			
*****Heteranthera yucatana*** Carnevali, J.L.Tapia & J.R.Grande	Herb	-	EN
Heteranthera limosa Willd.	Herb	0.235	
PORTULACACEAE			
Portulaca halimoides L.	Herb	1.034	
Portulaca oleracea L.	Herb	7.139	LC
Portulaca pilosa L.	Herb	0.506	
Portulaca rubricaulis Kunth	Herb	2.850	
PRIMULACEAE			
Bonellia macrocarpa (Cav.) B.Ståhl & Källersjö subsp. *macrocarpa*	Tree	0.241	LC
*****Bonellia flammea*** (Millsp. ex Mez) B.Ståhl & Källersjö	Tree	-	NT**
RUBIACEAE			
Ernodea littoralis Sw.	Subshrub	0.245	LC
Morinda royoc L.	Shrub	0.234	LC
Randia aculeata L.	Shrub	1.177	LC
Randia obcordata S.Watson	Shrub	0.877	LC
Spermacoce sp.	Herb	2.506	

Species	Plant habit	IVI	IUCN status
RUTACEAE			
Esenbeckia pentaphylla Griseb.	Tree	0.953	LC
SALICACEAE			
Casearia emarginata C.Wright ex Griseb.	Tree	0.289	LC
SANTALACEAE			
Phoradendron sp.	Herb (parasite)	-	
SAPINDACEAE			
Cardiospermum corindum L.	Vine	-	
SAPOTACEAE			
Sideroxylon americanum (Mill.) T.D.Penn.	Tree	0.299	LC
Sideroxylon celastrinum (Kunth) T.D.Penn.	Tree	1.049	LC
SCROPHULARIACEAE			
Capraria biflora L.	Herb	0.564	
SOLANACEAE			
Solanum houstonii Martyn	Subshrub	1.602	
VERBENACEAE			
Lantana camara L.	Shrub	1.021	
Phyla nodiflora (L.) Greene	Herb	5.956	LC
Stachytarpheta angustifolia (Mill.) Vahl	Herb	8.373	
Stachytarpheta jamaicensis (L.) Vahl	Subshrub	0.726	LC
Tamonea curassavica (L.) Pers.	Herb	3.303	
VITACEAE			
Cissus biformifolia Standl.	Vine	-	
Cissus microcarpa Vahl	Vine	-	

Results

Floristic characterization and species dominance. Our results recorded a total of 214 species (206 identified to species) belonging to 58 families and 164 genera of vascular plants (Table 1). *Marsilea vestita* Hook. & Grev. var. *vestita* was the only fern recorded. Herbs were the group with the highest number of species (46 %), followed by trees (22 %) and shrubs (14 %), while epiphytes and parasites were the least represented group, with 3 %. Vines and cacti are important and distinctive groups, with 11 and 4 %, respectively. Like most vegetation communities within the Yucatan peninsula, Fabaceae was the most representative plant family, with a higher number of species for trees (21) and shrubs (four), followed by Euphorbiaceae with nine species (three trees and six shrubs). Poaceae (13 species), Cyperaceae, and Malvaceae (seven species each) were the most representative families of herbs (Table 2). *Euphorbia* L. and *Ipomoea* L. were the most representative genera, with five species each, followed by *Portulaca* L. *and Eragrostis* Wolf with four species each (Table 2).

Five species showed the highest IVI (> 7), with *Sida ciliaris* L. as the species with the highest IVI value (IVI = 55.58), followed by *Haematoxylum campechianum* L. (IVI = 16.04), *Stachytarpheta angustifolia* (Mill.) Vahl (IVI = 8.37), *Agave angustifolia* var. *angustifolia* (7.42), and *Cienfuegosia yucatanensis* Millsp. (IVI = 7.36) (Table 1). Seventy-eight species had an IVI value greater than one, while 107 species recorded an IVI smaller than one (Table 1).

Table 2. Families and genera of plants most representative of the seasonally flooded Coquinal.

Family	Number of species	Genus	Number of species
Fabaceae	38	*Euphorbia*	6
Euphorbiaceae	16	*Ipomoea*	5
Malvaceae	13	*Portulaca*	4
Poaceae	13	*Eragrostis*	4
Convolvulaceae	9	*Croton*	3
Asteraceae	9	*Rhynchospora*	3
Cactaceae	7	*Tillandsia*	3
Cyperaceae	7	*Vachellia*	3
Acanthaceae	7	*Stachytarpheta*	2
Apocynaceae	5	*Bursera*	2
Verbenaceae	5	*Dictyanthus*	2

