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Vascular plants of the Médanos de Samalayuca natural protected area, Chihuahua, Mexico

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Abstract

Background: Inland sand dunes are expanding and increasing mobility. Knowledge on the plants growing on them is keystone for their management. One of the largest inland dune systems in Mexico is the Médanos de Samalayuca area.

Questions: How many and which species of vascular plants are in Samalayuca? Which is the distribution pattern of that flora? Are there endemisms? Are there species of conservation concern?

Studied species: Vascular plants.

Study site and dates: Médanos de Samalayuca protected area, northern Chihuahua, Mexico; 2017-2022.

Methods: A database was generated based on literature, electronic sources, herbarium specimens, photographing, and collection and identification of materials. Distribution, endemism level and conservation status were recorded.

Results: The updated checklist of vascular plants for Samalayuca includes 400 species of 246 genera and 65 families. Most species grow in Mixed desert scrub and in Sand dune vegetation. Almost a half are restricted to the Megamexico 1 region, followed by the North American element. One species is Threatened according to the Mexican Official Norm NOM-059, while two are Vulnerable and one is Almost threatened according to the IUCN. *Ribes fontinale* appears to be extinct.

Conclusions: Considering the arid, extreme climate and the low stability of the psammophilous vegetation, the flora of Samalayuca is richer than expected. The area is home to regional and local endemics. The data and information generated here is baseline for further management programs and action planning to protect these fragile ecosystems and the adjacent communities.

Keywords: Chihuahuan Desert, dune, endemic, psammophile, sand.

Resumen

Antecedentes: Las dunas de arena de interior se están expandiendo e incrementando movilidad. El conocimiento sobre sus plantas es clave para su manejo. En México, uno de los mayores sistemas de dunas de interior es el área de los Médanos de Samalayuca.

Preguntas: ¿Cuántas y cuáles especies de plantas vasculares hay en Samalayuca? ¿Qué patrón de distribución presenta esa flora? ¿Hay endemismos? ¿Existen especies en estado de riesgo?

Especies de estudio: Plantas vasculares.

Sitio y años de estudio: Área de protección Médanos de Samalayuca, Chihuahua, México; 2017-2022.

Métodos: Se generó una base de datos con base en revisión de literatura, fuentes electrónicas, especímenes de herbario, fotografías y colección e identificación de material botánico. Se registró la distribución, grado de endemismo y estado de conservación de cada especie.

Resultados: La lista florística incluye 400 especies de 246 géneros y 65 familias. La mayoría crecen en Matorral desértico micrófilo y en Vegetación de dunas arenosas. Casi la mitad se restringen a la región conocida como Megamexico 1 y 32 % son Norteamericanas. Una está Amenazada de acuerdo a la Norma Oficial Mexicana NOM-059, mientras dos son Vulnerables y una Casi amenazada de acuerdo a la IUCN. *Ribes fontinale* parece estar extinta.

Conclusiones: Considerando el clima árido y extremo y la inestabilidad de la vegetación psamófila, la flora de Samalayuca es más rica de lo esperado. El área alberga endemismos regionales y locales. La información generada puede apoyar programas de manejo y acciones para proteger estos frágiles ecosistemas.

Palabras clave: Arena, Desierto Chihuahuense, duna, endemismo, psamófila.

Sand dune fields and the psammophile organisms adapted to their extreme conditions have a great environmental and scientific value, and their knowledge is baseline for the management of these systems. Psammophytes, the plants able to grow on sandy, often unstable soils, are of special interest (Liu *et al*. 2016, Azizi *et al*. 2021, El-Sheikh *et al*. 2021, Macheroum *et al*. 2021). The plants of inland sand dunes are adapted to harsh environments of unstable substrates and extreme climates and have a high value as soil stabilizers, water collectors, and habitat for many organisms. As Earth warms, dune fields in arid zones are expanding and moving faster, posing danger to adjacent ecosystems and infrastructure (Redsteer *et al*. 2011, Baas & Delobel 2022). In southwestern USA, higher temperatures and prolonged droughts have increased dune mobility (Thomas & Redsteer 2016). Inland sand dunes are wind driven, generated by airflow erosion and by fragmentation of the rock surfaces due to the extreme temperatures of the deserts. There are different types, depending on the wind patterns and of the presence or lack of vegetation.

One of the largest inland dune systems in Mexico is the Médanos de Samalayuca area, in northern Chihuahua. Others are the Gran Desierto de Altar in the Sonoran Desert, and the gypsum dunes of Cuatro Ciénegas in the Chihuahuan Desert in Coahuila. The Samalayuca dune fields, locally known as Médanos de Samalayuca or just "Los Médanos", possesses dramatic landscapes, archeological sites and an interesting biota that provide the area of excellent touristic and recreational potential. The development of tourism in the area may help to diversify the activities and improve the economy of the local population, but also requires parallel conservation actions.

The Médanos de Samalayuca hold one of the most fragile ecosystems of the Chihuahuan Desert because the extreme temperatures, low and erratic precipitation, evaporation about 10 times higher than precipitation, and unstable soils (CONANP 2013). The extreme ecological conditions of the site give it a high biological value due to the development and adaptation of extremophile organisms. It is included as one of the conservation priority regions in Mexico (RTP-48) (Arriaga 2000, CONABIO 2004) and in 2009 it was declared as a natural protected area: Flora and Fauna Protection Area Médanos de Samalayuca (Área de Protección de Flora y Fauna Médanos de Samalayuca) (SEMARNAT 2009). One of the objectives of its management program is to get systematized and updated information about its biodiversity and ecosystems (Gatica Colima 2019). The first botanist passing through Samalayuca was Friedrich A. Wislizenus, in 1846 (Wislizenus 1848). As for not vascular plants, 12 species of Bryopsida in the families Pottiaceae, Grimmiaceae, Bryaceae, and Fabrionaceae have been recorded for the area (Delgadillo Moya 2015, Gatica Colima 2019).

