

## DIVERSITY OF CACTACEAE IN THE FLORA OF BAJÍO AND ADJACENT REGIONS (MEXICO)

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### Abstract

**Background:** Recent floristic lists indicate that the Mexican Bajío is a diverse area in terms of the number of species and endemism of Cactaceae.

**Questions and/or Hypotheses:** 1) How many taxa are distributed in the Bajío and adjacent regions? 2) What are the vegetation types and biogeographic provinces with the greatest species richness? 3) What are the areas with the highest level of endemism?

**Studied species:** Cactaceae family.

**Study site and dates:** Bajío region (Guanajuato, Querétaro and northern part of Michoacán), México, which was visited between 2014 and 2022.

**Methods:** With the use of herbarium, field collections and iNaturalist/iNaturalistMX records, a database was constructed from which species richness, weighted endemism and weighted endemism corrected by one-third degree cells were estimated.

**Results:** Thirty genera and 125 species of cacti are reported. Xerophilous scrub is the type of vegetation that hosts the greatest number of species. The Chihuahuan Desert is the province with the highest level of richness. The cells with the highest richness and weighted endemism are found between the provinces of the Chihuahuan Desert and the Sierra Madre Oriental. In contrast, there is a decrease toward the Trans-Mexican Volcanic Belt.

**Conclusions:** Of the three biogeographic provinces that converge in the Bajío region—the Trans-Mexican Volcanic Belt, the Chihuahuan Desert, and the Sierra Madre Oriental—the largest number of endemic species is found on the borders between the latter two, likely because this region was a climatic refuge during the Pleistocene.

**Keywords:** Bajío and adjacent regions, Chihuahuan Desert, species richness, Sierra Madre Oriental.

### Resumen

**Antecedentes:** Trabajos florísticos recientes indican que el Bajío mexicano es una zona diversa en número de especies y endemismos de Cactaceae.

**Pregunta y/o Hipótesis:** ¿Cuántos taxones se distribuyen en el Bajío y regiones adyacentes? 2) ¿Cuáles son los tipos de vegetación y provincias biogeográficas con mayor riqueza de especies? 3) ¿Cuáles son las áreas con mayor nivel de endemismos?

**Especie de estudio:** Familia Cactaceae.

**Sitio y fechas de estudio:** Región del Bajío (Guanajuato, Querétaro y porción septentrional de Michoacán) México, visitada entre 2014 y 2022.

**Métodos:** Con registros de herbario, colectas en campo y observaciones en iNaturalist/iNaturalistMX se construyó una base de datos a partir de la cual se estimó la riqueza de especies, el endemismo ponderado y el endemismo ponderado corregido por celdas de un tercio de grado.

**Resultados:** Se reportan 30 géneros y 125 especies de cactáceas. El matorral xerófilo alberga la mayor cantidad de especies. El Desierto Chihuahuense resultó la provincia con mayor nivel de riqueza. Las celdas con mayor riqueza y endemismo ponderado se encuentran en los límites entre las provincias del Desierto Chihuahuense y la Sierra Madre Oriental. En contraparte, hay un descenso hacia la Faja Volcánica Transmexicana.

**Conclusiones:** De las tres provincias biogeográficas que convergen en la región del Bajío—la Faja Volcánica Transmexicana, el Desierto Chihuahuense y la Sierra Madre Oriental— el mayor número de especies endémicas se encuentra en los límites entre estas dos últimas, probablemente porque esta región fue un refugio climático durante el Pleistoceno.

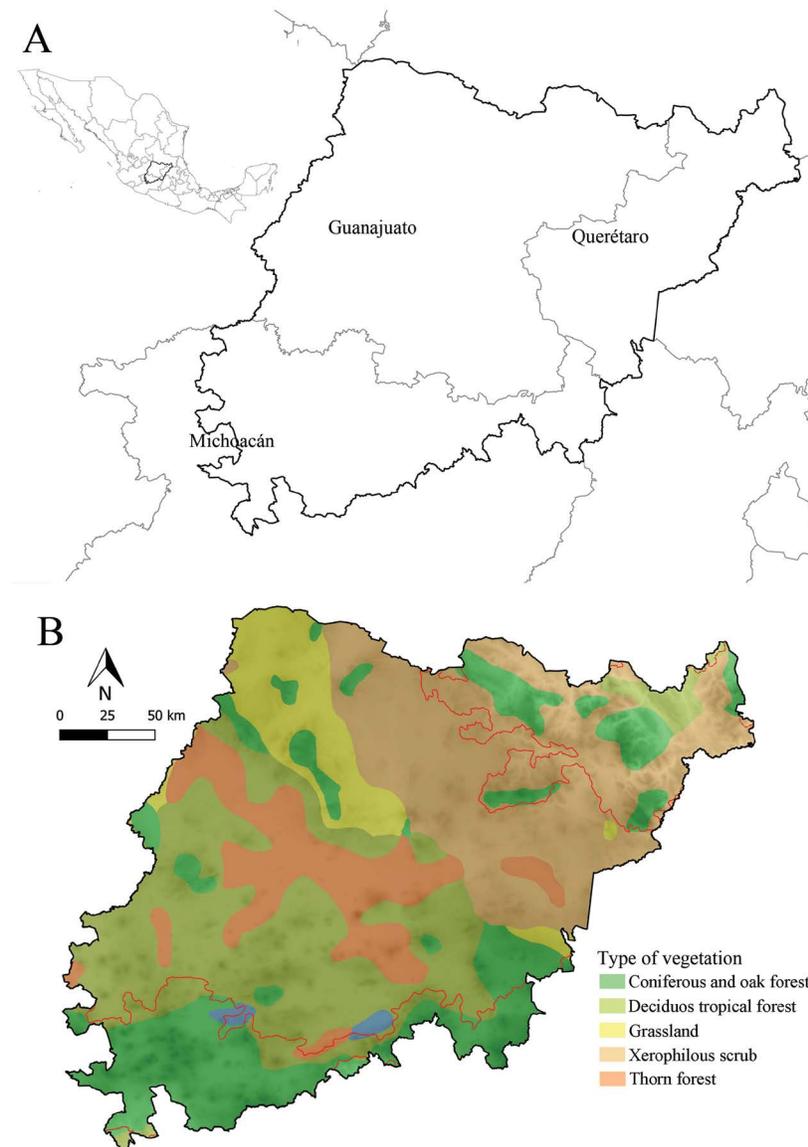
**Palabras clave:** Bajío y regiones adyacentes, Desierto Chihuahuense, riqueza de especies, Sierra Madre Oriental.