Vegetation classification. We propose the use of the term Seasonally Flooded Coquinal (SFC), to refer to this distinctive plant association. We classified the SFC as a subassociation of the tropical dry forest and particularly of the TDFCC based in the substratum, in which the predominance of the "coquina" stands out, preventing the filtration of water to the subsoil and remaining flooded during the rainy season. The SFC is a mosaic-like assemblage of continuous open, seasonally flooded areas, dominated mainly by herbs, with patches of woody vegetation of small trees and shrubs, including succulent plants (Figures 2A-C, 3A, B, G). Although its plant diversity is very similar to that of other regional dry forests as the tropical dry forest and the TDFCC, at least two species, *Zephyranthes orellanae* Carnevali, Duno & J.L. Tapia and *Ipomoea sororia* D.F. Austin & J.L. Tapia are endemic to this plant association. In addition, there are diagnostic plant species that give identity to the SFC such as *Cienfuegosia yucatanensis*, *Portulaca halimoides* L., *Stachytarpheta angustifolia*, *Justicia* sp. nov. (publication in process), and *Angelonia parviflora* Barringer. Except for the last two species, which are endemic to the Yucatan Peninsula Biotic Province (YPBP), they are not exclusive to this region. However, in the north of Yucatan the presence of them is commonly associated with the SFC. Furthermore, the SFC is the only type of vegetation where all these taxa occur together, which renders their co-occurrence diagnostic for the vegetation type.

Conservation status. Of the 206 species recorded and identified in this study, 111 have not yet been evaluated by the IUCN, while 84 are listed in the Least Concern (LC) category. Ten species are listed in a risk category: Three (*Zephyranthes orellanae*, *Lobelia yucatana* E. Wimm, and *Senna pallida* (Vahl) H.S. Irwin & Barneby var. *gaumeri* (Britton & Rose) H.S.Irwin & Barneby are considered Endangered (EN), six have been assigned the Near Threatened (NT) category, and *Ipomoea sororia* and *Gossypium hirsutum* Cav. have been classified as Vulnerable (VU). We recorded two endemic species to the SFC (*Zephyranthes orellanae* and *Ipomoea sororia*), whereas we also recorded twenty-eight species endemics to the YPBP. *Diphysa yucatanensis* A.M. Hanan & M. Sousa is quasi-endemic (with a few populations beyond yet near the border of the province (Table 1).

Heteranthera yucatana Carnevali, J.L.Tapia & J.R.Grande was not included as an endemic species of the SFC because it was not collected either in the transects or in surrounding areas. It is rare and seasonal species associated with muddy soils in peripheral areas of the SFC.

Discussion

Seasonally flooded Coquinal. Although this plant association is widely recognized by local botanists (Duno 2017, Pérez-Sarabia *et al*. 2017, Carnevali & Tapia-Muñoz 2017, Ramírez-Morillo 2019, Aguilar-Canché *et al*. 2022), very little has been done to document and thus protect it.

Figure 2. General view of the Seasonally flooded Coquinal (SFC) and some representative species. A. Panoramic view of the SFC in the dry season (Telchac Puerto). B. Panoramic view of the SFC in the wet season with *Cienfuegosia yucatanensis* Millsp. (Malvaceae), and *Stachytarpheta angustifolia* (Mill.) Vahl. (Verbenaceae) (El Corchito). C. Panoramic view of the SFC in the wet season with *Sesbania herbacea* (Mill.) McVaugh (Fabaceae) (El Corchito). D. *Justicia* sp. nov. (Acanthaceae; in process of publication) E. *Angelonia parviflora* Barringer (Plantaginaceae). F. *Zephyranthes orellanae* Carnevali, Duno & J. L. Tapia (Amaryllidaceae). Photos. A; Gustavo A. Romero González. B-E: Claudia J. Ramírez, F: Mayte del R. Aguilar Canche.

The results in our study clearly suggest that SFC represent an important area of plant biodiversity with local and peninsular endemism, which deserves to be preserved. Based on Velázquez *et al*. (2016) we recognize the SFC as a tropical dry deciduous shrubland; sub-spineless, microphyllous, non-succulent, with a series of Fabaceae associations dominating the landscape. *Sida ciliaris* and *Haematoxylum campechianum* as dominant floristic subassociation, and *Zephyranthes orellanae* and *Ipomoea sororia* as unique and characteristic species, while exposed coquina-type rock outcrops conform substratum subassociation.

Soil Features.- Several classifications of vegetation types have been proposed in Mexico (Miranda & Hernández-X 1963, Gómez-Pompa 1965, Rzedowski 1978, González-Medrano 2003). More recently, efforts have been made to establish criteria that allow better organization and standardization of the types of vegetation proposed over time (*e.g*., Faber-Langendoen *et al.* 2014, Velázquez *et al*. 2016).

