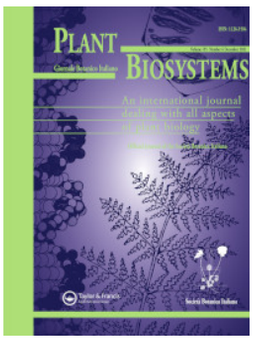

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Diversity, distribution and conservation of the Cactaceae (Caryophyllales) from Tamaulipas, Mexico

Leccinum J. García-Morales[a,b], Jesús García-Jiménez[b], Raúl Contreras-Medina[c], Othón Alcántara-Ayala[a] and Isolda Luna-Vega[a]

[a]Departamento de Biología Evolutiva, Laboratorio de Biogeografía y Sistemática, Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), Coyoacán, Mexico; [b]Tecnológico Nacional de México, Instituto Tecnológico de Ciudad Victoria, Departamento de Posgrado e Investigación, Victoria, Mexico; [c]Laboratorio de Biodiversidad, Escuela de Ciencias, Universidad Autónoma Benito Juárez de Oaxaca (UABJO), Oaxaca de Juárez, Mexico

ABSTRACT

Geographical distribution, diversity, endemism and conservation of Cactaceae in the Mexican state of Tamaulipas were analyzed based on distributional data obtained from specialized literature, fieldwork and herbarium specimens. Tamaulipas territory was divided into grid-cells of 10×10 min latitude/longitude and was used as units of analysis. Cactaceae comprises 174 taxa and 33 genera in Tamaulipas, representing a high proportion of the Mexican cacti with 65% at the generic level and 23% at the specific level. The richest genera are *Opuntia* (40), *Mammillaria* (35), *Echinocereus* (16) and *Turbinicarpus* (14). Thirty one Cactaceae taxa are new records for the state. The highest diversity of species occurs in the southwestern region associated with the Sierra Madre Oriental slopes and the Jaumave Valley. Cacti are well represented in the state natural protected areas (NPAs) of Tamaulipas compared to the federal conservation areas. We conclude that Tamaulipas constitutes a nodal area because it is located at the boundaries among four different biogeographic regions representing zones of biotic overlap promoted by historical and ecological changes allowing the mixture of different biotic elements and *in situ* speciation. For this, it is considered one of the richest Mexican states in terms of Cactaceae diversity.

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Biodiversity; endemicity; Mexican cacti; natural protected areas; threatened species

Introduction

Mexico is considered the main center of diversity of the family Cactaceae (Goettsch and Hernández 2006). From 50 to 63 genera and 518–593 species *sensu* Guzmán et al. (2003) and Hunt (2016) are recognized in the country; of these, approximately 40% of the genera and 75% of the species are endemic (Goettsch et al. 2019). It is, therefore, one of the richest families among the flora of Mexico after Asteraceae, Fabaceae, Poaceae and Orchidaceae (Rzedowski 1991; González-Elizondo et al. 2017). Cacti are mainly distributed in arid and semiarid regions, covering nearly 50% of the country's territory, especially in northern Mexico (Rzedowski 1991).

Mexican Cactaceae are important because 1) they are relevant components of the Mexican flora, dominating extensive landscapes, especially in the north (Rzedowski 1991); 2) they are economically significant because young stems, flowers and fruits of several species are edible for humans and cattle (Santa Anna del Conde et al. 2009), other species are used in house building and as living fences, whereas others have medicinal use or used in the production of alcoholic beverages (Casas 2002); 3) a high proportion of cactus species have small geographic ranges and exhibit high levels of endemism (Hernández et al. 2004; Goettsch et al. 2019); 4) their beauty and rarity have triggered their extraction from natural populations as well as land use cover changes, both factors promoting a high number of threatened species (31%) (Glass 1998; Goettsch et al. 2019; Santa Anna del Conde et al. 2009).

A current discussion on conservation efforts has been the biodiversity loss crisis. From this point of view, the family Cactaceae has high indexes of geographically restricted species and threatened taxa. In recent years, many populations of Mexican cacti changed their conservation status to critically endangered or presumably extinct in the wild (Gómez-Hinostrosa and Hernández 2000; Hunt 2016, among many others). As Nordal and Stedje (2005) pointed out, there are enough conservation reasons for recognizing paraphyletic taxa as valid, mainly because the loss of species is relatively faster than are being studied. The continuous description of new species and the recent phylogenetic approaches on the natural classification of groups and distribution analysis for several groups of Mexican cacti and the joining nomenclatural changes derived makes imperative the updating on the

CONTACT Isolda Luna-Vega luna.isolda@gmail.com Departamento de Biología Evolutiva, Laboratorio de Biogeografía y Sistemática, Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), C.P. 04510, Coyoacán, CDMX, Mexico

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knowledge of this family at different scales (Hernández et al. 2004; Godínez-Álvarez and Ortega-Baes 2007; Santa Anna del Conde et al. 2009; Rzedowski 2015; Vázquez-Sánchez et al. 2019; Korotkova et al. 2021).

Previous studies that analyze distributional patterns related to richness and endemism in Mexican cacti have been carried out in some Mexican regions and states, such as the study in the Chihuahuan Desert including parts of Nuevo León, San Luis Potosí, and Tamaulipas (Hernández et al. 2004; Goettsch and Hernández 2006); the study of Cactaceae in Tamaulipas (Martínez-Ávalos and Jurado 2005); research done in Coahuila, San Luis Potosí and Zacatecas (Hernández et al. 2008), and a study of the cacti in the biogeographic province of the Sierra Madre Oriental (Santa Anna del Conde et al. 2009). Some recent state studies on the richness and distribution of Cactaceae have been carried out in Durango (González-Elizondo et al. 2017) and Tabasco (Campos-Díaz et al. 2020).

One of the most critical areas for Cactaceae diversity is northern Mexico, where is located the state of Tamaulipas (Figure 1). Unfortunately, there are few studies carried out in Tamaulipas that integrate knowledge about this family, such as the distribution analysis carried out by Martínez-Ávalos and Jurado (2005); meanwhile, García-Morales (2005, 2006) deals with the richness and distribution of the cacti of the Sierra Madre Oriental and neighboring montane isolated regions of the Sierra de San Carlos and Sierra de Tamaulipas, both in Tamaulipas.

The sources of information to set the Cactaceae conservation strategies were specialized literature, fieldwork, floristic studies and specimens harbored in botanical collections. Our study integrates, updates and expands the knowledge on the Cactaceae of Tamaulipas, using a detailed geographic scale of grid-cells (10 min per side). This scale allowed us to recognize areas with high species richness, distributional information gaps, areas with a high concentration of endemic species and their conservation status. In addition, we offer an updated checklist of cacti species based on more than 25 years of fieldwork, revisions of herbarium specimens and virtual herbaria databases. We also analyzed the representativeness of cacti from Tamaulipas in natural protected areas (NPA) to determine the accuracy of the current protected areas and the diversity of cacti recorded.

Material and methods

Study area

The state of Tamaulipas is in northeastern Mexico (Figure 1), with an extension of 80,249 km^2 which represents 4.1% of the country's surface. Its extreme coordinates are 22°12′ –27°40′ N, 97°08′ –100°08′ W and it presents a wide range of elevation from sea level to 3500 m (Figure 1).

Based on the biogeographic regionalization of Mexico proposed by Morrone et al. (2017), in Tamaulipas are recognized four biogeographic provinces: I) the Chihuahuan Desert,

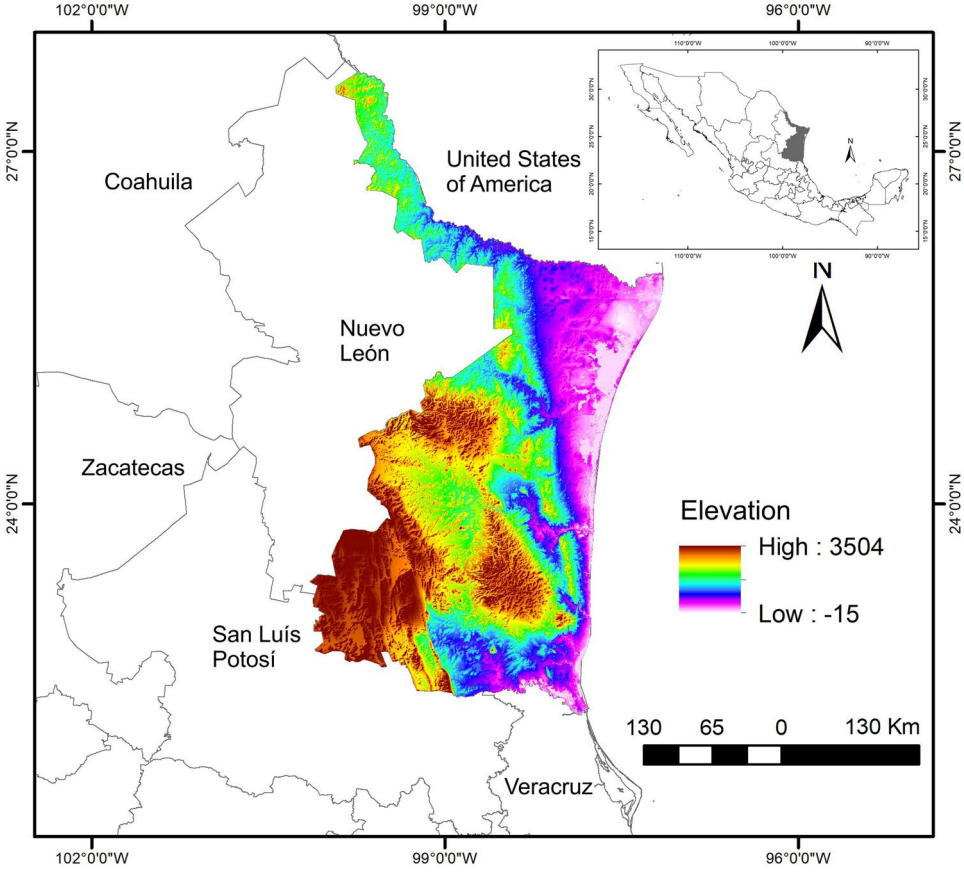

Figure 1. Map of the Mexican state of Tamaulipas showing different elevations.