**F**loras and floristic lists remain relevant as part of broad taxonomic work; these lists allow us to increase knowledge about plant diversity, offering more and better information to other biological disciplines and addressing current socio-environmental problems with greater discernment, such as the climate change crisis, endangered species or invasive species (Agababian *et al.* 2013, Morrone 2013, Villaseñor & Meave 2022). Since 1991, a continuous effort has been made in the Flora of Bajío (FBRA 2025), with more than 140 taxonomic treatments of families coordinated by Instituto de Ecología A.C. This effort is due in part to the fact that the change in land use is constant (Villaseñor & Ortiz 2012). Cactus-floristic studies for the region include the contribution of Bárcenas (1999), who recorded 20 genera and 92 species in Guanajuato. Hernández *et al.* (2004) documented 90 species in Guanajuato and 93 in Querétaro. Scheinvar (2004) reported 30 genera and 112 species in Querétaro, and Sánchez-Martínez *et al.* (2006) reported ca. 18 genera and 54 species in the arid zone of Querétaro. A comparative analysis carried out by Rzedowski & Bedolla (2021) revealed that Cactaceae contributes 2.4 % to the total richness of vascular plant species in the Flora of Bajío, which confirms the floristic importance of Cactaceae in this region. More recently, Arias & Aquino (2019) and Arias *et al.* (2024) reported 28 genera and 110 wild species of the Flora of Bajío, excluding species introduced: *Opuntia auberi* Pfeiff., *O. cochenillifera* (L.) Mill., *O. ficus-indica* (L.) Mill., *O. megacantha* Salm-Dyck, *O. undulata* Griffiths and *Selenicereus undatus* (Haw.) D. R. Hunt. Additionally, a significant portion of species from the region have been the subject of study; for example, Santa-Anna-del-Conde *et al.* (2009) carried out an analysis of endemism considering only the species listed in the NOM-059 (SEMARNAT-2001) distributed in the Sierra Madre Oriental; from a core from the eastern portion of the territories of Hidalgo, Guanajuato and Querétaro, the authors reported ca. seven endemic species distributed in this mountain chain. Further, recent phylogenetic and species delimitation analyses in Cactaceae (*e.g.*, Vázquez-Sánchez *et al.* 2019, Baker 2022, Franco 2020, Franco-Estrada *et al.* 2022, Rosas-Reinhold *et al.* 2022), as well as new taxa discovered in the region (González-Zamora *et al.* 2023a,b, Aquino *et al.* 2024), confirm that floristic knowledge of Mexico, particularly the Flora of Bajío, is dynamic and actively advancing. The vulnerability faced by this family originates from anthropogenic activities, such as the expansion of agriculture and livestock, residential development, and the collection of live plants and seeds for the horticultural trade (Hernández-Oria *et al.* 2007, Goettsch *et al.* 2015). Therefore, based on an updated list, the objectives of this contribution are 1) determine how many taxa are distributed in the Bajío and adjacent regions, 2) which types of vegetation and biogeographic provinces contain the greatest richness of species, and 3) which are the areas with the highest level of endemism.