Miranda (1958) classified some characteristic plant associations of the Yucatan peninsula as non-optimal primary associations ("edaphic associations" of Holdridge 1967), referring to plant associations that grow on soils or localities with less than favorable conditions. The SFC is undoubtedly a non-optimal ecosystem *sensu* Miranda (1958), and a tropical dry deciduous shrubland according to Velázquez *et al*. (2016) determined by the edaphic conditions and local climate (*i.e*., rock outcrops or rock outcrops + floods). Other non-optimal ecosystems *sensu* Miranda (1958) or subassociations sensu Velázquez *et al*. (2016) are also associated with the coast (*e.g*., tintal, associated mainly with the presence of *Haematoxylum campechianum*; carrizal, associated mainly to *Phragmites australis* (Cav.) Trin. ex Steud., saibal, associated mainly with *Cladium mariscus* subsp. *jamaicense* (Crantz) Kiik., and tular, associated mainly with *Typha domingensis*). However, no previously described vegetation association in Mexico matches the characteristics and conditions of the SFC. Beard (1944, 1955) proposed a classification system for tropical vegetation in America, which describes a plant association in the Guianas called "Rock Pavement Vegetation", growing on hard sandstone rock plates and granite outcrops (the Roraima formation) with scattered herbaceous and woody plants of less than two meters of height. In contrast, the SFC has shallow soils with outcrops of a highly permeable carbonated rock shell associated with the Carrillo Puerto geological formations, including bound stones or wackestones containing embedded fossils of mollusks, mainly bivalves and gastropods (Miranda-Huerta 2005, Shen *et al*. 2013). Rocks show surface cracks and cavities of different sizes, along with slight depressions and elevations that possibly determine the vegetation dynamics in the area.

Environmental conditions and plant associations.- The seasonality that characterizes the Yucatan peninsula with a dry season, a summer rainy season, and a winter rainy season influenced the dynamics of its plant populations (Flores & Espejel 1994, Islebe *et al.* 2018, SMN-CONAGUA 2022). This seasonality has a greater impact on the SFC, where the rainy season starts slightly later and, therefore, receives lower rainfall averages compared to the surrounding communities (Flores & Espejel 1994).

Two main structural elements can be recognized within the SFC. First, an open area with rock outcrops; during the rainy season, this area is flooded by a water layer of approximately 10-50 cm depth in which Cyperaceae and Poaceae thrive, along with other herbs and suffrutices up to one-meter high. In these flood-prone areas, hydrophilic or flood-resistant species grow seasonally, giving a distinctive profile to the area (see Figure 2B, C). Species adapted to anaerobic or hydric stress conditions, such as *Zephyranthes orellanae*, *Cienfuegosia yucatanensis*, *Ipomoea sororia*, and *Stachytarpheta angustifolia*, are abundant in flooded soils during the rainy season, but are difficult to observe during the dry season since they have either an annual life cycle (*e.g*., *S. angustifolia*) or persist through underground storage structures such as bulbs (*e.g*., *Z. orellanae*) and specialized roots (*e.g*., *C. yucatanensis*). *Sesbania herbacea* (Mill.) McVaugh is infrequent within the SFC, but can be highly abundant in flood-prone areas where it is usually found. The second structural element comprises patches of different sizes (commonly from 1 to 5 m in diameter, occasionally larger) on "islands" of imperceptibly higher microrelief that do not flood, with shrubs and trees such as *Bursera simaruba* Sarg., *Ipomoea carnea* Jacq. subsp. *carnea*, *Jatropha gaumeri* Greenm., *Neltuma juliflora* (Sw.) Raf. var. *juliflora*, and *Pithecellobium unguis-cati*. These species frequently serve as nurse plants for cacti, includ-

Figure 3. Some species of the Seasonally flooded Coquinal (SFC). A. *Acanthocereus tetragonus* (L.) Hummelinck (Cactaceae). B. Landscape within the SFC with *Agave angustifolia* Haw. var. *angustifolia* (Agavaceae) (Telchac Puerto). C. *Cyrtopodium macrobulbon* (La Llave & Lex.) G. A. Romero & Carnevali (Orchidaceae) growing under *Jatropha gaumeri* Greenm. D. *Ipomoea sororia* D.F. Austin & J.L. Tapia (Convolvulaceae). E. *Cuphea gaumeri* Koehne (Lythraceae). F. *Portulaca rubricaulis* Kunth (Portulacaceae). G. *Mammillaria gaumeri* (Britton & Rose) Orcutt (Cactaceae). H. *Jatropha gaumeri* Greenm. (Euphorbiaceae). Photos. A, D, E, H. Claudia J. Ramírez. B. Diego F. Angulo. C. Rodrigo Duno de Stefano. F-G. Mayte del R. Aguilar Canche.

ing species such as *Acanthocereus tetragonus*, *Opuntia inaperta* (A. Schott ex Griffiths) D.R. Hunt, and *Opuntia stricta* (Haw.) Haw., and the orchids *Cyrtopodium macrobulbon* (La Llave & Lex.) G.A. Romero & Carnevali and *Myrmecophila christinae* Carnevali & M. Gómez, all of which frequently grow on the periphery of these vegetation patches where light irradiance is higher. *Agave angustifolia* var. *angustifolia* is an abundant and distinctive species, particularly when in its reproductive phase, due to its long, conspicuous inflorescences and flowers, which can be found in both environments just described (Figure 3B).