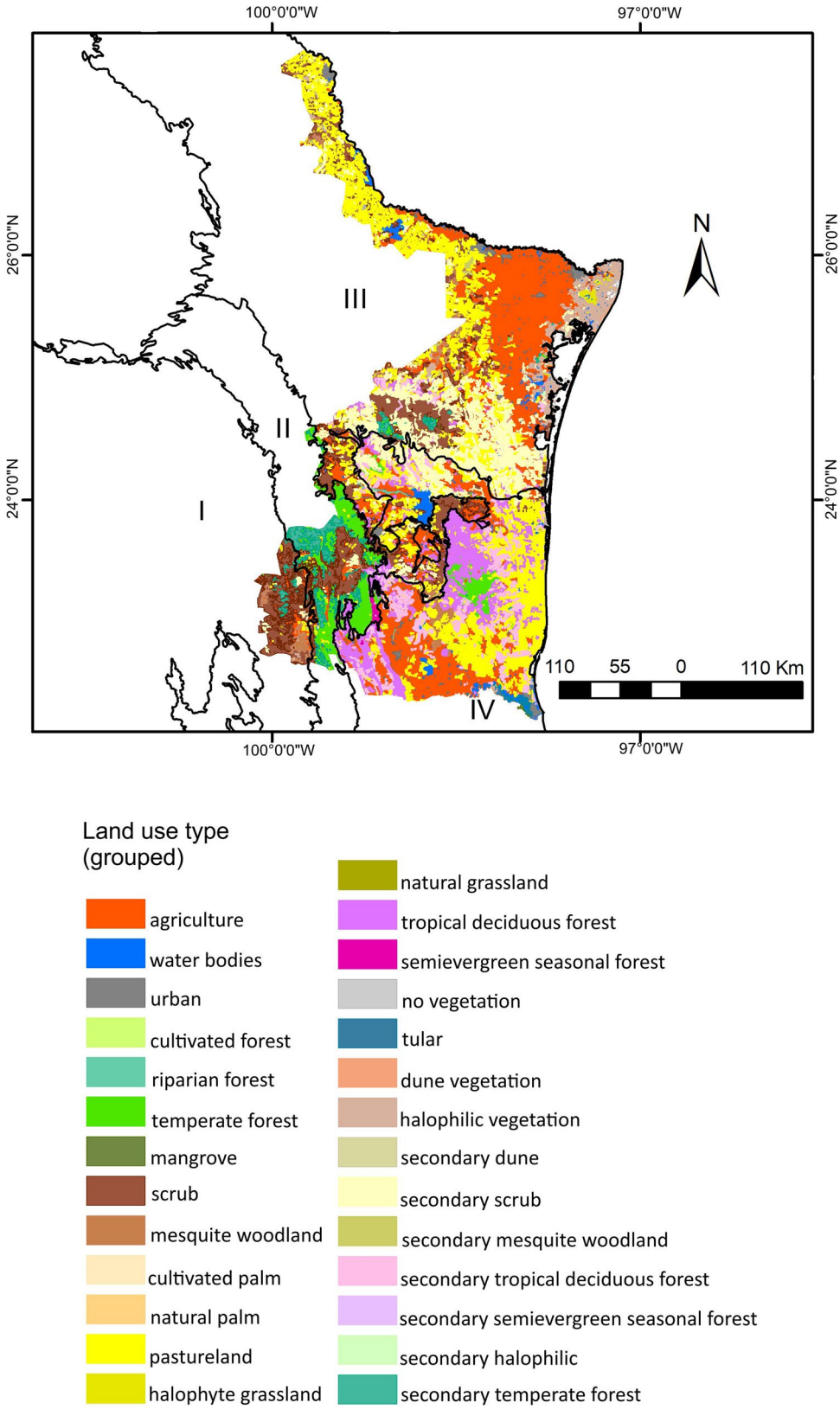

Figure 2. Biogeographic provinces, vegetation types and land use in Tamaulipas. Biogeographic provinces of Morrone et al. (2017): (I) Chihuahuan Desert, (II) Sierra Madre Oriental, (III) Tamaulipas and (IV) Veracruzan. Vegetation types and land use sensu INEGI (2017).

which is located in the southwestern portion and covers a small surface of territory; II) the Sierra Madre Oriental, a mountain province which occupies part of the southwestern territory with the highest elevations; III) Tamaulipas, located in the northern portion with lowland and coastal plains and IV) Veracruz, in the southern portion of the state (Figure 2).

A wide range of climates are found in the state: semi-warm in the lowland areas, dry in the northwestern and central

portions and temperate prevailing in the mountains (Figure 2). As a result, diverse vegetation types are present in Tamaulipas; xerophytic vegetation dominates 25% of the landscapes. Vegetation is represented by tropical deciduous forests, semievergreen seasonal forests, mesquite woodlands, grasslands and xerophytic scrub in the lowlands. In addition, different types of temperate forests occur in the mountain ranges, such as conifer, cloud, oak, pine forests and pine-oak woodland (Figure 2). A high proportion (26.5%) of the territory has been used for agriculture (Instituto Nacional de Estadística y Geografía [INEGI] 2017).

Data sources

Distributional data for the Cactaceae species were obtained from 25 years of field surveys, the revision of herbarium vouchers and type specimens deposited in selected herbaria: (ARIZ, ASU, CFNL, DES, GBH, ITCV, MEXU, MO, NY, P, UAT and US) and the revision of primary virtual herbaria databases for Mexican cacti, e.g. the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO 2020), the Herbario Nacional de México (MEXU) (https://datosabiertos.unam.mx/biodiversidad/, accessed August 2021) and the Missouri Botanical Garden (https://www.tropicos.org/home, accessed August 2021). The species' identity was verified for each specimen examined, the nomenclature was updated to the latest taxonomic revisionary study and the geographical coordinates were recorded accurately. For the databases of CONABIO and MEXU, a final depuration of taxa names without a clear identity, voucher references and accurate data was done, and a table of excluded taxa is presented according to vouchers revision in main herbaria and its cross-revision with the taxonomical lists proposed by main recent authorities. The last addition of herbaria and field observations to the composed database results in 3698 accessions records with complete UTM geographical coordinates prepared for the geographical and distribution analysis. With all this information, we created a distribution map that includes species records and collection localities using ArcGIS (Environmental Systems Research Institute [ESRI] 2012).

The foremost monographic, taxonomic and phylogenetic studies used to determine the species in this study and that support the recognition of genera and species are the following: Bravo-Hollis (1953, 1978), Bravo-Hollis and Sánchez-Mejorada (1991a, 1991b), Reppenhagen (1991, 1992), Guzmán et al. (2003), Butterworth and Wallace (2004), Bohata et al. (2005), Hunt et al. (2006), Hunt (2016), García-Morales (2005, 2006), García-Morales, González-Botello, et al. (2014), García-Morales, Estrada, González-Botello, et al. (2014), Lodé (2015), Bárcenas et al. (2011), Hernández-Hernández et al. (2011), Hernández and Gómez-Hinostrosa (2011, 2015), Majure et al. (2012), Vázquez-Sánchez et al. (2013, 2019), Hernández-Ledesma et al. (2015), Vázquez-Lobo et al. (2015), Korotkova et al. (2017), Vargas-Luna et al. (2018) and Alvarado-Sizzo et al. (2018). We prepared a final checklist of accepted taxa based

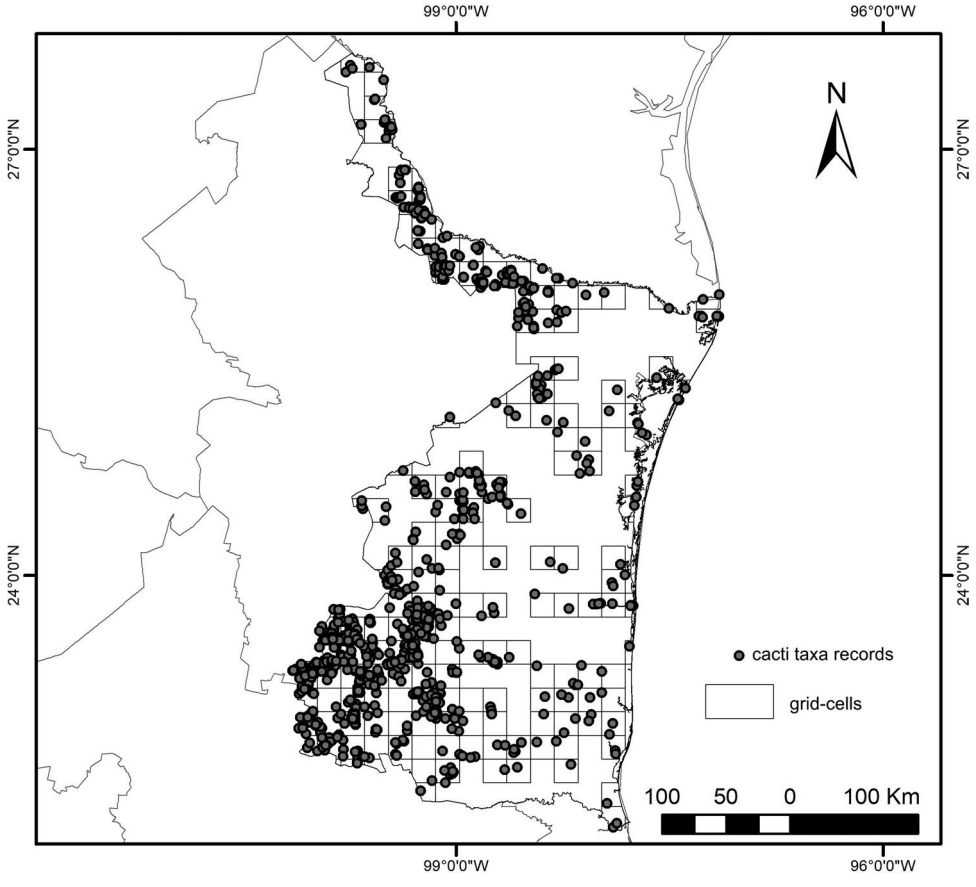

Figure 3. Grid cells and locality records of the Cactaceae in Tamaulipas.

on the validation of names through referenced phylogenetic tests and the cross reference of databases and revised vouchers from herbaria. Finally, we followed the philosophical proposal of De Queiroz (2020) that "subspecies are incompletely separated lineages within a more inclusive lineage".