## Materials and methods

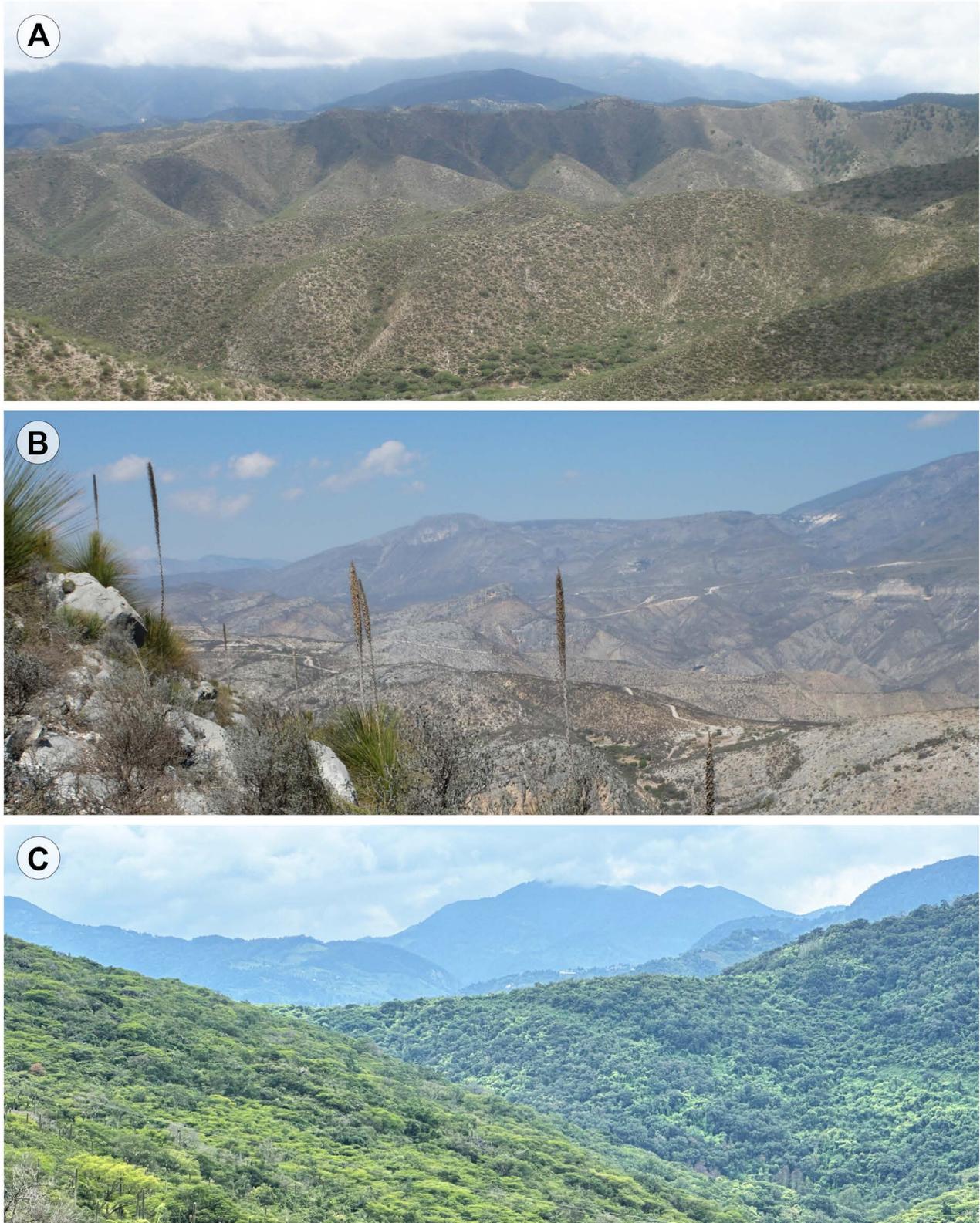
**Study area.** The Flora of Bajío includes that found in the states of Guanajuato and Querétaro in its entirety (46 and 18 municipalities respectively) and the northeastern part of the state of Michoacán (53 municipalities), delimited by the areas located east of the meridian 102° 10 ' W (Figure 1A, Villaseñor & Ortiz 2012). Xerophilous scrub has been recorded in large areas in the municipalities of San Luis de la Paz, Santa Catarina and Victoria in Guanajuato (Figure 2A, Rzedowski & Galván 1996). In Querétaro, this vegetation extends into the municipalities of Tolimán, Peñamiller and Cadereyta de Montes (Figures 1B and 2B, Rzedowski *et al.* 2012). The xerophilous scrub is found mainly in the Chihuahuan Desert, but also extends into areas within the Trans-Mexican Volcanic Belt in the foothills near Morelia, Michoacán (Contreras & Silva 2020). Deciduous tropical forests are present in Querétaro and Guanajuato; in the first cover the municipalities of Jalpan and Landa, but isolated patches have been also recorded in Tequisquiapan, San Juan del Río and Querétaro (Figures 1B and 2C, Zamudio *et al.* 1992). In Guanajuato, this vegetation type has been observed in the ravines of the municipalities of Xichú, Atarjea and Victoria, which correspond to Sierra Gorda, which is part of the Sierra Madre Oriental, as well as some remnants toward the central area of the state (Figures 1B, 3A, and 3B, Rzedowski & Galván 1996, Zamudio 2012, Rzedowski & Calderón 2013). The thorn forests extend into the municipalities of San Juan del Río, Pedro Escobedo and Querétaro. In addition, there is a strip of thorn forests that extends toward the states of Guanajuato and parts of Michoacán, surrounding the Trans-Mexican Volcanic Belt (Figure 1B, Rzedowski 2006, Zamudio 2012). The *Quercus* forests, associated or not associated with conifers, such

as *Pinus* and *Abies*, are distributed in Guanajuato on the Sierra Gorda, Sierra de Pénjamo and Agustinos; (Figures 1B and 3C, Zamudio 2012). In Querétaro, this type of vegetation is distributed toward the mountain ranges of Pinal de Amoles, San Joaquín, Arroyo Seco, Jalpan and Landa, extending toward Guanajuato in the municipalities of Xichú and Atarjea. Overall, the floristic composition indicates the influence of the Sierra Madre Oriental (Argüelles *et al.* 1991, Rzedowski *et al.* 2012, Zamudio 2012). *Quercus* and *Pinus* forests have been recorded to a lesser extent toward Amealco, which includes the Sierra del Rincón, whose extension reaches the northern part of Michoacán (Cabrera-Luna *et al.* 2015). The grassland is located in a small strip within the municipalities of San Juan del Río (Chihuahuan Desert), as well as in Amealco and Huimilpan (Trans-Mexican Volcanic Belt), although in some cases, the grassland was likely induced (Figure 3D, Zamudio *et al.* 1992).