Species dominance.- The Importance Value Index (IVI) has been used in different research areas such as pharmacology and ethnobiology (*e.g*., Dhar *et al*. 2000, Guèze *et al*. 2014), but is most widely used for assessing the ecological importance of plant species (*e.g*., Tadele *et al*. 2014). In the present study, the species featuring high IVI values cover a large proportion of the area in the plant community (Table 1). For example, *Sida ciliaris*, which yielded the highest IVI value, is a small herb that is common and widespread in open areas, while the logwood tree ("*palo de tinte"*; *Haematoxylum campechianum*), the species with the second highest IVI value, is a medium height erect to prostrate shrub or tree with a wide crown that is common in the seasonally flooded patches of the SFC. Other species with high IVI values were *Ipomoea carnea* subsp. *carnea*, a shrubby vine that can cover extensive areas, growing from suberect to prostrate on the ground or on bushes, and *Cienfuegosia yucatanensis*, that remains leafless for most of the year but that is conspicuous in flooded sites, within the SFC, during the rainy season. Species endemic to the YPBP and listed as Threatened, such as *Mammillaria gaumeri*, *Ipomoea sororia*, and *Zephyranthes orellanae*, had a relatively high IVI values, so they are species ecologically important within the YC. However, more than 70 % of the endemic species to YPBP had an IVI less than one, which indicates that they are ecologically scarce or rare (Rabinowitz 1981, Ahmed *et al.* 2020). Likewise, endemic species to YPBP included in the Least Concern category, such as *Jatropha gaumeri*, *Opuntia inaperta*, *Havardia albicans*, and *Cuphea gaumeri* Koehne, also obtained high IVI values (Table 1). These endemic species occur in the north of the Yucatan peninsula, not only in the SFC, but also in surrounding vegetation, mainly the TDFCC and the coastal dune shrubland.

Conservation status and threats to the SFC. The Yucatan peninsula contains a remarkable concentration of tropical dry forest (Miles *et al*. 2006, Carnevali *et al*. 2021), which has been referred to as probably the most threatened forest type, with projected low climatic stability (unstable climatic conditions) in the next 20 years (Janzen 1988, Miles *et al*. 2006, Pennington *et al.* 2018, Mesa-Sierra *et al*. 2022). Moreover, tropical dry forest is one of the least protected biomes in Mexico (Koleff *et al*. 2009, Mesa-Sierra *et al*. 2022), so actions to increase our knowledge and improve its conservation are necessary to warrant its short, medium, and long-term survival. In addition, the SFC is among the most highly threatened natural plant communities within the YPBP for several reasons. It is located between Merida -one of the main cities- and Progreso -one of the most important harbors- in the southeast of Mexico. In recent decades, both the city and the port have been growing vigorously, exerting increasing pressure on the TDFCC and, particularly, the SFC. The advancing coastal urbanization and, therefore, the growing population living in coastal cities is a global trend that has advanced exponentially in recent decades (Barragán & de Andrés 2015). On the other hand, the increasing socioeconomic importance of coastal areas, mainly associated with the recent expansion of tourism (Elliott *et al*. 2020), has also had adverse consequences on natural ecosystems. The Yucatan coasts are no exception to this issue, particularly in the geographically restricted SFC, currently being a major tourist attraction for locals and foreigners that has promoted urban growth, causing adverse environmental impacts on the plant and animal communities of the coast and adjacent areas (unpublished data). Finally, small-scale cattle-ranching and "traditional agriculture systems" = (*Cucurbita* spp.) and, along with natural events such as storms and hurricanes and the high incidence of natural and arson fires, cause adverse impacts on the natural communities of the SFC.

Despite its small geographic area (900 km^2 approximately), the SFC hosts a high diversity of plant species, two of which are endemic to the SFC and some 25 endemics to the YPBP, some of which are featured in the IUCN red list. However, the lack of its acknowledgement as a highly threatened plant associations, coupled with the fact that has it has mistakenly been thought of as a highly degraded successional stage of the tropical dry forest and of the TDFCC,

has made it difficult to establish mechanisms and policies for its protection and conservation. Although there are some sites featuring coquina outcrop in the northwestern edge of the SFC that are located within the "Ciénegas y Manglares de la Costa Norte de Yucatán" state reserve, to date, the TDFCC and the most of the SFC areas are not included in any Mexican conservation initiatives, and their ecological fragility merits high priority for conservation to prevent the loss and extinction of its unique assemblage of species.

Acknowledgements

We thank the three anonymous reviewers and Associate Editor, Guillermo Ibarra Manríquez, for comments on previous versions of the manuscript. Thanks also to Lilia Lorena Can for the review of the tables and figures. Authors are grateful to Silvia Hernández, Lilia Lorena Can, and Nestor Raigoza for help in the management of herbarium material. Finally, we thank our photographic collaborators: Gustavo A Romero and Claudia J. Ramírez.