The uniqueness of endemic species and their consecutive geographic isolation were found when analyzing the phylogenetic trees. These trees showed paraphyly in several species groups and previously synonymized species. The revision of protologues also showed enough morphological difference from several synonymized names. According to the ICN, we resurrected some names retaining the original combination as possible when a valid combination is available (Turland et al. 2018).

Data analysis

We divided Tamaulipas into grid-cells of 10 × 10 min latitude/longitude (322 grid-cells); we used these grids as study units for the biogeographical analysis. From this framework, only 165 grid-cells contain at least one cacti taxon (Figure 3). The geographical distribution of each taxon within the state was estimated considering the number of grid cells in which these were recorded. The size of the grid-cells used in our study (10′ × 10′) allows obtaining a reliable resolution of the distribution in comparison with other studies for Cactaceae (e.g. Martínez-Ávalos and Jurado 2005; González-Elizondo et al. 2017) in terms of biodiversity data and biological conservation (Ochoa-Ochoa et al. 2014). Concerning richness, those grid-cells with the high number of species in Tamaulipas were recognized and related with conservation priorities.

The degree of endemism of each species was determined considering different scales: 1) endemic to Mexico, taxa whose known distribution is restricted to Mexico; 2) regional endemic to northeastern Mexico (taxa whose known distribution is limited to the neighbor states of Tamaulipas, e.g. Nuevo León, San Luis Potosí and Veracruz (Figure 1); 3) endemic to Tamaulipas, taxa whose known distribution is restricted to the limits of the state of Tamaulipas. Associated with this last condition, those grid-cells with the high number of endemic species restricted to Tamaulipas were recognized and related with conservation priorities.

Conservation status and natural protected areas

The grid-cells with high species richness and the high number of endemic species were overlapped on the map of the federal NPAs decreed by the Mexican government (Secretaría de Medio Ambiente y Recursos Naturales-Comisión Nacional de Áreas Naturales Protegidas [SEMARNAT-CONANP] 2020), and with the map of the NPAs decreed by the government of Tamaulipas (CONABIO 2020). This task was done to determine the effectiveness of the current protected area system and the diversity of cacti recorded within each NPA, both federal and state levels (Figure 4). The NPAs of Tamaulipas are mainly distributed along with limited areas of the coastal

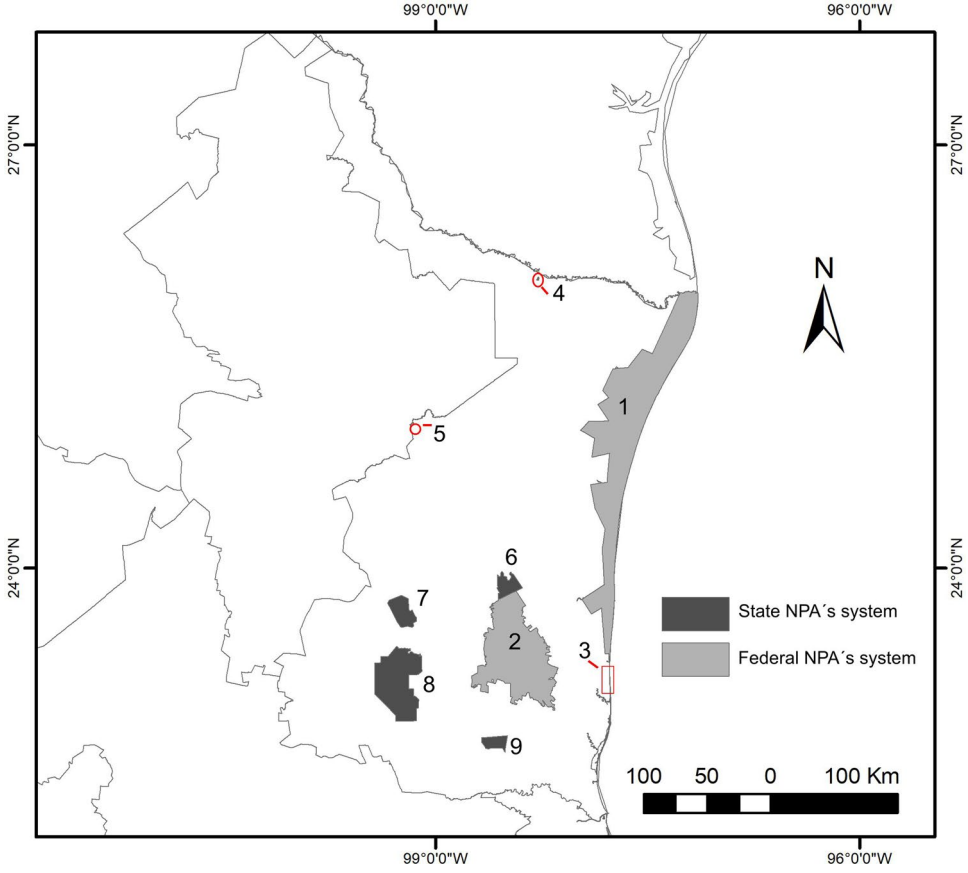

Figure 4. Natural protected areas (NPA's) in Tamaulipas. Federal NPA's: (1) Laguna Madre y Delta del Río Bravo; (2) Sierra de Tamaulipas; (3) Playa Rancho Nuevo. State NPA's; (4) Laguna La Escondida; (5) Las Flores; (6) Colonia Parras de la Fuente; (7) Altas Cumbres; (8) El Cielo; and (9) Bernal de Horcasitas.

Table 1. Cactaceae checklist of Tamaulipas.

Taxa	Endemism	NOM-059	IUCN	NPAs	Biogeo Prov	Grid-cells
Acanthocereus tetragonus (L.) Hummelinck			LC	1, 2, 7, 8, 9	II,III, IV	56
Ancistrocactus scheeri (Salm-Dyck) Britton & Rose					III, IV	46
Ariocarpus agavoides (Castañeda) E.F.Anderson	Regional	Pr	EN		I, II	4
Ariocarpus kotschkoubeyanus subsp. *albiflorus* (Backeb.) Glass	Tamaulipas	Pr			I, II	5
Ariocarpus retusus Scheidw.	Mexico	Pr	LC		I, II	9
Ariocarpus trigonus (F.A.C.Weber) K.Schum.	Regional	A	LC	7, 8	I, II, III, IV	26
Astrophytum asterias (Zucc.) Lem.		P	VU		II, III, IV	22
Astrophytum caput-medusae (Velazco & Nevárez) D.R.Hunt	Regional	P	CR		III, IV	3
Astrophytum myriostigma Lem.	Regional	A	LC	7	I,II, IV	10
Cephalocereus euphorbioides (Haw.) Britton & Rose	Regional			8	II, IV	7
Coryphantha delicata L.Bremer	Mexico	Pr	LC	8	I, II	25
Coryphantha georgii Boed.	Mexico	Pr	LC		I, II	3
Coryphantha glanduligera (Otto & A.Dietr.) Lem.	Mexico	A	LC		I, II	7
Coryphantha macromeris subsp. *runyonii* (Britton & Rose) N.P.Taylor					III	7
Coryphantha nickelsiae (K.Brandegee) Britton & Rose	Mexico	A	LC		III	3
Coryphantha octacantha (DC.) Britton & Rose	Mexico		LC	7	I, II	10
Coryphantha salinensis (Poselg.) A.D.Zimmerman ex Dicht. & A.Lüthy	Mexico		LC		III	1
Coryphantha sulcata (Engelm.) Britton & Rose			LC		III, IV	5
Coryphantha vaupeliana Boed.	Tamaulipas				II	3
Coryphantha wohlschlageri Holzeis	Regional	Pr	LC		I	1
Cumarinia odorata (Boed.) Buxb.	Mexico	Pr	LC		I	1
Cylindropuntia imbricata (Haw.) F.M.Knuth			LC	7, 8	I, II	22
Cylindropuntia kleiniae (DC.) F.M.Knuth			LC	8	I, II, III	9
Cylindropuntia leptocaulis (DC.) F.M.Knuth			LC	1, 2, 7, 8	I, II, III, IV	84
**Cylindropuntia rosea* (DC.) Backeb.	Mexico		DD		I	3
Cylindropuntia tunicata (Lehm.) F.M.Knuth			LC		I, II	8
Echinocactus horizonthalonius Lem.					I	4
Echinocactus platyacanthus Link & Otto	Mexico	Pr	NT	8	I, II	19
Echinocereus berlandieri (Engelm.) Haage			LC		III, IV	28
Echinocereus enneacanthus subsp. *brevispinus* (W.O.Moore) N.P.Taylor					III	20
Echinocereus enneacanthus subsp. *enneacanthus* Engelm.					I, II	4
Echinocereus fitchii subsp. *bergmannii* W.Blum	Regional				III, IV	5
**Echinocereus fitchii* subsp. *fitchii* Britton & Rose		A			III	7
Echinocereus knippelianus subsp. *kruegeri* (Glass & R.A.Foster) Glass	Regional	A			II	1
Echinocereus knippelianus subsp. *reyesii* (A.B.Lau) W.Blum & M.Lange	Regional	A			I, II	4
Echinocereus papillosus Linke ex Rümpler			LC		III	7
Echinocereus parkeri subsp. *gonzalezii* (N.P.Taylor) N.P.Taylor	Regional				I, II	7
Echinocereus pectinatus (Scheidw.) Engelm.	Mexico		LC		I	2
Echinocereus pentalophus subsp. *pentalophus* (DC.) Lem.	Mexico		LC	2, 7, 8	I, II, III, IV	40
Echinocereus pentalophus subsp. *procumbens* (Engelm.) W.Blum & M.Lange				1	III, IV	37
Echinocereus poselgeri Lem.		Pr	LC		II, III	25
Echinocereus tulensis Bravo	Regional				I	8
Echinocereus viereckii Werderm.	Tamaulipas		LC	7	II, III, IV	6
**Echinocereus waldeisii* Haugg	Regional	Pr			I	1
Escobaria emskoetteriana (Quehl) Borg			LC	7	III, IV	23
Ferocactus echidne var. *echidne* (DC.) Britton & Rose	Regional		LC	8	I, II	17
Ferocactus echidne var. *victoriensis* (Rose) G.E.Linds.	Tamaulipas			7, 8	II, III, IV	11
Ferocactus glaucescens (DC.) Britton & Rose	Mexico		LC		III	1
Ferocactus hamatacanthus subsp. *hamatacanthus* (Muehlenpf.) Britton & Rose		Pr	LC		I	4
**Ferocactus hamatacanthus* subsp. *sinuatus* (A.Dietr.) N.P.Taylor		Pr		1, 2, 7, 8	II, III, IV	51
Ferocactus histrix (DC.) Lindsay	Mexico	Pr	NT		I, II	4
Ferocactus pilosus (Galeotti ex Salm Dyck) Werderm.	Mexico	Pr	LC		I, II	12
Glandulicactus uncinatus (Pfeiff & Otto) Backeb.	Mexico	A			I	7
Grusonia schottii (Engelm.) H.Rob.			LC		III, IV	12
Homalocephala texensis (Hopffer) Britton & Rose				1	I, II, III, IV	57
Leuchtenbergia principis Hook.	Mexico	A	LC		I	2
Leuenbergeria zinniiflora (DC.) Lodé				2	IV	1
Lophocereus marginatus (DC.) S.Arias & Terrazas	Mexico				I, II	5
**Lophophora koehresii* (Ríha) Bohata, Mysak & Snicer	Regional	A			I	4
Lophophora williamsii (Lem. ex Salm-Dyck) J.M.Coult.		Pr	VU		I, II, III	13
Mammillaria albicoma Boed.	Regional	Pr	EN	7	I, II	4
Mammillaria anniana Glass & R.Foster	Tamaulipas	Pr	CR	9	IV	1
Mammillaria baumii Boed.	Tamaulipas	Pr	LC	7, 8	II	8
Mammillaria bucareliensis var. *tamaulipa* Repp.	Tamaulipas			8	II	3
Mammillaria candida Scheidw.	Mexico	A	LC	7, 8	I, II	20
Mammillaria carmenae Castañeda	Tamaulipas	P	CR	7	II	2
Mammillaria centralifera Repp.	Regional				I, II	13
**Mammillaria* aff. *chionocephala* Purpus	Mexico				I, II	8