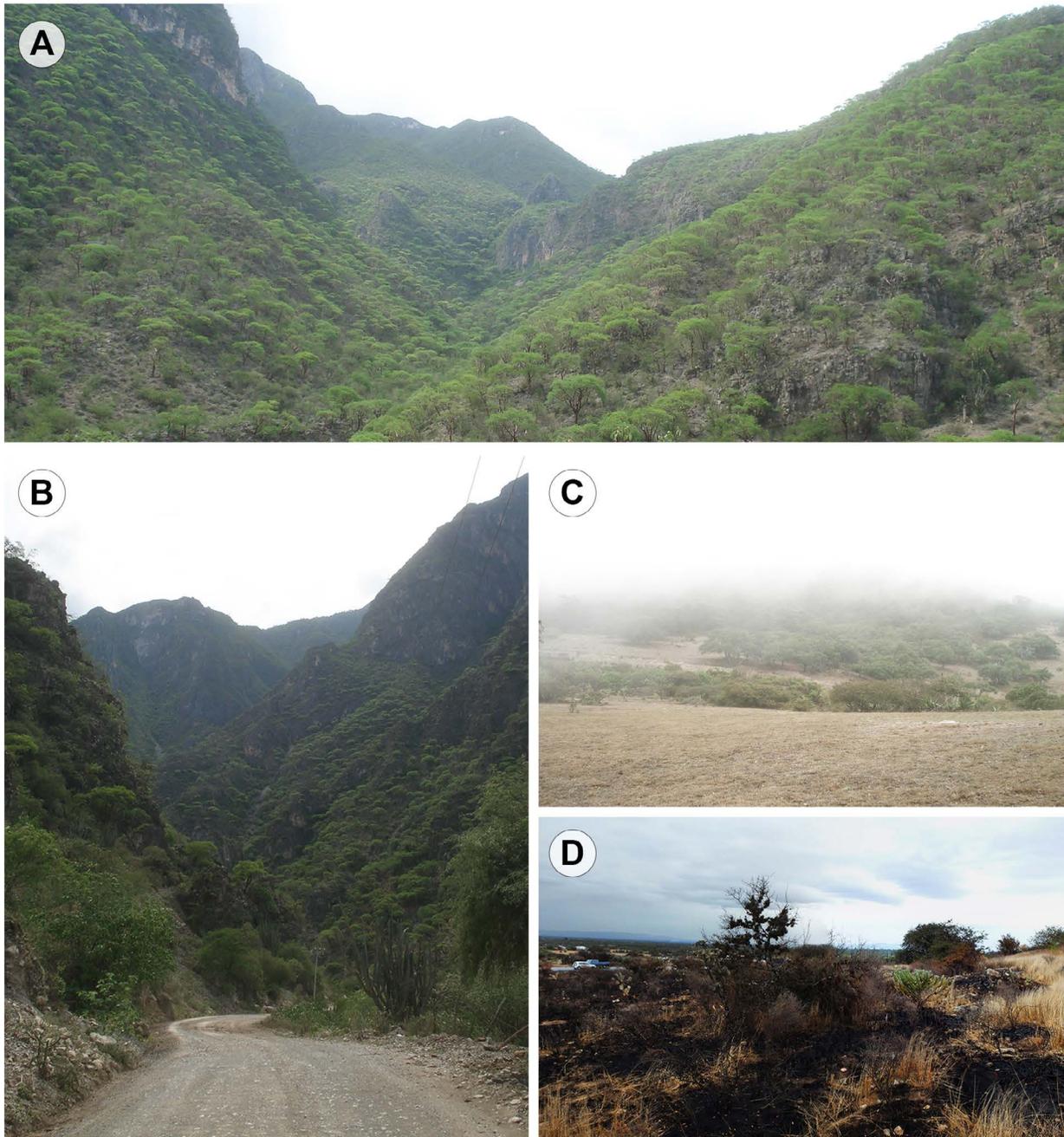


**Figure 1.** A. Flora of Bajío and adjacent regions, Mexico. The gray line indicates the state division, the bold black line indicates the boundaries of the Bajío Region. B. Map of vegetation types. The background shade shows the altitudinal range (light = low, dark = high). The red line indicates the biogeographic provinces. The northeast polygon is the Sierra Madre Oriental, the central polygon is the Chihuahuan Desert, and the southwest polygon is the Mexican Transvolcanic Belt. The blue polygons are water bodies.

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**Figure 2.** Vegetation types in the Bajío and adjacent regions. A. Xerophilous scrub in Atarjea, Gto., and B. Cadereyta de Montes, Qro. C. Tropical deciduous forest in Jalpan, Qro. Photo. D. Aquino (A, B), S. Arias (C).



**Figure 3.** Vegetation types. A, B. Tropical deciduous forest in Xichú, Gto. C. Secondary grassland with *Quercus* forest in the background in Santa Catarina, Gto. D. Xerophilous scrub disturbed to induce grasslands in San José Iturbide, Gto. Photo. D. Aquino.

*Field work.* Routes were established in the Flora del Bajío region between 2014 and 2022. Based on the type of vegetation and state of conservation of the locality, surveys were carried out in an area of approximately 500 m<sup>2</sup> of land and were inspected to locate individuals belonging to the Cactaceae family (Aquino & Arias 2010). For each location, the geographic position was recorded via a Garmin eTrex Vista H WGS84 geopositioner, photographs were taken, one or two samples of the Cactaceae' species found were collected, and phenological events were recorded. The collected samples were herborized and deposited in MEXU and IBUG (Thiers *et al.* 2023).

**Database.** A database was developed from the field collections and the herbarium records from ANSM, ASU, CIMI, ENCB, FEZA, IBUG, IEB, IZTA, MEXU, QMEX and UAMIZ (Thiers *et al.* 2023). Upon completion of herbarium and field work, three observations corresponding to species not listed in previous works (Arias & Aquino 2019) were added from iNaturalistMX (2023). The identification of the samples was carried out using the treatment for the Cactaceae family of the Flora del Bajío (Arias & Aquino 2019, Arias *et al.* 2024). The names were updated following the proposal of Korotkova *et al.* (2021). Additionally, recent taxonomic revisions were considered: *Coryphantha* (Engelm.) Lem. (Sánchez *et al.* 2022), *Echinocactus* Link & Otto (Vargas-Luna *et al.* 2018, Baker 2022) and *Stenocactus* (K.Schum.) A.Berger (Franco 2020). Cultivated species were excluded from the analyses.

**Analysis of richness and endemism.** Cactaceae richness was calculated by municipal political divisions (INEGI 2019), vegetation types (Rzedowski 2006) and biogeographic provinces (Morrone *et al.* 2017). In the present study, an endemism is a taxon restricted to the Bajío (Morrone 2008). To identify centers of endemism, weighted endemism (WE) was calculated, taking grid cells as the unit of comparison (Noguera-Urbano 2017). Furthermore, CWE seeks to reduce the correlation between species richness and endemism (Crisp *et al.* 2001, Noguera-Urbano 2017). Finally, the distribution of endemic taxa in the Flora of Bajío was represented in relation to the richness estimates. The visualization and editing of the maps were performed using QGIS 3.2.2 (QGIS Development Team 2009).