Literature cited

Aguilar-Canché M, Duno R, Angulo DF. 2022. La diversidad funcional en el calichal yucateco: una estrategia que permite entender su riqueza desde una perspectiva ecológica. *Desde el Herbario CICY* **14**: 234-240.

Ahmed MJ, Murtaza G, Shaheen H, Habib T. 2020. Distribution pattern and associated flora of Jurinea dolomiaea in the western Himalayan highlands of Kashmir: an indicator endemic plant of alpine phytodiversity. *Ecological Indicator* **116**: 106461. DOI: https://doi.org/10.1016/j.ecolind.2020.106461

Angulo DF, Tun-Garrido J, Arceo-Gómez G, Munguía-Rosas MA, Parra-Tabla V. 2018. Patterns of phylogenetic community structure of sand dune plant communities in the Yucatan peninsula: the role of deterministic and stochastic processes in community assembly. *Plant Ecology and Diversity* **11**: 515-526. DOI: http://doi.org/10.1080/17550874.2018.1534289

APG IV [Angiosperm Phylogeny Group], Chase MW, Christenhusz MJM, Fay MF, Byng JW, Judd WS, Soltis DE, Mabberley DJ, Sennikov AN, Soltis PS, Stevens PF. 2016. An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* **181**: 1-20. DOI: https://doi.org/10.1111/boj.12385

Balke T, Herman PMJ, Bouma TJ. 2014. Critical transitions in disturbance-driven ecosystems: identifying Windows of Opportunity for recovery. *Journal of Ecology* **102**: 700-708. DOI: https://doi.org/10.1111/1365-2745.12241

Barragán JM, de Andrés M. 2015. Analysis and trends of the world's coastal cities and agglomerations. *Ocean and Coastal Management* **114**: 11-20. DOI: https://doi.org/10.1016/j.ocecoaman.2015.06.004

Bautista-Zúñiga F. 2010. El Suelo. *In*: Durán R, Méndez M, eds. *Biodiversidad y Desarrollo Humano en Yucatán*. México: Centro de Investigación Científica de Yucatán A.C., Programa pequeñas donaciones-Fondo Mundial para el Medio Ambiente, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Secretaría de Desarrollo Urbano y Medio Ambiente, pp. 14-16. ISBN: 978-607-7823-08-7

Beard JS. 1944. Climax vegetation in tropical America. *Ecology* **25**: 127-158. DOI: https://doi.org/10.2307/1930688

Beard JS. 1955. The classification of tropical American vegetation-types. *Ecology* **36**: 89-100. DOI: https://doi.org/10.2307/1931434

Becerra JX. 2005. Timing the origin and expansion of the Mexican tropical dry forest. *Proceedings of the National Academy of Sciences USA* **102**: 10919-10923. DOI: https://doi.org/10.1073/pnas.0409127102

Boose ER, Foster DR, Plotkin AB, Hall B. 2003. Geographical and historical variation in hurricanes across the Yucatan Peninsula. *In*: Gómez-Pompa A, Allen MF, Fedick S, Jiménez-Osornio JJ, eds. *Lowland Maya Area: Three Millennia at the Human-Wild- Land Interface*. New York USA: Haworth Press, pp. 495-516. ISBN: 1-56022-971-3

Carnevali G, Tapia-Muñoz JL. 2017. El redescubrimiento de *Mammillaria columbiana* ssp. *yucatanensis* en Yucatán, II: no estaba extinta, estaba escondida. *Desde el Herbario CICY* **9**: 23-27.

Carnevali G, Tapia-Muñoz JL, Duno R, Ramírez-Morillo IM. 2010. *Flora Ilustrada de la Península de Yucatán*:

Listado Florístico. Mérida, México: Centro de Investigación Científica de Yucatán, AC. ISBN: 978-607-7823-07-0

Carnevali G, Ramírez-Morillo I, Pérez-Sarabia JE, Tapia-Muñoz JL, Estrada H, Cetzal-Ix W, Hernández-Aguilar S, Can LL, Raigoza NE, Duno R, Romero-González GA. 2021. Assessing the risk of extinction of vascular plants endemic to the Yucatan peninsula biotic province by means of distributional data. *Annals of the Missouri Botanical Garden* **106**: 424-457. DOI: https://doi.org/10.3417/2021661

Challenger A, Soberón J. 2008. Los ecosistemas terrestres. *In*: Soberón J, Halfter G, Llorente-Bousquets J, eds. *Capital natural de México*: *Conocimiento Actual de la Biodiversidad*. Volumen I. México: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, pp. 87-108. ISBN: 978-607-7607-03-8