(Continued)

Table 1. (Continued)

Mammillaria formosa Galeotti ex Scheidw.	Mexico		LC		I, II	14
Mammillaria giselae Mart.-Aval. & Glass	Tamaulipas				III	1
**Mammillaria glassii* subsp. *nominis-dulcis* (A.B.Lau) U.Guzmán	Regional		LC		II	4
Mammillaria hemisphaerica Engelm.				1, 2	II, III, IV	27
Mammillaria heyderi Muehlenpf.			LC	1	II, III, IV	18
Mammillaria huntiana García-Mor., A.Estrada, Gonz.-Bot. & Vargas-Vázq.	Tamaulipas			7	II	1
Mammillaria klissingiana Boed.	Tamaulipas	A	LC	8	I, II	7
Mammillaria laui subsp. *dasyacantha* (D.R.Hunt) D.R.Hunt	Tamaulipas	P	CR	7	II	1
Mammillaria laui subsp. *laui* D.R.Hunt	Tamaulipas	P	CR	7	II	1
Mammillaria laui subsp. *subducta* (D.R.Hunt) D.R.Hunt	Tamaulipas	P	CR	7	II	3
Mammillaria macracantha DC.	Tamaulipas			7, 8	II	3
Mammillaria meiacantha Engelm.					I, II	11
Mammillaria melaleuca Karw. ex Salm-Dyck	Tamaulipas	A	EN	8	II	4
Mammillaria microthele Muehlenpf.	Regional				I	2
Mammillaria picta Meinsh.	Regional		LC	7, 8	I, II	14
Mammillaria pilispina J.A.Purpus	Regional	Pr	LC	8	I, II	7
Mammillaria plumosa F.A.C.Weber	Mexico	A	NT		IV	1
Mammillaria prolifera subsp. *arachnoidea* (D.R.Hunt) D.R.Hunt	Regional			2, 7	II, III, IV	9
Mammillaria prolifera subsp. *texana* (Engelm.) D.R.Hunt				2, 7, 8	I, II, III, IV	37
Mammillaria roseoalba Boed.	Tamaulipas	Pr	DD	8	II	2
Mammillaria rubrograndis Repp. & A.B.Lau	Tamaulipas	Pr		7	II, III	7
Mammillaria sororia Meinsh.	Tamaulipas			7	II, III	2
Mammillaria sphaerica A.Dietr.			LC	7, 9	II, III, IV	25
Mammillaria surculosa Boed.	Regional	Pr	EN		I	4
**Mammillaria vallensis* Repp.	Regional			2	IV	4
Mammillaria viereckii Boed.	Tamaulipas			7, 8	II	7
Mammillaria zublerae Repp.	Tamaulipas		EN	8	II	3
Myrtillocactus geometrizans (Mart. ex Pfeiff.) Console	Mexico		LC	7, 8	I, II, III, IV	12
Neolloydia conoidea (DC.) Britton & Rose			LC	8	I, II, III, IV	16
**Neolloydia grandiflora* (Link & Otto ex Pfeiff.) F.M.Knuth	Regional			8	I, II	7
Neolloydia inexpectata Donati	Regional				I, II	3
Obregonia denegrii Fric	Tamaulipas	A	EN	8	II	3
**Opuntia aciculata* Griffiths			DD		III, IV	4
**Opuntia* aff. *elizondoana* E.Sánchez & Villaseñor	Mexico			8	II	2
**Opuntia auberi* Pfeiff.			LC	7, 9	II, IV	3
Opuntia cochenillifera (L.) Mill.			DD	1, 8	II, III, IV	11
**Opuntia cuija* (Griffiths & Hare) Rose	Mexico				I, II	17
Opuntia dejecta Salm-Dyck			DD	2, 7, 8, 9	II, III, IV	27
Opuntia dillenii (Ker-Gaw.) Haw.			LC	1, 7, 8	II, III, IV	15
Opuntia engelmannii Salm-Dyck			LC		I, II	12
**Opuntia ficus-indica* (L.) Mill.					I, II	5
**Opuntia glaucescens* Pfeiff.	Regional				I, II	3
**Opuntia gomei* Griffiths					III, IV	17
**Opuntia grandis* Pfeiff.	Regional				I, II	1
**Opuntia guilanchi* Griffiths	Mexico			8	II	3
**Opuntia hyptiacantha* F.A.C.Weber	Mexico		LC		I	2
**Opuntia inaperta* (Schott ex Griffiths) D.R.Hunt	Mexico			2	IV	2
**Opuntia joconostle* F.A.C.Weber	Mexico				I	2
Opuntia karwinskiana Salm-Dyck	Mexico			1	II, IV	7
Opuntia lasiacantha Pfeiff.	Mexico		LC	8	I, II, IV	17
Opuntia leucotricha DC.	Mexico		LC	8	I, II	27
Opuntia lindheimeri Engelm.				1, 6, 7, 8	II, III, IV	45
Opuntia megacantha Salm-Dyck	Mexico				I, II	6
Opuntia megarrhiza Rose	Regional		EN		I, II	3
Opuntia microdasys (Lehm.) Pfeiff.			LC		I, II, III	17
**Opuntia neochrysacantha* Bravo	Mexico				I	2
**Opuntia oligacantha* Pfieff.	Mexico				I, II	2
**Opuntia pachyrrhiza* H.M.Hern., Gómez-Hin. & R.T.Bárcenas	Mexico		EN		I, II	7
Opuntia phaeacantha Engelm.			LC		I, III	6
Opuntia puberula Pfeiff.	Mexico		LC	2, 7	II, III, IV	13
Opuntia pubescens J.C.Wendl. ex Pfeiff.	Mexico		LC	2, 7, 8	II, III, IV	12
Opuntia rastrera F.A.C.Weber	Mexico				I	8
Opuntia robusta J.C.Wendl.	Mexico		LC		I, II	6
**Opuntia spinulifera* Salm-Dyck	Mexico				I, II	4
Opuntia stenopetala Engelm.	Mexico		LC	7, 8	I, II, III	30
Opuntia streptacantha Lem.	Mexico		LC		I, II	4
Opuntia stricta subsp. *esparzae* Scheinvar	Regional			7	II, III	3
**Opuntia stricta* subsp. *stricta* Haw.			LC	1, 2, 7, 8	II, III, IV	52
Opuntia tomentosa Salm-Dyck	Mexico		LC	7, 8	I, II	7
Opuntia × *alta* Griffiths				1	III, IV	3
Opuntia × *andersonii* H.M.Hern., Gómez-Hin. & R.T.Bárcenas	Regional				I	4
**Opuntia zamudioi* Scheinvar	Mexico			7, 8	I, II	11
Pelecyphora strobiliformis (Werderm.) Fric & Schelle	Mexico	A	LC		I	1
Pilosocereus leucocephalus (Poselg.) Byles & G.D.Rowley			LC	1, 2, 7, 8, 9	II, III, IV	38