Data on the flora and vegetation of Samalayuca have been included in the Territorial Ecological Planning (Barraza-Pacheco *et al*. 1997) and in the Management Program (CONANP 2013), where 225 species of vascular plants were recorded; in a more recent inventory (Gatica Colima 2019), 50 more were added. Vegetation was described by Enríquez & Olivas (1999). Other studies of the flora have focused on Cactaceae (Enríquez Anchondo 2003, Esparza García 2017), Fabaceae (Rueda-Torres *et al*. 2022a), and the relation of plant communities and micorrhizae in the dry ecosystems (Quiñonez Martínez *et al*. 2018). The objective of this work is to present an updated checklist of the vascular flora of the Médanos de Samalayuca with data of their distribution and conservation status.

Materials and methods

Study area. The Médanos de Samalayuca protected area includes 63,182 ha. It is located at the northern part of the state of Chihuahua, Mexico, about 45 km south of the US-Mexico border where El Paso, Texas, and Ciudad Juárez, Chihuahua converge, in the municipalities of Juárez, Guadalupe, and a small portion of Ahumada (Gatica Colima 2019) (Figure 1). It lies among the extreme coordinates 31.10 °N to 31.38 °N, -106.19 °W to -106.64 °W, being part of the Chihuahuan Desert region and the North American Deserts ecoregion (Commission for Environmental Cooperation 1997), located on the belt of the greatest deserts north of the Tropic of Cancer.

It features dramatic landscapes that are visible from the Federal highway 45 south of Ciudad Juárez, with dune fields being continuously reshaped by the northwest prevailing winds. Dunes are *aklé* type (CONANP 2013, Gatica Colima 2019), like those found in western Sahara, forming a network of sinuous ridges at right angles to the wind and

crescent-shaped sections that alternately face it. The sand is whitish or tan, mostly siliceous, i.e., composed by quartz (SiO_2), 90-95 % silica and 5-10 % mixed rock particles of irregular, nodular and spheroid shapes (Cruz Sánchez *et al*. 2007). Located in an arreic basin, it includes the sand dune fields as well as other zones with stable soil, and valleys with alluvial and residual deposits. Soils are slightly saline to saline-sodic, alkaline (pH 7.8-8) (Quiñonez Martínez *et al*. 2018). There are two small sierras of sedimentary origin except for a narrow basaltic portion in the first: Sierra Samalayuca in the north and Sierra Presidio along the eastern limits. Because a legal modification of the delimitation of the protected area, the Sierra Samalayuca was recently excluded; but it was included in the management plan and sampled for this work. Elevations reach 1,450 m asl in the dune fields and up to 1,843 m asl in the Sierra Presidio. The high dunes originate because this sierra, which forms a 300 m high barrier perpendicular to the wind's predominant direction. The strong winds from the west collide on it and generate strong turbulence and intense revolving that drive the wind on the opposite direction near the ground, eroding the not consolidated sandstone and moving the dunes already formed (CONANP 2013). Loose substrate and strong winds cause dust storms (*tolvaneras*).

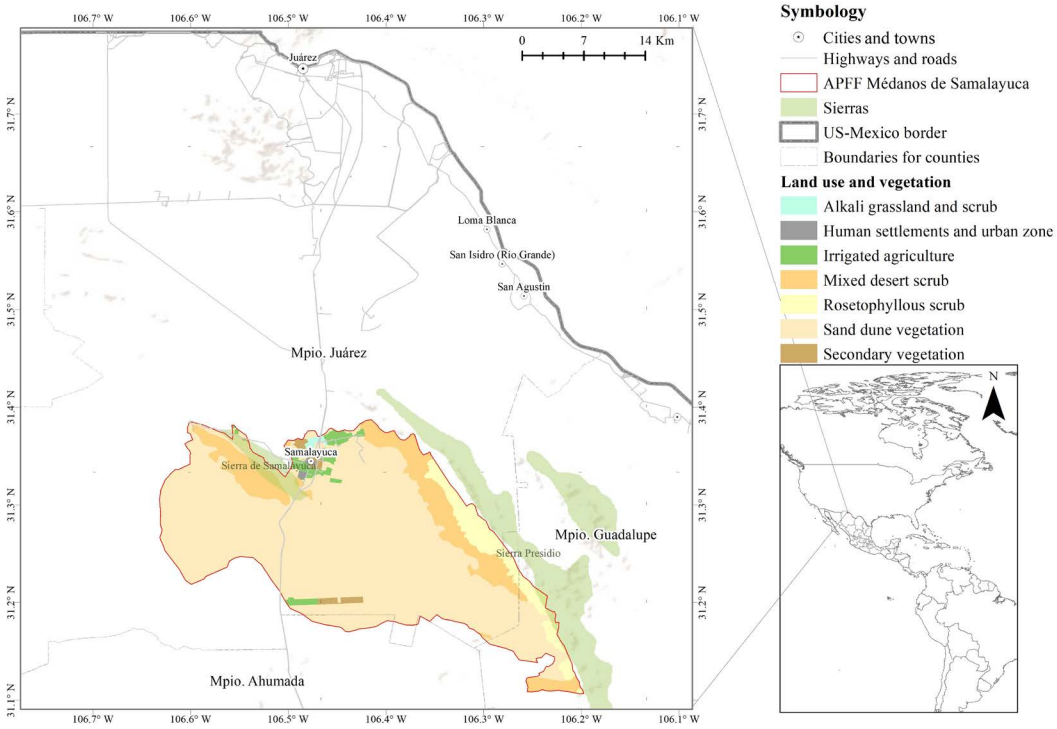

Figure 1. Localization, vegetation types and land use in the Médanos de Samalayuca natural protected area.