Corenblit D, Baas A, Balke T, Bouma TJ, Fromard F, Garófano-Gómez V, González E, Gurnell AM, Hortobágyi B, Julien F, Kim D, Lambs L, Stallins JA, Steiger J, Tabacchi E, Walcker R. 2015. Engineer pioneer plants respond to and affect geomorphic constraints similarly along water-terrestrial interfaces world-wide. *Global Ecology and Biogeography* **24**: 1363-1376. DOI: https://doi.org/10.1111/geb.12373

Curtis JT, McIntosh RP. 1950. The interrelations of certain analytic and synthetic phytosociological characters. *Ecology* **31**: 434-455. DOI: https://doi.org/10.2307/1931497

Curtis JT, McIntosh RP. 1951. An upland forest continuum in the pariré-forest border region of Wisconsin. *Ecology* **32**: 476-496. DOI: https://doi.org/10.2307/1931725

Dhar U, Rawat RS, Uprety J. 2000. Setting Priorities for Conservation of Medicinal Plants- A Case Study in the Indian Himalaya. *Biological Conservation* **95**: 57-65. DOI: https://doi.org/10.1016/S0006-3207(00)00010-0

Do TV, Sato T, Saito S, Kozana O, Yamagawa H, Nagamatsu D, Nishimura N, Manabe T. 2015. Effects of microtopographies on stand structure and tree species diversity in an old-growth evergreen broad-leaved forest, southwestern Japan. *Global Ecology and Conservation* **4**: 185-196. DOI: https://doi.org/10.1016/j.gecco.2015.06.010

Duch-Gary J. 1991. *Fisiografía del Estado de Yucatán*: *su relación con la agricultura*. México: Universidad Autónoma Chapingo, pp. 33-45. ISBN: 968-884-134-X

Duno R. 2017. El caliche yucateco, una vegetación compleja que falta por estudiar y definir. *Desde el Herbario CICY* **9**: 231-235.

Duno R, Ramírez-Morillo IM, Tapia-Muñoz JL, Hernández-Aguilar S, Can LL, Cetzal-Ix W, Méndez-Jiménez N, Zamora-Crescencio P, Gutiérrez-Báez C, Carnevali G. 2018. Aspectos generales de la flora vascular de la Península de Yucatán Mexicana. *Botanical Sciences* **96**: 515-532. DOI: https://doi.org/10.17129/botsci.1868

Elliott LR, White MP, Grellier J, Garrett JK, Cirach M, Wheeler BW, Bratman GN, van den Bosch MA, Ojala A, Roiko A, Lima ML, O`Connor A, Gascon M, Nieuwenhuijsen M, Fleming LE. 2020. Research Note: Residential distance and recreational visits to coastal and inland blue spaces in eighteen countries. *Landscape and Urban Planning* **198**: 103800. DOI: https://doi.org/10.1016/j.landurbplan.2020.103800

Espejel I. 1984. La vegetación de las dunas costeras de la Península de Yucatán. I. Análisis florístico del estado de Yucatán. *Biótica* **9**: 183-210.

Faber-Langendoen D, Keeler-Wolf T, Meidinger D, Tart D, Hoagland B, Josse C, Navarro G, Ponomarenko S, Saucier J, Weakley A, Comer P. 2014. EcoVeg: a new approach to vegetation description and classification. *Ecological Monographs* **84**: 533-561. DOI: https://doi.org/10.1890/13-2334.1

Flores JS, Espejel I. 1994. *Tipos de vegetación de la Península de Yucatán*. Etnoflora Yucatanense 3. México: Universidad Autónoma de Yucatán, pp. 135. ISBN: 968-6843-44-2

Gagnon E, Bruneau A, Hughes CE, De Queiroz LP, Lewis GP. 2016. A new generic system for the pantropical Caesalpinia group (Leguminosae). *PhytoKeys* **71**: 1-160. DOI: https://doi.org/10.3897/phytokeys.71.9203

García E. 1998. *Climas de la República Mexicana (clasificación de Köppen, modificado por García)*. *Escala 1: 000 000*. México: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. http://www.conabio.gob.mx/informacion/gis/ (Accessed July 10, 2023).

Gómez-Pompa A. 1965. La vegetación de México. *Botanical Sciences* **29**: 76-120. DOI: https://doi.org/10.17129/botsci.1090

González-Medrano F. 2003. *Las comunidades vegetales de México*: *propuesta para la unificación de la clasificación y nomenclatura de la vegetación de México*. DF, México: Instituto Nacional de Ecología-Secretaría de Medio Ambiente y Recursos Naturales. ISBN: 968-817-611-7

Guèze M, Luz AC, Paneque-Gálvez J, Macía MJ, Orta-Martínez M, Pino J, Reyes-García V. 2014. Are ecologically important tree species the most useful? a case study from indigenous people in the Bolivian Amazon. *Economic Botany* **68**: 1-15. DOI: https://doi.org/10.1007/s12231-014-9257-8

Holdridge LR. 1967. *Life Zone Ecology*. San José, Costa Rica: Tropical Science Center.