(Continued)

Table 1. (Continued)

Rapicactus beguinii (N.P.Taylor) Lüthy	Mexico	Pr			I, II	5
Rhipsalis baccifera (J.S.Muell.) Stearn			LC	8	II, IV	9
Selenicereus grandiflorus (L.) Britton & Rose			LC	2, 8	II, IV	16
Selenicereus pteranthus Britton & Rose			DD	2, 8	II, IV	5
Selenicereus spinulosus (DC.) Britton & Rose			LC	1, 2, 7, 8, 9	II, III, IV	35
**Selenicereus undatus* (Haw.) D.R.Hunt	Mexico				II, IV	7
Stenocactus dichroacanthus (C.Mart. ex Pfeiff.) Berger ex Backeb. & Knuth	Mexico				I, II	6
Stenocactus aff. *multicostatus* (Hildm. ex Schum.) Berger ex Backeb. & Knuth	Mexico		DD	7	II	1
Stenocactus pentacanthus (Lem.) Berger ex Backeb. & Knuth	Mexico				I	2
Stenocereus huastecorum Alvarado-Sizzo, Arreola-Nava & Terrazas	Mexico			1, 2, 7, 8, 9	I, II, III, IV	48
Thelocactus bicolor (Galeotti) Britton & Rose		A	LC		I, III	6
**Thelocactus conothelos* subsp. *argenteus* (Glass & R.A.Foster) Glass	Regional				I	1
Thelocactus conothelos subsp. *conothelos* (Regel & Klein) Knuth	Regional		LC		I, II	11
Thelocactus garciae Glass & M.L.Mend.	Tamaulipas				I	1
Thelocactus hexaedrophorus (Lem.) Britton & Rose	Mexico		LC		I	4
Thelocactus schwarzii Backeb.	Tamaulipas	Pr			III, IV	10
Thelocactus setispinus (Engelm.) E.F.Anderson			LC	1	III, IV	31
Thelocactus tulensis (Poselg.) Britton & Rose	Mexico	A	LC		I	10
**Turbinicarpus graminispinus* Matusz., Mysak & Jiruse	Regional				I	1
**Turbinicarpus major* (Glass & R.A.Foster) D.Donati	Regional				I	1
Turbinicarpus nieblae García-Mor., Mart.-Aval. & Bergm.-Beck.	Tamaulipas				III, IV	2
Turbinicarpus pseudopectinatus (Backeb.) Glass & R.Foster	Regional	Pr	LC		I, II	6
Turbinicarpus saueri subsp. *gonzalezii* Pavlícek & Zatloukal	Regional				II, III	2
Turbinicarpus saueri subsp. *nelissae* Halda & Panar.	Tamaulipas				I, II	1
Turbinicarpus saueri subsp. *saueri* (Boed.) V.John & Ríha	Tamaulipas	A	VU		II	2
Turbinicarpus saueri subsp. *verduzcoi* Zachar & Lux	Tamaulipas				I	1
Turbinicarpus schmiedickeanus subsp. *sanchezii-mejoradae* García-Mor., Gonz.-Bot. & Vargas-Vázq.	Tamaulipas				I	2
Turbinicarpus schmiedickeanus subsp. *schmiedickeanus* (Boed.) Buxb. & Backeb.	Tamaulipas	A	NT		I, II	1
Turbinicarpus viereckii subsp. *neglectus* D.Donati & Zanov.	Tamaulipas			8	II	1
Turbinicarpus viereckii subsp. *reconditus* Labhart	Tamaulipas				II	1
Turbinicarpus viereckii subsp. *viereckii* (Werderm.) V.John & Ríha	Tamaulipas	A	LC		II	1
Turbinicarpus ysabelae (Schlange) V.John & Ríha	Tamaulipas	A			I	1

The Cactaceae taxa risk categories are based on the NOM-059 (SEMARNAT 2010) and the IUCN (2021). In addition, we include information about the occurrence of Cactaceae taxa in each NPA and the biogeographical provinces of Morrone et al. (2017). The grid cells record each taxon and endemism level (Mexico, regional – more than two northeastern Mexican states – and Tamaulipas). Those species marked with an asterisk (*) represent new records of Cactaceae for Tamaulipas. Risk categories: NOM-059: A, threatened; P, endangered; Pr, with special protection. IUCN: (CR) critically endangered; (EN) endangered; (VU) vulnerable; (NT) near threatened; (DD) data deficient; (LC) least concern. The ANP's are: 1, Laguna Madre y Delta del Río Bravo; 2, Sierra de Tamaulipas; 3, Playa Rancho Nuevo; 4, Laguna La Escondida; 5, Las Flores; 6, Colonia Parras de la Fuente; 7, Altas Cumbres; 8, El Cielo; 9, Bernal de Horcasitas. The biogeographic provinces are: I, Chihuahuan Desert; II, Sierra Madre Oriental; III, Tamaulipas; IV, Veracruzan.

plains facing the Gulf of Mexico and in the state's center near to the capital city of Ciudad Victoria (Figure 4).

Finally, we revised the Official Mexican Norm NOM-059 (SEMARNAT 2010) to recognize how many Cactaceae of Tamaulipas are listed and verify the corresponding risk category for each species. The NOM-059 is the official document generated by the Mexican government, including threatened species of animals, plants and fungi. In the same sense, the conservation status was also considered according to the Red List of Threatened Species (IUCN 2021).

Results

Based on herbarium specimens examined, web databases, photographic records and specimens collected during fieldwork, we obtain a data matrix with 3698 accession georeferenced records (Figure 3) corresponding to 174 taxa (157 species and 17 subspecies) in 33 genera of cacti. In addition, we found 31 new records of Cactaceae (included in 10 genera and corresponding to 26 species and five subspecies) never registered elsewhere for the state (Table 1).

According to Guerrero et al. (2019), the subfamily Cactoideae is represented by 127 species and infraspecific categories, whereas 46 taxa represent Opuntoideae. Only one species, *Leuenbergeria zinniiflora*, represent Pereskioideae. The genera with the highest species richness are *Opuntia* (40), *Mammillaria* (35), *Echinocereus* (16) and *Turbinicarpus* (14). The remaining 29 genera are represented by one to five species each.

Geographic distribution, richness and endemism

The species found in most grid-cells were *Cylindropuntia leptocaulis* (recorded in 84 grid-cells), *Homalocephala texensis* (57), *Acanthocereus tetragonus* (56), *Opuntia stricta* subsp. *stricta* (52) and *Ferocactus hamatacanthus* subsp. *sinuatus* (51) (Table 1). Other well-represented taxa were *Stenocereus huastecorum* and *Ancistrocactus scheeri*, recorded in 48 and 46 grid-cells, respectively. In contrast, 44 species were recorded only in one or two grid-cells; among these, we found those taxa endemic to Tamaulipas: *Mammillaria anniana*, *Mammillaria carmenae* and *Mammillaria laui* subsp. *laui*. A total of 124

Table 2. Cactaceae taxa cited from Tamaulipas excluded in our study.

Guzmán et al. (2003)	Martínez-Ávalos and Jurado (2005)	Villaseñor (2016)
Ariocarpus fissuratus (Engelm.) K. Schum. in Engl. & Prantl.	*Coryphantha guerkeana* (Boed.) Britton & Rose	*Ariocarpus fissuratus* (Engelm.) K. Schum. in Engl. & Prantl.
Coryphantha pulleineana (Backeb.) Glass	*Coryphantha pulleineana* (Backeb.) Glass	*Astrophytum ornatum* (DC.) F.A.C. Weber ex Britton & Rose
Echinomastus gautii (L.D. Benson) Mosco & Zanovello	*Echinocereus reichenbachii* (Terscheck ex Walp.) Haage	*Aztekium hintonii* Glass & Fitz Maurice
Epithelantha micromeris (Engelm.) F.A.C. Weber ex Britton	*Echinocereus stramineus* (Engelm.) Engelm. ex F. Seitz	*Cephalocereus senilis* (Haw.) Pfeiff.
Grusonia dumetorum (A. Berger) E.F. Anderson	*Echinocereus triglochidiatus* Engelm.	*Coryphantha compacta* Engelm.) Britton & Rose
Mammillaria compressa DC.	*Echinomastus gautii* (L.D. Benson) Mosco & Zanovello	*Coryphantha guerkeana* (Boed.) Britton & Rose
Mammillaria magnimamma Haw.	*Epithelantha micromeris* (Engelm.) F.A.C. Weber ex Britton	*Coryphantha maiz-tablasensis* Backeb.
Mammillaria melanocentra Poselg.	*Grusonia dumetorum* (A. Berger) E.F. Anderson	*Coryphantha pulleineana* (Backeb.) Glass
Mammillaria winterae Boed.	*Mammillaria compressa* DC.	*Coryphantha radians* (DC.) Britton & Rose
Opuntia humifusa (Raf.) Raf.	*Mammillaria glassii* R.A. Foster	*Echinocereus reichenbachii* (Terscheck ex Walp.) Haage
Opuntia macrorhiza Engelm.	*Mammillaria perbella* Hildm. ex K. Schum.	*Echinocereus pulchellus* (Mart.) C.F. Först. ex F. Seitz
Opuntia strigil Engelm.	*Mammillaria winterae* Boed.	*Echinocereus rayonesensis* N.P. Taylor
Turbinicarpus jauernigii Gerhart Frank	*Opuntia humifusa* (Raf.) Raf.	*Echinocereus stramineus* (Engelm.) Engelm. ex F. Seitz
	Opuntia macrorhiza Engelm.	*Echinocereus triglochidiatus* Engelm.
	Opuntia strigil Engelm.	*Echinomastus gautii* (L.D. Benson) Mosco & Zanovello
	Pereskia lychnidiflora DC.	*Epithelantha micromeris* (Engelm.) F.A.C. Weber
	Stenocactus crispatus (DC.) A. Berger ex A.W. Hill	*Ferocactus macrodiscus* (Mart.) Britton & Rose
	Stenocereus pruinosus (Otto ex Pfeiff.) Buxb.	*Geohintonia mexicana* Glass & Fitz Maurice
	Turbinicarpus gielsdorfianus (Werderm.) Vác. John & Ríha	*Mammillaria aureilanata* Backeb.
		Mammillaria cielensis Mart.-Aval., Golubov, S.Arias & Villarreal
		Mammillaria densispina (J.M. Coult.) Orcutt
		Mammillaria erythrosperma Boed.
		Mammillaria geminispina Haw.
		Mammillaria longimamma DC.
		Mammillaria magnimamma Haw.
		Mammillaria melanocentra Poselg.
		Mammillaria orcuttii Boed.
		Mammillaria weingartiana Boed.
		Opuntia humifusa (Raf.) Raf.
		Opuntia macrorhiza Engelm.
		Opuntia strigil Engelm.
		Peniocereus greggii (Engelm.) Britton & Rose
		Pereskiopsis aquosa (F.A.C. Weber) Britton & Rose
		Stenocactus crispatus (DC.) A. Berger ex A.W. Hill
		Stenocactus obvallatus (DC.) Berger ex Backeb. & Knuth
		Turbinicarpus gielsdorfianus (Werderm.) Vác. John & Ríha
		Turbinicarpus hoferi Lüthy & A.B. Lau
		Turbinicarpus subterraneus (Backeb.) A.D. Zimmerman in D.R. Hunt & N.P. Taylor
		Turbinicarpus zaragozae (Glass & R.A. Foster) Glass & A. Hofer ex Glass