Climate.- It is continental, very dry, with a mean annual precipitation of 257 mm (almost 60 % of which are received in the summer), a mean evaporation of about 2,218 mm (8.6 times higher than the mean annual precipitation), mean annual temperature of 17 °C with warm summers, and very extreme (BWkw(x') according Köppen classification) (SEGOB 2015). Temperatures are warm in summer and cool in winter, with periods of freezing and occasional snow (Henrickson & Johnston 1986; Enríquez Anchondo 2003); the highest temperatures are above 46 °C and the lower of -16 °C. Differences among the medium temperature in the warmer and coldest months can be up to 23 °C and the daily oscilation of temperatures can reach 24 °C (adapted from different sources).

Vegetation.- The plant communities and land use categories were defined on the basis on the physognomic dominance of one or a few species (Figure 1), mainly following the classification of Henrickson & Johnston (1986) for the ChD, as follows: a) Mixed desert scrub (Chihuahuan Desert scrub), often dominated by *Larrea* -creosote bush,

or sometimes by *Fouquieria* or *Prosopis*; b) Sand dune vegetation; c) Rosetophyllous scrub dominated by *Agave lechuguilla*, *Yucca*, or *Dasylirion leiophyllum*; d) Alkali grassland and scrub; e) Woodland elements scattered on the higher parts of the sierras; f) Secondary vegetation in disturbed places, induced grassland on old agricultural fields, and in human settlements and urban zone in the village of Samalayuca; g) Irrigated agriculture. Additionally, a few aquatic, subaquatic and riparian plants are recorded from natural and artificial water bodies.

Data gathering and analysis. A database was generated based on field work, collection and identification of specimens, specialized literature, databases (CONABIO 2022, SEINet 2022, Red de Herbarios del Noroeste de México 2022), and digital images of herbarium materials from the following collections: ARIZ, ASU, BRYV, CCIB, CIIDIR, COLO, DES, HCIB, HNT, MEXU, MDE, MICH, MSC, NMC, NLU, NY, RSA, SBBG, TEX-LL, UACJ, UASLP, UCR, USF, UTEP, WIS and WLM. Acronyms according to Thiers (2022, continuously updated).

Field work for the project Inventario multitaxonómico del ANP Médanos de Samalayuca (CONABIO PJ018) allowed the collection of 713 plant specimens and additional georeferenced observations (collection permit SGPA/DGVS/04785/17). An additional source of information was the digital platform NaturaLista (www.naturalista.mx/projects) where the project "Inventario multitaxonómico del ANP "Médanos de Samalayuca" was created (https://www.naturalista.mx/projects/inventario-multitaxonomico-del-anp-medanos-de-samalayuca-pj018). Identification was made using taxonomic treatments and floras, including the Chihuahuan Desert Flora (Henrickson & Johnston 2007), as well as revision of herbarium specimens, mainly at CIIDIR and UACJ, where the vouchers were deposited, and of type images at JSTOR. Names of families are according to PPG I (2016) for ferns and allies, Christenhusz *et al*. (2011) for gymnosperms, and APG IV (2016) / Stevens (2001 onwards) for angiosperms; species names are according recent taxonomic treatments and Tropicos (www.tropicos.org). Data on general distribution, origin (native or non-native), endemism level and conservation status were recorded and assessed.

Results

A checklist of the wild and naturalized vascular flora from the Médanos de Samalayuca natural protected area was compiled, including 400 species of 246 genera and 65 families (Table S1). Nineteen additional species are known from the area only as cultivated and were not included in in the analyses (Table S2). Richness by taxonomic groups is shown in Table 1. The most diverse families are Asteraceae and Poaceae (Table 2), while the richest genera are *Euphorbia*, *Opuntia*, *Boerhavia*, and *Aristida*. Examples of the plant communities and flora in the zone are in Figures 2 and 3.

Distribution by vegetation type or land use. Most species grow in Mixed desert scrub and in Sand dune vegetation (Table 3; Table S1).

General distribution and origin. Almost a half of the species (48.5 %) are restricted to the Megamexico 1 region, as defined by Rzedowski (1991); a second set is composed by the North American elements (31.7 %); additional patterns of distribution are shown in Table 4. As about the geographic origin, most species are native but there are also 26 (6.5 %) exotics (Table S1).

Conservation status. Five species with a risk category in the Mexican Official Norm NOM-059 and/or in the IUCN Red List are indicated in Table 5. One species is classified as Threatened according to the Mexican Official Norm NOM-059 while two are Vulnerable and one is Near Threatened according to the IUCN. The complete list of species in the NOM-059 and the IUCN Red List (including those listed as of Low concern, LC) are in Table S3. One species not included on those lists, *Ribes fontinale*, appears to be extinct.

Table 1. Richness of vascular plants by taxonomic group in the Médanos de Samalayuca protected area.

Group	Families	Genera	Species	Subsp./var.
Ferns and fern allies	2	5	9	
Pinophyta	2	2	4	
Magnoliophyta – Monocots	6	41	70	
Magnoliophyta – Dicots	55	198	317	2
Total	65	246	400	2

Discussion

The Médanos de Samalayuca are part of the Chihuahuan Desert (ChD), a relatively well studied ecoregion. The flora of the ChD has been recorded in papers and in a superb assessment coordinated by Henrickson & Johnston (2007). Yet, many areas and many groups still require be explored. Precise information on the species and their ecological requirements is useful to scholars, land managers and general users (Villaseñor & Meave 2022). The updated checklist of the wild and naturalized vascular flora of Samalayuca compiled here adds 117 species (30 %) to the previous inventory (Gatica Colima 2019) and to a preliminary list included in the Management Program (CONANP 2013).