## Results

The Cactaceae family was represented in the Flora of Bajío by 125 species of the ca. 700 reported for Mexico (17.8 %, Korotkova *et al.* 2021), grouped into 30 genera of the ca. 58 recognized (51.7 %, Korotkova *et al.* 2021, [Table 1](#)). The most diverse genus was *Mammillaria* Haw., with 45 species representing 30 % of the ca. 150 species (Korotkova *et al.* 2021, Aquino *et al.* 2024). Next in importance was *Opuntia* (L.) Mill. with 18 species of the 78 reported for Mexico, representing 23 % (Arias *et al.* 2024). Only three species were represented with more than 100 records: *Cylindropuntia imbricata* (Haw.) F.M.Knuth, *Myrtillocactus geometrizans* (Mart. ex Pfeiff.) Console and *Coryphantha cornifera* (DC.) Lem.; in contrast, 11 species presented between one and three records: *Echinocereus weinbergii* Weing. *Mammillaria bombycina* Quehl; *M. monochrysacantha* Gonz.-Zam., D.Aquino & Dan.Sánchez, *M. multihamata* Boed. *M. occulta* Zamudio & U.Guzmán, *M. scheinvariana* R.Ortega V. & Glass, *M. schwarzii* Shurly, *M. rzedowskiana* Zamudio & U.Guzmán; *Selenicereus ocamponis* (Salm-Dyck) D.R.Hunt, *Stenocactus sulphureus* (A.Dietr.) Bravo, and *S. wippermannii* (Muehlenpf.) A.Berger. We report here four species not listed by Arias & Aquino (2019), including *Echinocereus weinbergii*, which was located via herbarium records (IBUG) and three more records found in the review of iNaturalistMX (2023): *Mammillaria bombycina*, *Selenicereus ocamponis* and *Stenocactus wippermannii* ([Table 1](#)).

**Species richness.** The analysis revealed that the municipalities of Cadereyta de Montes and Peñamiller in Querétaro, as well as San Luis de la Paz in Guanajuato, presented the highest richness of cacti, with 60, 44 and 50 species, respectively ([Figure 4A](#)). Other municipalities with a high level of richness were Atarjea, San Miguel de Allende, Victoria and Xichú in Guanajuato, with 34, 32, 40 and 37 species, respectively; and Colón, Pinal de Amoles and Tolimán in Querétaro, with 33, 32, and 39 species, respectively ([Figure 4A](#)). *Myrtillocactus geometrizans* was recorded in 40 municipalities of the study area; followed by *Opuntia streptacantha* Lem., which was recorded in 31 municipalities; *O. lasiacantha* Pfeiff. and *O. tomentosa* Salm-Dyck, which were observed in 30 municipalities.

The analysis of richness by vegetation type revealed that the xerophytic scrub had the greatest diversity of species, with 112 ([Table 2](#)). *Cylindropuntia imbricata*, *Isolatocereus dumortieri* (Berge ex K.Schum.) N. P. Taylor, *Mammillaria gilensis* Boed., *M. polythele* Mart., *Myrtillocactus geometrizans* and five species of *Opuntia* occurred in all types of vegetation in the study area ([Table 1](#)), whereas 37 species inhabited only one vegetation type ([Table 1](#)). With 97 species the Chihuahuan Desert was the biogeographic province with the greatest number of species ([Table 3](#)). *Mammillaria rhodantha* Link & Otto and five species of *Opuntia* inhabited the three biogeographic provinces in

the study area (Table 1). Cell-based richness analysis revealed two quadrants with the highest cactus richness, *i.e.*, 55 and 54 species, respectively, as well as two secondary cells, with 47 and 41 species (Figure 4B). Species richness was concentrated to the east of the Flora of Bajío area and decreased in the extreme southwest, mainly in the portion of Michoacán included in the Trans-Mexican Volcanic Belt, as well as the southern end of Guanajuato (Figure 4B).

**Table 1.** List of Cactaceae in the Flora of Bajío and adjacent regions; risk category NOM-059 (SEMARNAT 2019), IUCN (2022); CITES Appendix I (Lüthy & Moser 2001), vegetation type (Rzedowski 2006), biogeographic province (Morrone *et al.* 2017), registered municipalities (INEGI 2019), and supporting specimens. Interpretation: + recently described taxon. \* New record for the area. ε Endemic taxon to the Flora of Bajío. CAOF: coniferous and *Quercus* forest; BE: thorn forest; TDF: tropical deciduous forest; XS: xerophilous scrub; G: grassland. DC: Chihuahuan Desert, TVB: Trans-Mexican Volcanic Belt, SMOr: Sierra Madre Oriental.