taxa are endemic to Mexico (69%), among which 36 taxa are regional endemics (northeastern Mexico), and 34 taxa of Cactaceae are endemic to Tamaulipas (Figure 5); from these, 54 taxa are widespread in Mexico (Table 1).

The distribution of the Cactaceae richness in Tamaulipas is heterogeneous and the richness values of the grid-cells range from one to 51 species. Grid-cells with high richness are concentrated in the southwestern part of the state, related to the Sierra Madre Oriental mountain chain (Figure 6). These richest grid-cells are located at Bustamante, Jaumave, Miquihuana, Palmillas, Tula and Victoria municipalities, located in southwestern Tamaulipas. In contrast, grid-cells with one to six taxa are mainly located in the eastern portion.

Natural protected areas and conservation status

Our analysis shows that six NPAs include at least one species or subspecies of Cactaceae. El Cielo NPA contains the highest number with 48, followed by Altas Cumbres with 43, Sierra de Tamaulipas with 19, Laguna Madre with 17 and Bernal de Horcasitas with eight. In contrast, Colonia Parras de la Fuente includes only one species (Figure 4). We recorded 77 taxa (64 species, 13 subspecies and varieties) in the NPA System; the species recorded in five NPAs are *A. tetragonus*, *Pilosocereus leucocephalus*, *Selenicereus spinulosus* and *S. huastecorum*, whereas taxa recorded in four NPAs are *C. leptocaulis*, *F. hamatacanthus* subsp. *sinuatus*, *Opuntia lindheimeri*, *Opuntia dejecta* and *O. stricta* subsp. *stricta*. In contrast, 44 taxa were recorded only in one NPA (Table 1).

Concerning NPAs without records of Cactaceae within their limits are las Flores and Laguna Escondida, both state NPAs, whereas one federal NPA is the Playa Rancho Nuevo. We counted 97 taxa (76 species and 21 subspecies) that were not recorded in any NPA.

Fifty-three taxa of Cactaceae are included in the NOM-059 (SEMARNAT 2010) (Table 1). Of these, 22 taxa are in the threatened category (A), 25 are in the special protection category (Pr), and six taxa are considered at risk of extinction (P) (abbreviations of each category correspond to those established in the NOM-059 (SEMARNAT 2010). In the case of the IUCN, 96 cacti taxa are recognized under particular conservation categories (see Table 1). Of these, 68 taxa are in the minor concern category (LC), whereas the other categories include less than nine taxa (Table 1 and Figure 5).

Figure 5. Cactus of Tamaulipas endemics (Ed) and/or included in the Red List of the IUCN (CR, LC, EN, DD, NT and VU). First records in Tamaulipas (*). A. *Ariocarpus kotschoubeyanus* subsp. *albiflorus* (Ed); B. *Mammillaria zublerae* (Ed, EN); C. *Echinocereus viereckii* (Ed); D. *Coryphantha vaupeliana* (Ed); E. *Mammillaria klissingiana* (Ed, LC); F. *Mammillaria carmenae* (Ed,CR); G. *Mammillaria laui* subsp. *subducta* (Ed, CR); H. *Mammillaria bucareliensis* var. *tamaulipa* (Ed); I. *Mammillaria baumii* (Ed, LC); J. *Mammillaria giselae* (Ed); K. *Ferocactus echidne* var. *victoriensis* (Ed); L. *Mammillaria huntiana* (Ed); M. *Mammillaria anniana* (CR); N. *Mammillaria laui* subsp. *laui* (Ed, CR); O. *Mammillaria laui* subsp. *dasyacantha* (Ed, CR); P. *Mammillaria viereckii* (Ed); Q. *Mammillaria macracantha* (Ed); R. *Mammillaria rubrograndis* (Ed); S. *Mammillaria roseoalba* (Ed, DD); T. *Mammillaria melaleuca* (Ed, EN); U. *Mammillaria sororia* (Ed); V. *Astrophytum caput-medusae* (CR) ; W. *Mammillaria zublerae* (Ed, EN); X. *Obregonia denegrii* (Ed, EN); Y. *Turbinicarpus schmiedickeanus* subsp. *sanchezii-mejoradae* (Ed); Z. *Turbinicarpus schmiedickeanus* subsp. *schmiedickeanus* (Ed, NT); AA. *Thelocactus schwarzii* (Ed); AB. *Turbinicarpus nieblae* (Ed); AC. *Thelocactus garciae* (Ed); AD. *Turbinicarpus viereckii* subsp. *neglectus* (Ed); AE. *Turbinicarpus saueri* subsp. *saueri* (Ed, VU); AF. *Turbinicarpus saueri* subsp. *nelissae* (Ed); AG. *Turbinicarpus viereckii* subsp. *reconditus* (Ed); AH. *Mammillaria glassii* subsp. *nominis-dulcis* (*); AI. *Turbinicarpus ysabelae* (Ed); AJ. *Cylindropuntia rosea* (*); AK. *Echinocereus fitchii* (*); AL. *Echinocereus waldeisii* (*); AM. *Ferocactus hamatacanthus* subsp. *sinuatus* (*); AN. *Mammillaria* aff. *chionocephala* (*); AO. *Lophophora koehresii* (*); AP. *Mammillaria vallensis* (*); AQ. *Turbinicarpus viereckii* subsp. *viereckii* (Ed, LC); AR. *Turbinicarpus saueri* subsp. *verduzcoi* (Ed); AS. *Opuntia aciculata* (*); AT. *Neolloydia grandiflora* (*); AU. *Opuntia* aff. *elizondoana* (*); AV. *Opuntia oligacantha* (*); AW. *Opuntia ficus-indica* (*); AX. *Opuntia auberi* (*); AY. *Opuntia pachyrrhyza* (*); AZ. *Opuntia gomei* (*); BA. *Opuntia grandis* (*); BB. *Opuntia glaucescens* (*); BC. *Opuntia inaperta* (*); BD. *Opuntia guilanchi* (*); BE. *Opuntia spinulifera* (*); BF. *Opuntia joconostle* (*); BG. *Opuntia zamudioi* (*); BH. *Thelocactus conothelos* subsp. *argenteus* (*); BI. *Opuntia stricta* (*); BJ. *Selenicereus undatus* (*); BK. *Turbinicarpus graminispinus* (*); BL. *Turbinicarpus major* (*); BM. *Opuntia cuija* (*). Photo credits: L. García-Morales, except M: W. Ten Hoeve and AG: C. Pérez-Badillo.

Figure 5. Continued.

Finally, we did not find herbaria specimens of the taxa mentioned in Table 2 and our systematic fieldwork does not support their presence in Tamaulipas. In this sense, Guzmán et al. (2003) cited 13 taxa, Martínez-Ávalos and Jurado (2005) cited 19 and Villaseñor (2016) cited 39. Furthermore, except for the specimens of Martínez-Ávalos and Jurado (2005), the above authors did not provide additional data or reference vouchers for collating purposes nor discussion and references about the identity of these specimens.