Floristic richness. Dicots (Magnoliopsida) is the most diverse group, as is in Mexico and in most of the world, but ferns and gymnosperms are scarcely represented. Ferns in the area are associated to rock outcrops and soil crust. As for gymnosperms, only four species were found (0.1 % of the flora, as compared with 0.8 % for northern Mexico) (González-Elizondo *et al.* 2017), including only a conifer (*Juniperus arizonica*). The most diverse families are Asteraceae (17 %) and Poaceae (14 %), followed by Cactaceae (7 %), Fabaceae (6.5 %), Amaranthaceae (4.7 %), and Nyctaginaceae (4.5%). A comparison with Villaseñor (2016) data for Mexico reveals that Nyctaginaceae is almost 10 times richer in Samalayuca than in general for Mexico (4.5 vs 0.47 %) (despite Mexico having a surface > 3,000-fold larger than Samalayuca), Amaranthaceae (including Chenopodiaceae) is five times richer, while Poaceae and Brassicaceae are three times richer. Cactaceae and Euphorbiaceae are also well represented in Samalayuca in relation to Mexico (Table 6). On the other hand, some families are underrepresented. Fabaceae downs to the fourth position in Samalayuca from the second place in Mexico, but the most striking differences are Lamiaceae and Cyperaceae. Those two are among the most diverse families in the country but are barely represented in Samalayuca; Lamiaceae is proportionally 5 times richer in Mexico than in Samalayuca, and Cyperaceae is almost twice richer in Mexico than in Samalayuca. Although, our inventory is still preliminary, and it is almost certain that more members of those families will be recorded later. The arid conditions of the area are unfavorable for these families: Lamiaceae is better adapted to temperate climates in mountain regions (Martínez-Gordillo *et al.* 2017), while many Cyperaceae grow better in humid places, which are very scarce in Samalayuca. Relative differences in the diversity of several families

Table 2. Most diverse families of vascular plants of the Médanos de Samalayuca protected area.

Family	Number of genera	Number of species
Asteraceae	51	68
Poaceae	32	55
Cactaceae	12	28
Fabaceae	15	26
Nyctaginaceae	7	18
Euphorbiaceae	4	17

Figure 2. Landscape and vegetation of the Médanos de Samalayuca protected area. A) Mixed desert scrub dominated by *Larrea*; B) Sand dune vegetation with *Artemisia filifolia*; C) Sand dune vegetation with *Artemisia* sp.; D) Rosetophyllous scrub with *Yucca and Agave lechuguilla*; E) *Echinocereus dasyacanthus* in mixed desert scrub with *Larrea*; F) *Artemisia filifolia* scrub on semi-fixed dunes; G) Grasses on sand dunes; H) *Sphaeralcea hastulata* in secondary vegetation; I) Aquatic vegetation.

with regards to Mexico and several geographically close areas in northern Mexico and southwestern United States are presented in Table 6.

When comparing the flora of Samalayuca with other sandy areas, we found strong similitudes regarding the representation of the families: Asteraceae and Poaceae, in the gypsophylous area of White Sands, NM (Table 6). The same two are also the most important in a steppe zone of north-west Algeria (Habib *et al.* 2020), while in another zone in northern Algeria the larger are Asteraceae and Fabaceae (Macheroum *et al*. 2021). Poaceae and Brassicaceae, well represented in Samalayuca, are the most important in sandy soils of northern Sahara (Azizi *et al.* 2021).

The richest genera in Samalayuca are *Euphorbia*, *Opunia*, *Boerhavia*, and *Aristida*. *Euphorbia* is also the richest genus in the gypsum dunes of Cuatro Ciénegas, White Sands, USA, the halophytic grasslands of Janos, and in different Mexican coastal sand dunes (Pinkava 1984, Anderson 2007, Vega-Mares *et al.* 2014, Espejel *et al.* 2017). As for *Opuntia*, nine species are recognized following the criteria of specialists, but a lot of taxonomic work is still needed in that genus. For example, *Opuntia camanchica* is part of the *Opuntia phaeacantha* complex and may represent a morphotype of that species. However, since there is no clear understanding yet in the group, *O.* aff. *camanchica* is kept in the list. On the other hand, *Salvia*, the largest genus in Mexico and in the Lamiaceae (Martínez-Gordillo *et al.* 2017; González-Gallegos *et al.* 2019), has not been found yet in Samalayuca; although, it is well represented in gyp-