Hughes CE, Ringelberg JJ, Lewis GP, Catalano SA. 2022. Disintegration of the genus Prosopis L. (Leguminosae, Caesalpinioideae, mimosoid clade. *PhytoKeys* **205**: 147-189. DOI: https://doi.org/10.3897/phytokeys.205.75379

Ibarra-Manríquez G, Martínez-Ramos M. 2002. Landscape variation of liana communities in a Neotropical rain forest. *Plant Ecology* **160**: 91-112. DOI: https://doi.org/10.1023/A:1015839400578

Ibarra-Manríquez G, González-Espinosa M, Martínez-Ramos M, Meave J. 2022. From vegetation ecology to vegetation science: current trends and perspectives. *Botanical Sciences* **100**: S137-S174. DOI: https://doi.org/10.17129/botsci.3171

Islebe GA, Calmé S, León Cortés J, Schmook B. 2015. *Biodiversity and conservation of the Yucatan Peninsula*. Springer International Publishing AG Switzerland. ISBN: 978-3-319-06528-1

Islebe GA, Torrescano-Valle N, Aragón-Moreno AA, Vela-Peláez AA, Valdez-Hernández M. 2018. The Paleoanthropocene of the Yucatán Peninsula: palynological evidence of environmental change. *Boletín de la Sociedad Geológica Mexicana* **70**: 49-60. DOI: https://doi.org/10.18268/bsgm2018v70n1a3

IUCN [International Union for Conservation of Nature] 2021. *The IUCN Red List of Threatened Species*. Version 2020-2. https://www.iucnredlist.org (accessed July 28, 2023).

Janzen DH. 1988. Tropical dry forests, the most endangered major tropical ecosystem. *In*: Wilson EO, Peter FM, eds. *Biodiversity*. Washington, EUA, National Academic Press. pp. 130-137. ISBN: 0-309-03783-2

Koleff P, Tambutti M, March I, Esquivel R, Cantú C, Lira-Noriega A. 2009. Identificación de prioridades y análisis de vacíos y omisiones en la conservación de la biodiversidad de México. *In*: Sarukhán J. ed. *Capital natural de México*, *vol. II*: *Estado de conservación y tendencias de cambio*. DF, México: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, pp. 651-718. ISBN: 978-607-7607-08-3

Lundell CL. 1938. *The 1938 botanical expedition to Yucatan and Quintana Roo, Mexico*. Carnegie Institution of Washington Year Book.

Méndez-Toribio M, Meave JA, Zermeño-Hernández I, Ibarra-Manríquez G. 2016. Effects of slope aspect and topographic position on environmental variables, disturbance regime and tree community attributes in a seasonal tropical dry forest. *Journal of Vegetation Science* **27**: 1094-1103. DOI: https://doi.org/10.1111/jvs.12455

Mesa-Sierra N, de la Peña-Domene M, Campo J, Giardina CP. 2022. Restoring Mexican Tropical Dry Forests: A National Review. *Sustainability* **14**: 3937. DOI: https://doi.org/10.3390/su14073937

Miles L, Newton A, Defries R, Ravilious C, May I, Blyth S, Kapos V, Gordon J. 2006. A global overview of the conservation status of tropical dry forests. *Journal of Biogeography* **33**: 491-505. DOI: https://doi.org/10.1111/j.1365-2699.2005.01424.x

Miranda F. 1958. Rasgos fisiográficos de interés para estudios botánicos. *In*: Beltrán E, ed. *Los Recursos Naturales del Sureste y su Aprovechamiento II*. DF, México: Instituto Mexicano Recursos Naturales Renovables, pp. 215-271.

Miranda F, Hernández-XE. 1963. Los tipos de vegetación de México y su clasificación. *Botanical Sciences* **28**: 29-179. DOI: https://doi.org/10.17129/botsci.1084

Miranda-Huerta A. 2005. *Carta geológico-minera Tizimín F16-7*, *escala 1:250000*: *Estado de Yucatán*. Yucatán, México: Servicio Geológico Mexicano. https://mapserver.sgm.gob.mx/InformesTecnicos/CartografiaWeb/T312005MIHA0001_01.PDF (accessed August 13, 2023).

Orellana R, Balam M, Bañuelos I. 1999. Evaluación climática. *In*: García FA, Córdoba OJ, Chico PLP, eds. *Atlas de Procesos Territoriales de Yucatán*. Facultad de Arquitectura, Universidad Autónoma de Yucatán, México, pp: 163-182. ISBN: 9687-5569-27

Pennington RT, Lehmann CER, Rowland LM. 2018. Tropical savannas and dry forests. *Current Biology* **28**: R541-R545. DOI: https://doi.org/10.1016/j.cub.2018.03.014

Pérez-García EA, Meave JA. 2005. Heterogeneity of xerophytic vegetation of limestone outcrops in a tropical deciduous forest region in southern México. *Plant Ecology* **175**: 147-163. DOI: https://doi.org/10.1007/s11258-005-4841-8