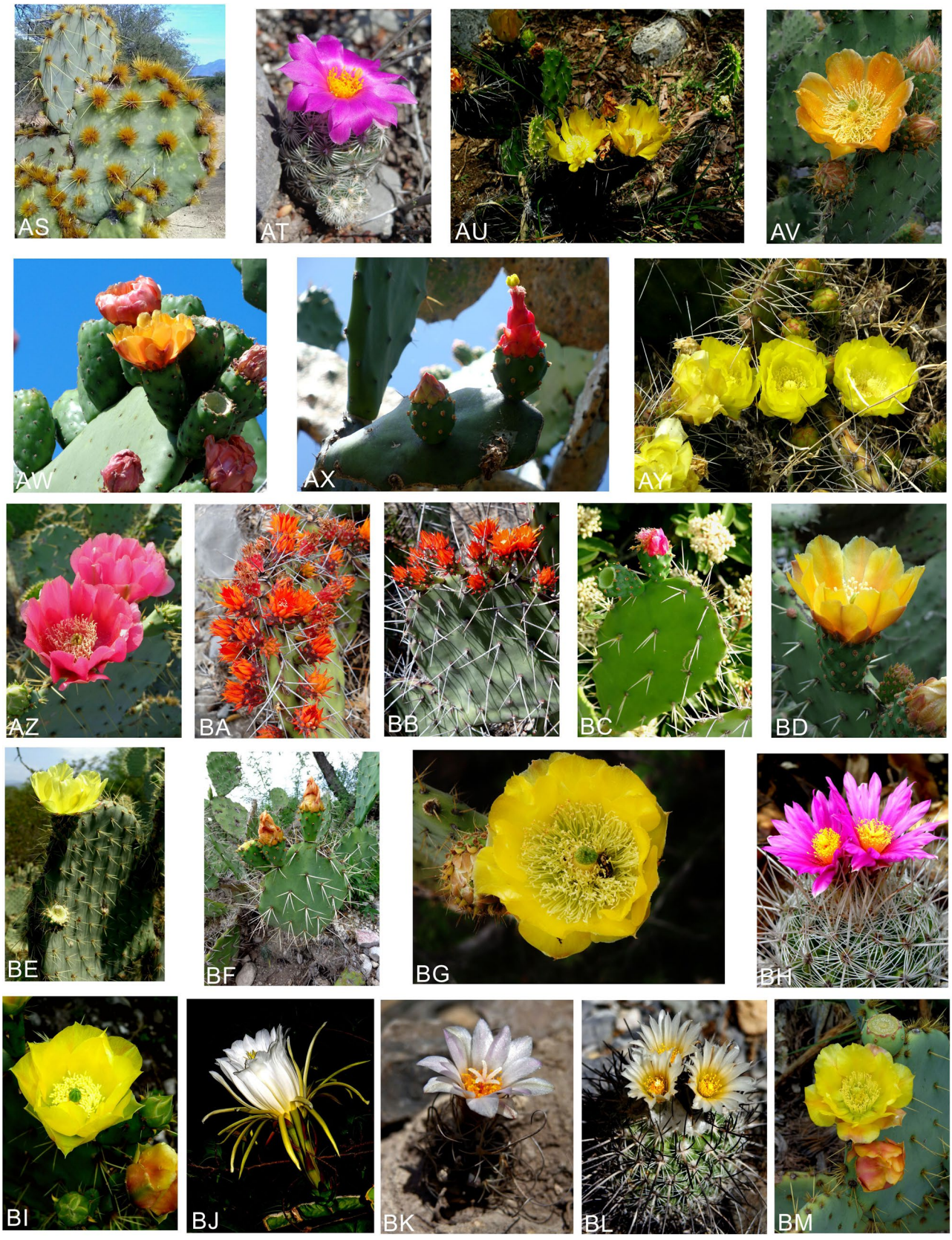

Figure 5. Continued.

Discussion

Four biogeographic provinces coincide in Tamaulipas *sensu* Morrone et al. (2017): two lowland areas, one mountain and one xerophytic. Thus, the complex geologic past and the biogeographical history created a heterogeneous mosaic of conditions allowing the development of different vegetation types. In this sense, we confirm Tamaulipas as a nodal area (Luna-Vega et al. 2000) because it is located at the boundaries among four different biogeographic regions and

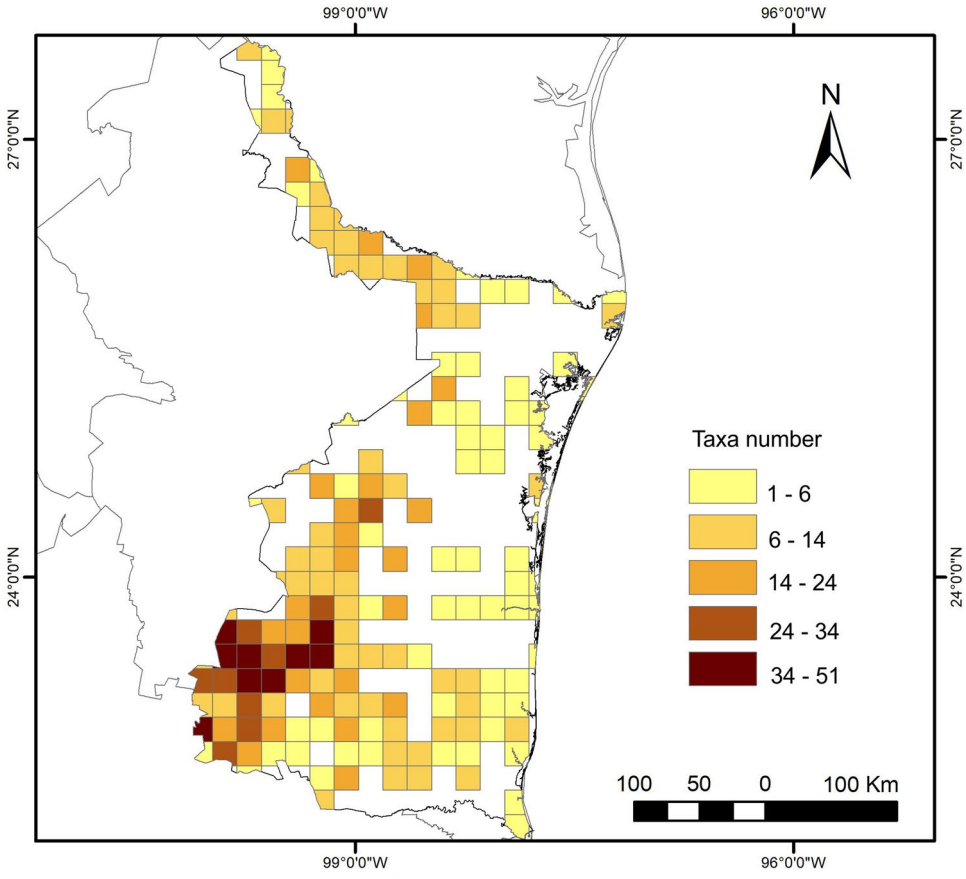

Figure 6. Grid cells and taxa richness of Cactaceae in Tamaulipas.

represents zones of biotic overlap promoted by historical and ecological changes allowing the mixture of different biotic elements. Therefore, this state includes more than 4000 species of vascular plants (Villaseñor 2016) and is considered among the more diverse Mexican states, mainly in Cactaceae.

In the last 20 years, the representativeness of Cactaceae taxa in Tamaulipas in local herbaria (as is the case of the ITCV) has increased substantially, adding 31 new records not mentioned in the Mexican Cactus Inventory (Guzmán et al. 2003), the checklist of Cactaceae (Martínez-Ávalos and Jurado 2005) and the checklist of Mexican vascular plants (Villaseñor 2016). Thus, our new checklist (Table 1) updates the nomenclature and Cactaceae taxa numbers following the recent phylogenetic and monographic studies.

Guzmán et al. (2003) recorded three most species-rich genera in Tamaulipas: *Mammillaria* (160 in Mexico; 35 in Tamaulipas), *Opuntia* (83/40) and *Echinocereus* (56/16). This situation is also presented in other Mexican northern states, such as Chihuahua (Lebgue-Keleng and Quintana-Martínez 2013) and Durango (González-Elizondo et al. 2017). *Mammillaria* and *Echinocereus* stand out in the flora of Tamaulipas because they represent about one-quarter of the total known taxa from Mexico, whereas *Opuntia* species represent nearly 50%.

Our field explorations in the last years allowed us to recognize a greater number of *Opuntia* species in Tamaulipas. Guzmán et al. (2003) cited 14 species and four subspecies, whereas Martínez-Ávalos and Jurado (2005) listed 13 species and four subspecies. Furthermore, in our study, we found in Tamaulipas several taxa of *Mammillaria* not previously reported in this state. Thus, the taxa richness in this genus also increased because 23 species and 8 subspecies were cited by Guzmán et al. (2003), and 23 species and 21 subspecies were reported by Martínez-Ávalos and Jurado (2005).

Guzmán et al. (2003) argued that the Cactaceae family in Tamaulipas is represented by 62 genera and 108 species, representing 54% of genera and 16% of species represented in Mexico. On the other hand, Hunt et al. (2006) registered in their checklist of Cactaceae 80 of the 593 species (13%) and 30 of the 50 genera (60%). Finally, the checklist of Mexican vascular plants of Villaseñor (2016) records for the state 154 species and 39 genera of Cactaceae, representing 65% of the genera and 23% of the species in Mexico. Therefore, after analyzing the most representative studies on Cactaceae and the inclusion of our results, we conclude that Tamaulipas harbors a high proportion of the Mexican Cactaceae, ranging from 54% to 65% at the genus level (more than 50% of the represented genera in the Mexican territory) and 13–23% from the species and infraspecific taxa level.

Finally, our extended, systematic fieldwork does not support the presence of many taxa cited by local and national lists. For example, we did not find herbarium vouchers that support their presence in Tamaulipas nor photographic records in the Naturalista platform (www.naturalista.mx) that allow us the inclusion of any other cacti within our final checklist. Therefore, we corrected the names of herbarium vouchers species (Table 2). From this point of view, Guzmán et al. (2003) cited 13

misidentified taxa, Martínez-Ávalos and Jurado (2005) cited 19 and Villaseñor (2016) cited 39. Unfortunately, these authors omitted the localities for these taxa or/and herbarium vouchers revised to resolve their taxonomic identity.