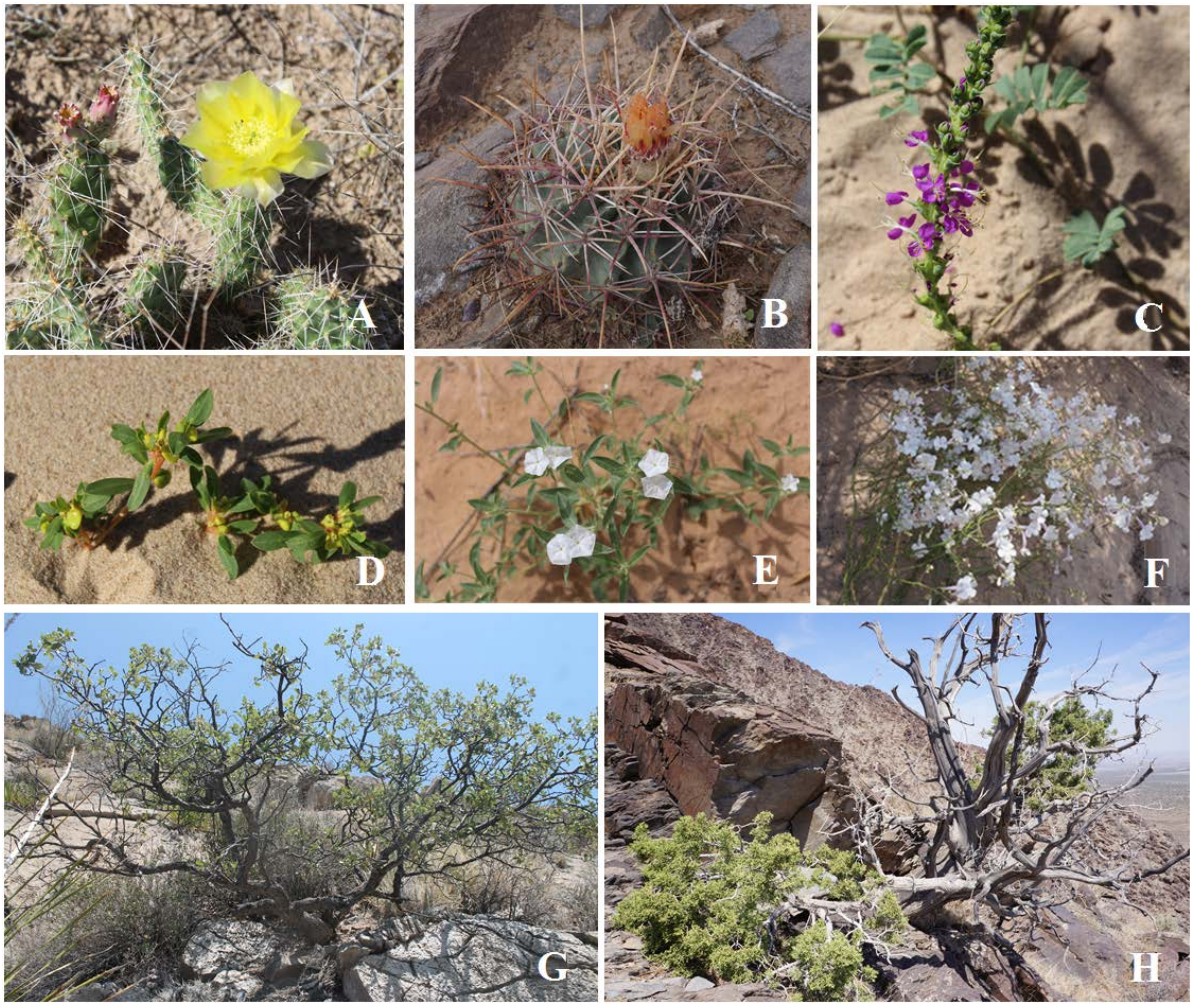

Figure 3. Examples of the flora of the Médanos de Samalayuca protected area. A) *Opuntia arenaria*; B) *Homalocephala parryi*; C) *Dalea lanata*; D) *Euphorbia carunculata*; E) *Euploca convolvulacea*; F) *Penstemon ambiguus*; G) *Quercus pungens*; H) *Juniperus arizonica*.

Table 3. Distribution of the flora by vegetation type and land use in the Médanos de Samalayuca protected area. Distribution data are not mutually exclusive.

Vegetation or land use	Species
Mixed desert scrub (MDS)	330
Sand dune vegetation (SD)	224
Woodland element (W)	103
Secondary vegetation (SV)	56
Humid places and wetlands (HP)	46
Rosetophyllous scrub (RS)	40
Irrigated agriculture (IA)	27
Alkali grassland and scrub (A)	25
Riparian (R)	25

sophylous areas as Cuatro Cienegas (eight species) (Pinkava 1984) and White Sands (six species) (Anderson 2007), as well as in the nearby Franklin mountains of Texas and New Mexico (five species) (Worthington 2014).

Samalayuca is relatively close to the gypsum sand dunes from Cuatro Ciénegas, Coahuila. (Pinkava 1979, 1984) and the New Mexico's White Sands dune fields, that are also gypsum rich (Worthington 2003, Anderson 2007), but it differs in its mostly siliceous (composed by quartz) sand. Cuatro Ciénegas harbors more than 860 species (871 taxa) of native and naturalized vascular plants, which is more than twice than in Samalayuca. The explanation for this is the wide elevational span in Cuatro Ciénegas (2,260 m, from 740 to 3,000 m asl) in about 2,000 km^2, hence a high variety of ecosystems range from gypsum dunes and wetlands to pine-oak woodlands and conifer forests (Pinkava 1984). Samalayuca, on the other hand, is a smaller area less than a third the surface of Cuatro Ciénegas and only 393 m of difference among the lowest and the highest points, so only xerophytic communities develop there, aside scarce woodland elements restricted to the colder places. Still, the plant diversity in Samalayuca is higher than the found in other zones with predominancy of dune fields. For example, Azizi *et al*. (2021) recorded only 29 species for a zone in northern Sahara, Algeria. It could be due to drier conditions (annual precipitation is < 36-76 mm) and to the fact that no other plant communities were sampled aside the sand dunes vegetation. For another area in northern Algeria, Macheroum *et al*. (2021) recorded 63 species. This area is half the surface of Samalayuca (28,600 ha), receives a higher precipitation (372 mm/yr), and harbors steppe vegetation.

Distribution by vegetation type. As around the world, in the ChD, the plant communities strongly intergrade. The distribution of species in the recognized categories is not mutually exclusive, so we indicate their relative proportions. The highest diversity was found in the Mixed desert scrub (38 %) and Sand dune vegetation (26 %). The first is the most broadly distributed community in the ChD; in Samalayuca it is often dominated by *Larrea*, along with *Fouquieria*, *Vachellia*, *Opuntia*, *Prosopis*, and other shrubs. Some elements, as *Hedeoma nana* and *Oenothera brachycarpa*, while growing to Mixed desert scrub, require special rocky microhabitats. Others, as the association of *Artemisia-Poliomintha*, are found on fixed dunes but also on active sand dunes. While *Flourensia cernua* is co-dominant with *Larrea tridentata* in many areas of the ChD, this association does not occur in Samalayuca, where *F. cernua* is infrequent. In fact, it was not observed during this study, and its inclusion in the inventory is based in its record in the Management Program. The rareness of *F. cernua* in the area might be due to the prevalence of sandy soils, given that this species prefers soils of finer texture (LTER Network 2019), particularly loams (Ji *et al*. 2019).