No.	Taxon	NOM	UICN	CITES	Endemic	Vegetation	Province	Voucher (herbarium or iNaturalistMX)
SUBFAMILIA Cactoideae								
1	<i>Acanthocereus tetragonus</i> (L.) Hummelinck					CAOF, TDF, XE	SMOr	E. Sánchez 02 (QMEX)
2	<i>Aporocactus flagelliformis</i> (L.) Lem.	Pr				CAOF, TDF, XE	SMOr	U. Guzmán 3382 (IEB)
3	<i>Ariocarpus kotschoubeyanus</i> (Lem.) K.Schum.	Pr	NT	I		XE	CD	S. Arias <i>et al.</i> 1704 (MEXU)
4	<i>Astrophytum ornatum</i> (DC.) F.A.C.Weber ex Britton & Rose	A				CAOF, XS	SMOr, CD	S. Arias <i>et al.</i> 1718 (MEXU)
5	<i>Cephalocereus polylophus</i> (DC.) Britton & Rose					CAOF, TDF, XE	SMOr	E. Sánchez & G. Galin- do 27 (MEXU)
6	<i>Coryphantha clavata</i> (Scheidw.) Backeb.					CAOF, XE	SMOr, CD	H. Bravo-Hollis s.n. (MEXU)
7	<i>Coryphantha cornifera</i> (DC.) Lem.					CAOF, TDF, XE	SMOr, CD	D. Aquino & S. Arias 275 (MEXU)
8	<i>Coryphantha elephantidens</i> (Lem.) Lem.	A				CAOF, TDF, XE, G	CD	A. Cabrera 1074 (QMEX)
9	<i>Coryphantha erecta</i> (Lem.) Lem.					CAOF, XS, G	CD, SMOr	D. Aquino & S. Arias 273 (MEXU)
10	<i>Coryphantha glassii</i> Dicht & A.Lüthy					TDF, XS	SMOr	S. Arias & D. Aquino 2214 (MEXU)
11	<i>Coryphantha jalpanensis</i> Bu- chenau					CAOF, TDF, XE	SMOr	S. Arias 111 (MEXU)
12	<i>Coryphantha octacantha</i> (DC.) Britton & Rose					XS, G	CD, SMOr	S. Arias & T. Terrazas 1705 (MEXU)
13	<i>Coryphantha ottonis</i> (Pfeiff.) Lem.					CAOF, XS, G	CD, SMOr	E. Sánchez <i>et al.</i> 52 (IEB)
14	<i>Disocactus speciosus</i> (Cav.) Barthlott					CAOF, TDF	CD, TVB	G. Cornejo 3985 (IEB)
15	<i>Echinocactus horizontalonius</i> Lem.							
15a	<i>Echinocactus horizontalonius</i> subsp. <i>australis</i> M. A.Baker +					XS	CD, SMOr	G. Navarro 23 (MEXU)

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No.	Taxon	NOM	UICN	CITES	Endemic	Vegetation	Province	Voucher (herbarium or iNaturalistMX)
16	<i>Echinocactus platyacanthus</i> Link & Otto	Pr				CAOF, XS, G	CD, SMOr	S. Arias & T. Terrazas 1679 (MEXU)
17	<i>Echinocereus acifer</i> (Otto ex Salm-Dyck) Jacobi					CAOF, G	CD, SMOr	D. Sánchez & S. Arias 01 (MEXU)
18	<i>Echinocereus cinerascens</i> (DC.) Rumlper					XS, G	CD, SMOr	E. Sánchez 159 (MEXU, QMEX)
19	<i>Echinocereus pectinatus</i> (Scheidw.) Engelm.					XS	CD, SMOr	G. Navarro 79 (MEXU)
20	<i>Echinocereus pentalophus</i> (DC.) Lem.					CAOF, XS	CD, SMOr	J. Rzedowski 42999 (MEXU)
21	<i>Echinocereus schmollii</i> (Weing.) N.P.Taylor	P		I	ε	XS	CD, SMOr	S. Arias 91 (MEXU)
22	<i>Echinocereus weinbergii</i> Weing.							
22a	<i>Echinocereus weinbergii</i> subsp. <i>venustus</i> (W.Blum & W.Rischer) Gómez-Quint. & Dan.Sánchez					G	CD	J. P. Ortiz-Brunel 773 (IBUG)
23	<i>Ferocactus echidne</i> (DC.) Brit- ton & Rose					CAOF, TDF, XE, G	CD, SMOr	S. Arias & T. Terrazas 1682 (MEXU)
24	<i>Ferocactus glaucescens</i> (DC.) Britton & Rose					CAOF, XS	CD, SMOr	S. Arias & T. Terrazas 1701 (MEXU)
25	<i>Ferocactus hystrix</i> (DC.) G.E.Linds.	Pr				CAOF, XS, G	CD, SMOr	U. Guzmán 14 (MEXU)
26	<i>Ferocactus latispinus</i> (Haw.) Britton & Rose					XS, G	CD, SMOr	J. Gutiérrez 641 (MEXU)
27	<i>Ferocactus macrodiscus</i> (Mart.) Britton & Rose							
27a	<i>Ferocactus macrodiscus</i> subsp. <i>septentrionalis</i> (J.Meyrán) N.P.Taylor				ε	CAOF, XS	CD, SMOr	U. Guzmán 2553 (IEB)
28	<i>Ferocactus mathssonii</i> (Berge ex K.Schum.) N.P.Taylor	A			ε	XS	CD, SMOr	H. Sánchez-Mejorada 3891 (MEXU)
29	<i>Isolatocereus dumortieri</i> (Scheidw.) Backeb.					CAOF, TF, TDF, XS, G	CD, SMOr	E. Sánchez <i>et al.</i> 251 (MEXU, QMEX, IEB)
30	<i>Kadenicarpus pseudomacro- chele</i> (Backeb.) Doweld							
30a	<i>Kadenicarpus pseudomacro- chele</i> subsp. <i>pseudomacro- chele</i>	P	VU	I		XS	CD	L. Scheinvar <i>et al.</i> 5050 (MEXU)
30b	<i>Kadenicarpus pseudomacro- chele</i> subsp. <i>krainzianus</i> (Ger- hart Frank) Vázquez-Sánchez			I		XS	CD	C. Glass <i>et al.</i> 9217 (IEB)
30c	<i>Kadenicarpus pseudomacro- chele</i> subsp. <i>lausseri</i> (Diers & Gerhart Frank) Doweld			I		XS	CD	G. B. Hinton 2605 (GBH)