Certain species like *Opuntia humifusa*, *Opuntia macrorhiza* and *Opuntia strigil* have been cited by Bravo-Hollis (1978) as probably represented in Mexico, without references in herbaria. We found a single photographic record of *O. humifusa* in the Naturalista platform (https://www.naturalista.mx/observations/36179469), but it was impossible to confirm its identity. The type of *Grusonia dumetorum* resulted in a synonym of *Opuntia pubescens* (POWO 2022). *Echinomastus gautii* is a synonym of *Echinomastus warnockii,* an endemic species from the northern part of the Chihuahuan Desert (POWO 2022). *Epithelantha micromeris* and *Ariocarpus fissuratus* are not present in Tamaulipas (Korotkova et al. 2021). The records of *Coryphantha guerkeana* from Tamaulipas cited by Martínez-Ávalos and Jurado (2005) are misidentified, corresponding to *Coryphantha delicata* according to the UAT vouchers revisited. The *Coryphantha pulleineana* records cited by Guzmán et al. (2003) and Martínez-Ávalos and Jurado (2005) correspond with *Coryphantha wohlschlageri* according to the UAT vouchers revision; *C. pulleineana* is a microendemic species from the area of El Huizache, northern San Luis Potosí. The records of *Mammillaria compressa*, *Mammillaria glassii*, *Mammillaria magnimamma*, *Mammillaria melanocentra*, *Mammillaria perbella* and *Mammillaria winterae* are misidentifications for *Mammillaria centralifera*, *M. glassii* subsp. *nominis-dulcis*, *Mammillaria macracantha*, *Mammillaria rubrograndis*, *Mammillaria microthele* and *Mammillaria roseoalba,* respectively. *Turbinicarpus jauernigii* is a well-known microendemic species from the northern part of San Luis Potosí, cited by some authors from Tamaulipas based in approximate highway locations. *Turbinicarpus gielsdorfianus* is known only from a single location in the San Luis Potosí state. The records of *Echinocereus reichenbachii* reported by Martínez-Ávalos and Jurado (2005) are misidentifications for *Echinocereus fitchii* subsp. *fitchii* and *E. fitchii* subsp. *bergmanii* (Blum et al. 2005). The records of *Echinocereus stramineus* and *Echinocereus triglochidiatus* are misidentifications for *E. ennecanthus* subsp. *brevispinus* and *Echinocereus viereckii*. The record of *Pereskia lycnhindiflora* is probably a misidentification of *Leuenbergeria ziniiflora*. The records of *Stenocereus pruinosus* corresponds to the recently described *S. huastecorum* (Alvarado-Sizzo et al. 2018). *Stenocactus crispatus* is a wrong identification of *S. dichroacanthus*; *S. crispatus* inhabits the Mexican Plateau.

Several records from the Villaseñor checklist (2016) are excluded from our study since he included undocumented species from Tamaulipas (as is the case of *A. fissuratus*, *C. guerkeana*, *C. pulleineana*, *E. reichenbachii*, *E. stramineus*, *E. triglochidiatus*, *E. gautii*, *E. micromeris*, *M. magnimamma*, *M. melanocentra*, *O. humifusa*, *O. macrorhiza*, *O. strigil*, *S. crispatus* and *T. gielsdorfianus*). Another excluded species from this cited checklist are the records of *Astrophytum ornatum*, an endemic species from the arid regions of Hidalgo, Querétaro and Guanajuato (Hernández and Gómez-Hinostrosa 2011, Vázquez-Lobo et al 2015). *Aztekium hintonii* and *Geohintonia mexicana* live together in a narrow habitat of gypsum hills in Galeana, Nuevo León, not yet found in the neighboring Tamaulipas border (Hernández and Gómez-Hinostrosa 2011). *Cephalocereus senilis* is a well-known endemic species from the states of Hidalgo and Veracruz (Tapia et al. 2017). *Coryphantha compacta* is endemic from Chihuahua, Durango and Sonora, meanwhile *C. maiz-tablasensis* is endemic to some gypsum flats in San Luis Potosí and southern Nuevo León. *Coryphantha radians* is now a synonym of *C. cornifera* (DC.) Lem., an endemic species to Central Mexico (Dicht and Luthy 2005). *Echinocereus pulchellus* is endemic to the states of Hidalgo and Puebla (Sánchez et al. 2020). *Echinocereus rayonesensis* is endemic to the Galeana, Iturbide and Rayones municipalities, Nuevo León (Felix and Blum 2011). *Ferocactus macrodiscus* is endemic and present from Central Mexico to Oaxaca (Bravo-Hollis and Sánchez-Mejorada 1991b). *Mammillaria aureilanata*, *Mammillaria erythrosperma* and *Mammillaria orcuttii* are endemic species to San Luis Potosí (Hernández and Gómez-Hinostrosa 2015), meanwhile *Mammillaria densispina* is known only from Aguascalientes, Durango, Guanajuato, Jalisco, Querétaro, San Luis Potosí and Zacatecas (Linzen 2020). *Mammillaria geminispina* is known from Hidalgo and Querétaro, *Mammillaria longimamma* from Guanajuato, Hidalgo and Querétaro and *M. weingartiana* is a narrow endemic to the grasslands in Galeana, Nuevo León (Linzen 2020). *Mammillaria cielensis* is considered now a synonym of *Mammillaria zublerae* (POWO 2022). *Peniocereus greggii* is another endemic species of the northern part of the Chihuahuan Desert, not yet found in Tamaulipas (Arias et al. 2005). *Pereskiopsis aquosa* is an introduced species found in several house backyards from the Jaumave Valley (García-Morales 2006). *Stenocactus obvallatus* is another endemic from central Mexico (Bravo-Hollis and Sánchez-Mejorada 1991b). Finally, *Turbinicarpus hoferi*, *T. subterraneus* and *T. zaragozae* (the latter two now transferred to *Rapicactus sensu* Donati and Zanovello (2004) and Vázquez-Sánchez et al. (2019) have a limited distribution in the state of Nuevo León.

According to the data analyzed and recent field observations, we propose new conservation assessments and their potential inclusion within the NOM-059 (SEMARNAT 2010) and the IUCN Red List of threatened species (2021) for the following taxa: *Cephalocereus euphorbioides*, *Coryphantha macromeris* subsp. *runyonii*, *Coryphantha sulcata*, *Coryphantha vaupeliana*, *Echinocereus papillosus*, *Mammillaria bucareliensis* var. *tamaulipa*, *M. giselae*, *M. glassii* subsp. *nominis-dulcis*, *M. huntiana*, *M. zublerae*, *Thelocactus conothelos* subsp. *argenteus*, *Thelocactus garciae*, *Turbinicarpus graminispinus*, *T. major*, *T. nieblae*, *T. saueri* subsp. *gonzalezii*, *T. saueri* subsp. *nelissae*, *T. saueri* subsp. *verduzcoi*, *T. schmiedickeanus* subsp. *sanchezii-mejoradae*, *T. viereckii* subsp. *neglectus* and *T. viereckii* subsp. *reconditus*.

At the same time, new conservation assessments are imperative for previously included species within the NOM-059 (SEMARNAT 2010), as recent field surveys suggest rapid population and habitat changes have occurred for the following taxa in Tamaulipas: *Ariocarpus agavoides*, *Ariocarpus kotschoubeyanus* subsp. *albiflorus*, *Astrophytum asterias*, *A. caput-medusae*, *M. anniana*, *M. carmenae*, *M.*

laui subsp. *laui*, *M. laui* subsp. *dasyacantha*, *M. laui* subsp. *subducta*, *Obregonia denarii*, *Turbinicarpus saueri* subsp. *saueri*, *T. schmiedickeanus* subsp. *schmiedickeanus* and *T. ysabelae*.

The percentage of endemic cacti in Tamaulipas is high (20%), highlighting new diversity, ecological, biogeographical and molecular studies. Thirty-four taxa are restricted to Tamaulipas, and 22 are narrowly restricted to a single or few localities (Table 1). These microendemic taxa are: *M. anniana, M. baumii, M. bucareliensis* var. *tamaulipa, M. carmenae, M. giselae, M. huntiana, M. laui, M. laui* subsp. *dasyacantha, M. laui* subsp. *subducta, M. roseoalba, Obregonia denegrii, Thelocactus garciae, Turbinicarpus nieblae, T. saueri, T. saueri* subsp. *nelissae, T. saueri* subsp. *verduzcoi, T. schmiedickeanus, T. schmiedickeanus* subsp. *sanchezii-mejoradae, T. viereckii, T. viereckii* subsp. *neglectus, T. viereckii* subsp. *reconditus* and *T. ysabelae*.

Tamaulipas has only three federal NPAs decreed by the Mexican government in contrast with the neighboring states of San Luis Potosí and Veracruz, both with six NPAs (SEMARNAT-CONANP 2020). We recorded 28 cacti in only two NPAs showing low representativeness, coinciding with other taxa of the Mexican biota (Vázquez and Valenzuela-Galván 2009 with mammals). In contrast, the state NPAs in Tamaulipas play a significant role in Cactaceae conservation as 67 taxa were found inside their limits.

A high proportion of species of Cactaceae are included in National and International lists at different risk categories (Álvarez et al. 2004). The main threats of cacti are their characteristically slow growth rates and long-life cycles. Several species only grow in particular environmental conditions and have greatly restricted distributions, with low population densities, recruitment, rates of seed germination, and seedling survival (Álvarez et al. 2004; González-Elizondo et al. 2017). Fifty-three cacti from Tamaulipas (30%) are included in a risk category in the NOM-059 (SEMARNAT 2010), and ninety-six (55%) in the Red Lists of the IUCN (2021). Sixty-eight cacti are included in the least concern category (LC). The six taxa under the critically endangered (CR) category are *Astrophytum caput-medusae, M. anniana, M. carmenae* and the three subspecies of *M. laui*. The last three species of *Mammillaria* endemic to Tamaulipas are found within the state NPA system, particularly well represented in the Altas Cumbres Natural Protected Area with two species and two subspecies (García-Morales, Estrada Castillón, García-Jiménez, et al. 2014).

This study updates and provides new information about the geographic distribution of the cacti inhabiting Tamaulipas. We listed here 31 new records from Tamaulipas never registered by other authors, highlighting the richness of taxa and areas with high endemism, essential for conservation plans and management purposes.

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Disclosure statement

The authors reported no potential conflict of interest.

ORCID

Leccinum J. García-Morales http://orcid.org/0000-0003-0907-0673
Jesús García-Jiménez http://orcid.org/0000-0001-9290-1460

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