For Sand dune vegetation, 224 species were recorded. In strong contrast with this relatively high diversity, the plant cover is so sparse that most of its surface has been represented in previous maps in a category named "*Sin vegetación aparente*" (With no apparent vegetation) (*e.g.,* INEGI 2005). Physiognomic dominants, often in separate areas, are of the genera *Prosopis*, *Atriplex*, *Artemisia-Poliomintha*, as well as grasses. The sand dune communities

cover large surfaces but can be also intercalated with other communities. Movement of sand dunes prevents the formation of true soils; these substrates lacking horizons are called psamment Entisoils (Steila 1976, in Pavlik 1979). The term psammophytes, for the plants adapted to grow on those sandy, unstable soils, was coined by M. Vahl in Warming' Oecology of plants (1909). Many psammophytes are extremophiles (Azizi *et al*. 2021), very valuable as keepers of the ground moisture, potential stabilizers, enrichers of the substrate, habitat for other species, and pioneers for other vegetation stages. Assessing the types and characteristics of psammophytes allows to identify those useful to stabilize rangeland dunes (Thomas & Redsteer 2016). Obligated psammophytes in Samalayuca are *Dysphania atriplicifolia* and *Euphorbia carunculata*. However, most species growing on the dunes are not strict psammophytes. While many grow preferentially on sand dunes, they are not restricted to them, *e.g*., *Artemisia carruthii*, *A. filifolia*, *Mimosa rupertiana*, *Euploca convolvulacea, Penstemon ambiguus*, *Poliomintha incana*, and several Nyctaginaceae. The genus *Prosopis* includes recognized dune stabilizers, *e.g*., *Prosopis juliflora* (Sw.) DC. (Pasiecznik 2017); this name has been widely applied to plants of the Chihuahuan Desert, but it corresponds to a species restricted to coastal zones of the Yucatán peninsula and south (Palacios 2006). While the three species of *Prosopis* in Samalayuca (Table S1) have not been recorded as dune stabilizers, they also act as such (personal observation). There are also tolerant

Table 4. General distribution of the vascular flora of the Médanos de Samalayuca protected area.

Distribution	Species	%
Megamexico 1*	194	48.5
North America**	127	31.75
American continent	26	6.5
Pantropical and subtropical	23	5.75
Near Cosmopolitan	11	2.75
Megamexico 3	5	1.25
Southwestern United States to South America	4	1.00
Other	3	0.75
Microendemic***	2	0.50
Non available data	5	1.25
Total	400	100

*Rzedowski's (1991) Megamexico concept is based in the natural continuity and sharing of ecosystems and flora between Mexico and its neighboring countries. Megamexico 1 encompasses the Sonoran and Chihuahuan deserts and the Tamaulipan scrub in Mexico and southern United States; Megamexico 2 includes Mexico and the zone of Central America northern of the Nicaraguan depression, while Megamexico 3 applies to species whose distribution combines the former two.

** North America including Canada, the United States and Mexico (Nearctic realm).

***Only known for Samalayuca or northern Chihuahua.

elements from the xerophytic scrub that grow on sand, and other species growing well on semi-stabilized dunes or sandy soils in other types of vegetation, e.g., *Baccharis wrightii*, *Fouquieria splendens*, and *Salsola* spp.

Woodland elements. The oak or juniper woodland and chaparral are communities not represented in Samalayuca. However, there are elements of those communities (12 % of the flora) restricted to the coldest sites of the small sierras (Samalayuca and Presidio) in spots that are not depicted in the vegetation map. Among those are *Castilleja* spp., *Juniperus arizonica*, *Quercus pungens*, *Fendlera rupicola*, and *Philadelphus mearnsii*. As relics of a colder

past, they are particularly vulnerable to the regional climate trend to higher and extreme heat (Union of Concerned Scientists 2016).

Other communities. About 6.4 % of the plants in Samalayuca grow in Secondary vegetation, which covers disturbed places, human settlements, and induced grassland on old agricultural fields. Many of the wild and naturalized plants recorded for the secondary vegetation grow also in the agriculture fields (3.1 %). The Rosetophyllous scrub, a xerophytic scrub dominated by *Agave lechuguilla*, *Yucca*, or *Dasylirion leiophyllum*, holds about 4.4 % of the species, while Alkali scrub and grassland, with halophytic species, includes only 2.9 %. Additionally, 5.3 % of the species grow in Humid places, including few aquatic, subaquatic and water tolerant plants that develop in the natural and artificial water bodies of the area; the most conspicuous of them are *Typha* and *Arundo*. Related with the former category are 2.9 % of Riparian species, herbs, shrubs and a few trees (*Populus*, *Tamarix*) bordering the water bodies. The three springs known from Samalayuca are at present highly modified and a species described from that habitat (*R. fontinale*) was not found during this work.

The names of the plant communities recognized here are adapted from the classification of Henrickson & Johnston (1986) for the ChD. Of 16 plant communities recognized by them, six are represented in Samalayuca: Chihuahuan Desert scrub (with three of its five facies), lechuguilla scrub, *Yucca* woodland, *Prosopis-Atriplex* scrub, Alkali scrub, and Montane Chaparral. The last is represented by scattered woodland elements. The facies of the Chihuahuan Desert scrub present in Samalayuca are the *Larrea* scrub (Gobernadora), the Mixed desert scrub (Chaparrillo or *Acacia* scrub), and Sand dune scrub (Matorral de Dunas or Médanos). The first two facies (*Larrea* scrub and Chaparrillo or *Acacia* scrub) are recognized in this work as part of the Mixed desert scrub, while the last is part of the Sand dune vegetation. According to Muldavin (2002), the three northernmost communities of the ChD in its limits with the Colorado Plateau are dominated by *Larrea tridentata*, *Bouteloua eriopoda*, and *B. gracilis*; *Larrea* and *Bouteloua eriopoda* are present in Samalayuca, not so *B. gracilis*, a species broadly distributed in North America but not located here. Previous classifications of the vegetation of Samalayuca (Enríquez & Olivas 1999), include plant communities

Table 5. Species with conservation status of the Médanos de Samalayuca protected area. NOM-059 - Risk category in the Mexican Official Norm NOM-059 (SEMARNAT 2010): A - Threatened, Pr - special protection category. IUCN - Risk category in the IUCN Red List: LC - Low concern, NT - Near threatened, VU - Vulnerable, dec - population decreasing, st - population stable.