Pérez-García EA, Sevilha AC, Meave JA, Scariot A. 2009. Floristic differentiation in limestone outcrops of southern Mexico and central Brazil: a beta diversity approach. *Botanical Sciences* **84**: 45-58. DOI: https://doi.org/10.17129/botsci.2294

Pérez-Sarabia JE, Duno R, Carnevali G, Ramírez-Morillo I, Méndez-Jiménez N, Zamora-Crescencio P, Gutiérrez-Báez C, Cetzal-Ix W. 2017. El conocimiento florístico de la península de Yucatán, México. *Polibotánica* **44**: 39-49. DOI: https://doi.org/10.18387/polibotanica.44.3

Rabinowitz D. 1981. Seven forms of rarity. *In*: Synge H, ed. *The biological aspects of rare plant conservation*. England: John Wiley & Sons, Chichester, pp 205-217. ISBN: 0471-2800-46

Ramírez-Morillo IM. 2019. La flora de la Península de Yucatán: ¿diversa? ¿bien conocida? ¿protegida? No, no y ¿no? *Desde el Herbario CICY* **11**: 130-137.

Reyes-Palomeque G, Dupuy JM, Portillo-Quintero CA, Andrade JL, Tun-Dzul FJ, Hernández-Stefanoni JL. 2021. Mapping forest age and characterizing vegetation structure and species composition in tropical dry forests. *Ecological Indicators* **120**: 106955. DOI: https://doi.org/10.1016/j.ecolind.2020.106955

Rzedowski J. 1978. *Vegetación de México*. DF, México: Editorial Limusa. ISBN: 9681-8000-28

Sánchez-Reyes UJ, Niño-Maldonado S, Barrientos-Lozano L. Treviño-Carreón J, Meléndez-Jaramillo E, Sandoval-Becerra FM, Jones RW. 2021. Structural changes of vegetation and its association with microclimate in a successional gradient of low thorn forest in northeastern Mexico. *Plant Ecology* **222**: 65-80. DOI: https://doi.org/10.1007/s11258-020-01088-z

Shen JW, Long JP, Pedoja K, Yang HQ, Xu HL, Sun JL. 2013. Holocene coquina beachrock from Haishan Island, east coast of Guangdong Province, China. *Quaternary International* **310**: 199-212. DOI: https://doi.org/10.1016/j.quaint.2013.05.011

Simpson MG. 2006. *Plant Systematics*. Burlington, San Diego & London. Elsevier Academic Press. ISBN: 0-12-644460-9

SMN-CONAGUA [Servicio Meteorológico Nacional-Comisión Nacional del Agua] . 2022. *Precipitación y temperatura de Yucatán*. México. www.smn.conagua.gob.mx (accessed July 19, 2023).

Tadele D, Lulekal E, Damtie D, Assefa A. 2014. Floristic diversity and regeneration status of woody plants in Zengena Forest, a remnant montane forest patch in northwestern Ethiopia. *Journal of Forestry Research* **25**: 329-336. DOI: https://doi.org/10.1007/s11676-013-0420-3

Thiers B. 2023. *Index Herbariorum. Part I: The herbaria of the world.* New York Botanical Garden. https://www.sweetgum.nybg.org/ih (accessed September 25, 2023).

Torres W, Méndez M, Dorantes A, Durán R. 2010. Estructura, composición y diversidad del matorral de duna costera en el litoral yucateco. *Botanical Sciences* **86**: 37-51. DOI: https://doi.org/10.17129/botsci.2319

Velázquez A, Medina C, Durán E, Amador A, Gopar LF. 2016. Standardized Hierarchical Vegetation Classification - Mexican and Global Patterns. Berlin: Springer Verlag. ISBN: 3030317196

Viles HA, Coombes MA. 2022. Biogeomorphology in the Anthropocene: A hierarchical, traits-based approach. *Geomorphology* **417**: 108446. DOI: https://doi.org/10.1016/j.geomorph.2022.108446

Associate editor: Guillermo Ibarra Manríquez

Author contributions: RDS and DFA conceived the ideas and designed the research. RDS secured funding. RDS, GC, MAC, JLT and DFA conducted fieldwork, collected data and analyzed the results. GRP elaborated the map and RDS the plates. DFA wrote the initial draft of the manuscript and led the writing of the paper. All authors discussed results, and reviewed drafts of the paper. GC and IR greatly contributed to improving the way questions and hypotheses were framed/discussed and provided extensive early revisions to the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Supporting Agencies (alphabetical order): This research has been funded by competitive grants (2020/44938) from the Botanic Gardens Conservation International awarded to Rodrigo Duno de Stefano. Diego F. Angulo thanks CONAHCyT-Mexico for the postdoctoral fellowship support (2022-2023).

Conflict of interests. The authors declare that there is no conflict of interests, financial or personal, in the information, presentation of data and results of this article.