No.	Taxon	NOM	UICN	CITES	Endemic	Vegetation	Province	Voucher (herbarium or iNaturalistMX)
31	<i>Kroenleinia grusonii</i> (Hildm.) Lodé	P	CR			XS	CD	L. Scheinvar 5742 (MEXU, QMEX)
32	<i>Lophocereus marginatus</i> (DC.) S.Arias & T.Terrazas					CAOF, XS, G	CD, SMOr	E. Sánchez 142 (MEXU)
33	<i>Lophophora diffusa</i> (Croizat) Bravo	A	VU		ε	XS	SMOr	S. Arias & T. Terrazas 1698 (MEXU)
34	<i>Mammillaria albiflora</i> (Werderm.) Backeb.		CR		ε	XS	CD	D. Aquino <i>et al.</i> 506 (MEXU)
35	<i>Mammillaria ariasii</i> U.Guzmán & D.Aquino+				ε	CAOF, XS	SMOr	D. Aquino <i>et al.</i> 510 (MEXU)
36	<i>Mammillaria bombycina</i> Quehl							
36a	<i>Mammillaria bombycina</i> subsp. <i>perezdelarosae</i> (Bravo & Scheinvar) D.R.Hunt*	Pr				CAOF	CD	<a href="https://mexico.inaturalist.org/observations/221031599">https://mexico.inaturalist.org/observations/221031599</a>
37	<i>Mammillaria candida</i> Scheidw.	A				CAOF, XS	SMOr	T. Hernández-Hernández 103 (MEXU)
38	<i>Mammillaria compressa</i> DC.					CAOF, XS	CD, SMOr	J. Rzedowski 46456 (MEXU)
39	<i>Mammillaria crinita</i> DC.							
39a	<i>Mammillaria crinita</i> subsp. <i>crinita</i>					CAOF, XS, P	CD, SMOr	W. A. Fitz Maurice & B. Fitz Maurice 2187 (MEXU)
39b	<i>Mammillaria crinita</i> subsp. <i>leucantha</i> (Boed.) D.R.Hunt*					XS	CD	U. Guzmán 3541 (IEB)
40	<i>Mammillaria decipiens</i> Scheidw.							
40a	<i>Mammillaria decipiens</i> subsp. <i>decipiens</i>					XS	CD, SMOr	R. Bárcenas 371 (MEXU)
40b	<i>Mammillaria decipiens</i> subsp. <i>albescens</i> (Tiegel) D.R.Hunt	Pr			ε	XS	CD	E. Sánchez <i>et al.</i> 20 (MEXU)
40c	<i>Mammillaria decipiens</i> subsp. <i>camptotricha</i> (Dams) D.R.Hunt				ε	XS	CD, SMOr	A. Cabrera 5916 (QMEX)
41	<i>Mammillaria densispina</i> (J.M.Coult.) Orcutt					CAOF, TDF, XS, G	CD, SMOr	S. Arias & D. Sánchez 1756 (MEXU)
42	<i>Mammillaria duwei</i> Rogoz. & P.J.Braun	Pr	EN		ε	XS	CD	W. A. Fitz Maurice & B. Fitz Maurice 1641 (MEXU)
43	<i>Mammillaria elongata</i> DC.					CAOF, XS	CD, SMOr	S. Arias & T. Terrazas 1697 (MEXU)
44	<i>Mammillaria formosa</i> Galeotti ex Scheidw.							
44a	<i>Mammillaria formosa</i> subsp. <i>pseudocrucigera</i> (R.T.Craig) D.R.Hunt				ε	CAOF, XS, G	CD, SMOr	S. Arias & T. Terrazas 1696 (MEXU)

Cactaceae in the Flora of Bajío

No.	Taxon	NOM	UICN	CITES	Endemic	Vegetation	Province	Voucher (herbarium or iNaturalistMX)
45	<i>Mammillaria geminispina</i> Haw.					CAOF, XS	CD, SMOr	D. Aquino <i>et al.</i> 515 (MEXU)
46	<i>Mammillaria gigantea</i> Hildm. ex K.Schum.					XS	CD, SMOr	G. Navarro 74 (MEXU)
47	<i>Mammillaria gilensis</i> Boed.					CAOF, TF, TDF, XS, G	CD	W. A. Fitz Maurice & B. Fitz Maurice 1761 (MEXU)
48	<i>Mammillaria hahniana</i> Werderm.	A				CAOF, TDF, XS	SMOr	U. Guzmán 3389 (IEB)
49	<i>Mammillaria herrerae</i> Werderm.	P	CR		ε	XS	CD	L. Scheinvar <i>et al.</i> 5735 (MEXU)
50	<i>Mammillaria jaliscana</i> (Britton & Rose) Boed.					TF, TDF	CD	R. Bárcenas & C. Gómez-Hinostrosa 450 (MEXU)
51	<i>Mammillaria longimamma</i> DC.	A				XS	CD, SMOr	U. Guzmán 1378 (MEXU)
52	<i>Mammillaria magnimamma</i> Haw.					CAOF, TDF, XS, G	CD, SMOr	E. Sánchez 216 (MEXU)
53	<i>Mammillaria mathildae</i> Kraehenb. & Krainz	P	VU		ε	XS, TF, TDF	CD	W. A. Fitz Maurice & B. Fitz Maurice 1647 (MEXU)
54	<i>Mammillaria microhelia</i> Werderm.	Pr	VU		ε	XS	CD	U. Guzmán <i>et al.</i> 577 (MEXU)
55	<i>Mammillaria monochrysacantha</i> Gonz.-Zam., D.Aquino & Dan.Sánchez+				ε	XS	SMOr	P. González-Zamora <i>et al.</i> 84 (IBUG, IEB)
56	<i>Mammillaria morganiana</i> Tiegel				ε	CAOF, XS	SMOr	H. Hernández <i>et al.</i> 3536 (MEXU)
57	<i>Mammillaria muehlenpfordtii</i> Foerster					CAOF, XS	CD, SMOr	S. Arias & T. Terrazas 1692 (MEXU)
58	<i>Mammillaria multihamata</i> Boed.		CR		ε	CAOF	SMOr	U. Guzmán 1462 (MEXU)
59	<i>Mammillaria nana</i> Backeb. ex Mottram	Pr				XS	CD	W. A. Fitz Maurice & B. Fitz Maurice 2371 (MEXU)
60	<i>Mammillaria occulta</i> Zamudio & U.Guzmán				ε	CAOF	SMOr	R. Hernández <i>et al.</i> 11315 (QMEX)
61	<i>Mammillaria painteri</i> Rose				ε	XS	CD	E. Sánchez 70 (MEXU)
62	<i>Mammillaria parkinsonii</i> Ehrenb.	Pr			ε	XS	SMOr	L. Scheinvar <i>et al.</i> 2386 (MEXU)
63	<i>Mammillaria perbella</i> Hildm. ex K.Schum.					XS, G	CD, SMOr	G. Navarro 81 (MEXU)
64	<i>Mammillaria petterssonii</i> Hildm.					CAOF, XS, G	CD	H. Bravo-Hollis s.n. (MEXU)
65	<i>Mammillaria polythele</i> Mart.					CAOF, TF, TDF, XS, G	CD, SMOr	S. Arias & U. Guzmán 234 (MEXU)