Species	NOM-059	IUCN
Agave havardiana Trel.		VU dec
Epithelantha micromeris (Engelm.) F.A. C.Weber ex Britton & Rose	Pr	LC st
Ferocactus wislizeni (Engelm.) Britton & Rose		VU dec
Homalocephala parryi (Engelm.) Vargas & Bárcenas	A	NT st
Opuntia arenaria Engelm.	Pr	

names that are not recognized in this work (*e.g*., Microphyllous desert scrub, Small-leafed spineless scrub, Subspineless dune scrub, among others).

General distribution and endemism. The flora of Samalayuca has a strong Nearctic and regional endemic component. Almost a half of the species are distributed in "Megamexico 1" (MM1) (Rzedowski 1991) and a third that are distributed in North America. MM1 is a region concept based in the natural continuity of ecosystems between Mexico and southwestern United States, mainly from the Chihuahuan and Sonoran deserts, hence it represents a regional endemism. Some species have a rather restricted distribution inside MM1, *e.g*., *Agave havardiana*, known only for SW Texas, N Chihuahua, and N Coahuila; *Agave* x *gracillipes*, from SE New Mexico, SW Texas, and N Chihuahua, as well as several Nyctaginaceae.

The separation among the distribution patterns of the MM1 and North American elements is subtle for some species that go a little further north of the southwestern region. Our criterion was to leave as MM1 to species that reach

southern Utah, but not for those that may be present in northern Utah. Species as *Argyrochosma limitanea*, *Palafoxia sphacelata*, *Pectis angustifolia* and *Sporobolus giganteus* are considered as North American because their distribution reach Wyoming, northern Utah, Nebraska, and/or eastern Texas. Others, as *Notholaena standleyi* and *Parthenium incanum*, while reaching southern Nevada, Utah, Colorado or Kansas, are still MM1.

Additionally, in Samalayuca there are two microendemics, one to northern Chihuahua (*Homalocephala parryi*/ *Echinocactus parryi*) and one to Samalayuca (*Ribes fontinale*). No other taxa were found restricted to the limits of Mexico, besides these two microregional endemics, which is explained by the closeness of Samalayuca with the international border Mexico - USA. This is also the reason for the high proportion of endemics from the MM1 region. Among these, stand out many Asteraceae as well as most Cactaceae and *Agave*, as occurs for northern Mexico (González-Elizondo *et al.* 2017) and the ChD (Villarreal-Quintanilla *et al*. 2017). Nyctaginaceae, Boraginaceae and Brassicaceae are distributed either in MM1 or NA.

The second largest contingent of the flora (32 %) are the North American elements (distributed from Canada to Mexico), which belong to the Nearctic realm. Some of them barely reach Mexico at northern Chihuahua, e.g., *Mirabilis glabra* (S. Watson) Standl., which is known for the country only for Samalayuca and near Casas Grandes, Chih. (Hernández-Ledesma & Flores-Olvera 2023).

Other biogeographic elements are scarcely represented. The species distributed in the American continent are 6.5 %, the pantropical and subtropical element is 5.7 %, and others still scarcer. Some of the American species (*e.g.*, *Scleropogon brevifolius*, *Hoffmannseggia glauca*) grow from the southwestern United States to southern South America, often as disjunct.

Introduced species.- Most of the recorded species are native, except for 26 exotic (6.5 % of the flora). From these, 10 are Poaceae, most of them from Africa. Among the introduced, two Poaceae and two Amaranthaceae are invasive. What we cite as *Salsola* x *gobicola* (a hybrid between *S. paulsenii* and *S. tragus*), may be *S. paulsenii*; the taxonomic revision of this complex is beyond of the scope of this work. The introduced and native successful colonizers thrive mainly in secondary vegetation and in disturbed places. The only family that includes only introduced species (3) is Tamaricaceae.

Conservation status. The species catalogued as threatened or vulnerable in the Mexican Official Norm NOM-059 (SEMARNAT 2010) and in the Red List of the IUCN are listed in Table 5. Most of the species with a risk category are cacti, as also pointed out by Royo-Márquez *et al.* (2014) for Chihuahua. *Sclerocactus papyracanthus* is listed in Appendix I of CITES (Threatened with extinction, trade only in exceptional circumstances) (UNEP WCMC 2003). The Mexican Official Norm NOM-059 (SEMARNAT 2010) is the official report that lists the wild flora in Mexico

Table 6. Comparison of richness (%) of plant families among several floras. 1. This work; 2. Estrada-Castillón & Villarreal-Quintanilla (2010); 3. Royo-Márquez & Melgoza-Castillo (2001); 4. Vega-Mares *et al.* (2014); 5. Villaseñor (2016); 6. Pinkava (1984); 7. Anderson (2007). The data for Mexico (Villaseñor 2016) involve only native species; all the others are based on native and introduced species.

Region	Aster	Poac	Cact	Fabac	Amar	Nyctag	Euph	Brass	Lam	Cype
Samalayuca[1]	17	13.7	7.0	6.5	4.7	4.5	4.2	3.2	0.5	1.0
Central Chihuahua[2]	17.8	12.3	2.3	10.1	2.3	1.6	2.8	1.9	2.0	1.5
La Campana[3]	17.8	27.2	0.2	12.5	3.9	0.9	2.1	1.6	1.1	1.4
Janos[4]	16.8	18.3	4.0	8.5	3.0	0.91	6.7	2.7	1.2	0.9
Mexico[5]	13.1	4.5	2.9	8.1	0.9	0.46	3.1	0.9	2.6	1.8
Cuatro Ciénegas[6]	14.6	8.7	5.9	2.9	2.4	1.5	3.4	2.4	2.3	1.8
White Sands, NM[7]	17.1	14.4	3.2	5.7	2.8	1.7	3.5	3.4	1.8	1.1

Amaranthaceae s.l., including Chenopodiaceae.

catalogued as with some risk category. For example, *Homalocephala parryi* (assessed as *Echinocactus parryi* in the NOM-059) is an endemic with the category of Threatened.

For the plants with some risk category according to the IUCN (included those of Low concern), the population tendencies are: 5 decreasing, 5 increasing, and 57 stable.

Species previously recorded and not found during this study.- *Ribes fontinale* was described from springs in Samalayuca. The three springs, which are seasonal and have somewhat saline water, are now highly transformed (one of them is dry, while the borders of the other two have been cemented). *Ribes fontinale* was known only from the type collection and it may be considered as probably extinct. However, the taxonomy of the species needs to be assessed; it is worth to explore its taxonomic position as part of the complex of *R. aureum* Pursh, a highly variable species known from Canada to Chihuahua (www.tropicos.org/collection/4795281). If materials from southwestern United States and Chihuahua that are presently identified as *R. aureum* prove to be *R. fontinale*, then this species may be locally extinct in Samalayuca but still extant elsewhere. Another option could be that *R. fontinale* represents a morphotype of *R. aureum*.

Hoffmannseggia drepanocarpa was cited by Simpson (1999) in her revision of the genus and included here with basis in an herbarium specimen at LL. It has not been recently recorded, being probably an unfrequent plant.

Other unfrequent species are *Houstonia humifusa* and *Ayenia microphylla*, which are known for the area exclusively from the records in Naturalista. *Flourensia cernua*, as mentioned above, was not observed during this work, indicating rareness or probable absence in Samalayuca. It was recorded in the Management Program and is included here since its absence from the area is not certain.

Sclerocactus papyracanthus was recently recorded for the first time for Mexico (Ortiz-Brunel et al. 2023). Although in the second edition of the Cites Cactaceae Checklist, Hunt (1999) included Mexico in the distribution of *S. papyracanthus*, no voucher or record was mentioned; later, in the third edition of the same list (Hunt 2016), Mexico was deleted. In the assessment for the IUCN (Heil *et al.* 2013), *S. papyracantus* was also treated as an endemic to the United States (Arizona, New Mexico and Texas).

Excluded species.- Among the 225 species recorded in the Management Program (CONANP 2013) and other references, the following are based on misidentifications and hence, excluded from this work: *Myriopteris microphylla* (Sw.) Grusz & Windham, known from Florida to South America and West Indies; *Escobaria chihuahuensis* Britton & Rose, known from central Chihuahua to eastern Durango; *Sphaeralcea axillaris* S. Watson, distributed in eastern Sonora and Baja California; *Lappula redowskii* (Hornem.) Greene, a species from the old world whose citation may be based in the fact that *L. occidentalis* (S. Watson) Greene (which occurs in the area), has been considered as a synonym or as a subspecies of *L. redowskii*; *Nama parvifolia* (Torr.) Greenm. and *Nama retrorsa* Howell have been recorded with basis in misidentified specimens in UACJ; the first is known from southeastern Texas and northeastern Mexico, while *N. retrorsa* is recorded for southern Colorado and northern Arizona and New Mexico; *Penstemon alamosensis* Pennell & G.T. Nisbet, endemic to the Sacramento Mts. and surroundings of Alamos, New Mexico. An unidentified *Penstemon* from Samalayuca differs in having not pubescent corollas. *Salsola kali* L. is a coastal species. *Urochloa ciliatissima* (Buckley) R.D. Webster, recorded with basis in misidentified *U. texana*. A specimen in UACJ previously identified as *Abronia carletonii* Coult. & Fisher is a wide-leaved form of *A. angustifolia*.

Anthropogenic activities and the associated flora.- In some areas, the original plant cover has been replaced by irrigated crops, mainly pecan (*Carya illinoinensis*), with about 400 ha (Rueda-Torres *et al*. 2022b), as well as vines (*Vitis vinifera*) and pistachios (*Pistacia vera*), besides the impact of extensive cattle farming. The area is also a popular recreational destination for ecotourism and adventure tourism, has been the scenery for some movies (Chihuahuan Frontier 2009), and has been considered with potential industrial use (Cruz Sánchez *et al*. 2007). The plants associated with crops are mainly species of Poaceae, Asteraceae, Solanaceae, and Boraginaceae (Rueda-Torres *et al*. 2022b). Land use change, mainly to irrigated crops and urbanization, as well as ecoturism/recreational activities pose threats to the biodiversity and the fragile ecosystems of Samalayuca, so policies focused on a better interaction among people and the natural system are needed (Gatica Colima 2019).

Probably because the extreme climate and the moving substrates that reduce the stability of the vegetation, the flora of the Médanos de Samalayuca has a relatively low diversity. Still, it is richer than we expected prior to this work, with many elements adapted to extreme edaphic and climatic conditions. The area is home to regional endemics and threatened species, and more work is needed to know the status of rare species and if some plants previously cited for the area but not located during this study, may still be found. Understanding the composition and ecology of sand dunes communities is keystone to improve the strategies to protect these fragile ecosystems from anthropogenic impacts and invasive organisms and, at the same time, to prevent the ecological and economic damages that dune expansion poses on adjacent ecosystems and infrastructure.

Supplementary material

Supplemental material for this article can be accessed here: https://doi.org/10.17129/botsci.3369

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