No.	Taxon	NOM	UICN	CITES	Endemic	Vegetation	Province	Voucher (herbarium or iNaturalistMX)
66	<i>Mammillaria pringlei</i> (J. M. Coult.) K.Brandegee	Pr				XS, G	CD	M. Rivas 2903 (MEXU)
67	<i>Mammillaria prolifera</i> (Mill.) Haw.					CAOF, TDF, XS	SMOr	U. Guzmán 797 (IEB)
68	<i>Mammillaria rettigiana</i> Boed.	Pr	VU			XS, G	CD	W. A. Fitz Maurice & B. Fitz Maurice 2098A (MEXU)
69	<i>Mammillaria rhodantha</i> Link & Otto							
69a	<i>Mammillaria rhodantha</i> subsp. <i>rhodantha</i>					CAOF, XS	CD, TVB, SMOr	J. Rzedowski 44425 (MEXU)
69b	<i>Mammillaria rhodantha</i> subsp. <i>fera-rubra</i> (Schmoll ex R.T.Craig) D.R.Hunt					TDF, XS	CD	J. Rzedowski 49239 (IEB)
70	<i>Mammillaria rzedowskiana</i> Zamudio & U.Guzmán					CAOF	SMOr	S. Zamudio <i>et al.</i> 15083 (MEXU)
71	<i>Mammillaria scheinvariana</i> R.Ortega V. & Glass				ε	XS	CD	D. Sánchez & A. Martínez-Poiré 884 (IBUG)
72	<i>Mammillaria schiedeana</i> C. Ehrenb.	A				CAOF, XS	SMOr	D. Aquino & S. Arias 270 (MEXU, IBUG)
73	<i>Mammillaria schwarzii</i> Shurly	P	CR		ε	G	CD	W. A. Fitz Maurice & B. Fitz Maurice 1687B (MEXU)
74	<i>Mammillaria sempervivi</i> DC.					XS	CD	U. Guzmán <i>et al.</i> 28 (MEXU)
75	<i>Mammillaria uncinata</i> Zucc. ex Pfeiff.					CAOF, TDF, XS, G	CD, SMOr	R. Bárcenas 17 (MEXU, IEB)
76	<i>Mammillaria vetula</i> Mart.							
76a	<i>Mammillaria vetula</i> subsp. <i>vetula</i>					XS, CAOF	SMOr	R. Bárcenas 1494 (MEXU)
76b	<i>Mammillaria vetula</i> subsp. <i>gracilis</i> (Pfeiff.) D.R.Hunt					XS, CAOF	SMOr	E. Sánchez 97 (MEXU)
77	<i>Mammillaria zeilmanniana</i> Boed.	Pr	EN		ε	XS, CAOF, G	CD	W. A. Fitz Maurice & B. Fitz Maurice 1764 (MEXU)
78	<i>Mammillaria zephyranthoides</i> Scheidw.	A				TDF, XS, G	CD	D. Aquino & S. Arias 287 (MEXU)
79	<i>Myrtillocactus geometrizans</i> (Mart. ex Pfeiff.) Console					CAOF, TF, TDF, XS, G	CD, SMOr	G. Navarro 30 (MEXU)
80	<i>Neolloydia conoidea</i> (DC.) Britton & Rose					CAOF, TDF, XS, G	CD, SMOr	S. Arias & T. Terrazas 1695 (MEXU)
81	<i>Nyctocereus serpentinus</i> (Lag. & Rodr.) Britton & Rose					CAOF, TDF, XS, G	CD, SMOr	E. Sánchez <i>et al.</i> 259 (MEXU)

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No.	Taxon	NOM	UICN	CITES	Endemic	Vegetation	Province	Voucher (herbarium or iNaturalistMX)
82	<i>Pilosocereus leucocephalus</i> (Poselg.) Byles & G.D.Rowley					CAOF, TDF, XS	SMOr	S. Zamudio & E. Carranza 9965 (MEXU, IEB, QMEX, UAMIZ)
83	<i>Rhipsalis baccifera</i> (J.S.Muell) Stearn					TDF, XS	SMOr	J. Rzedowski 42969 (IEB)
84	<i>Selenicereus spinulosus</i> (DC.) Britton & Rose					CAOF, TDF, XS	SMOr	U. Guzmán 3429 (IEB)
85	<i>Selenicereus ocamponis</i> (Salm-Dyck) D.R.Hunt*					CAOF	TVB	<a href="https://www.naturalista.mx/observations/27771446">https://www.naturalista.mx/observations/27771446</a>
86	<i>Stenocactus coptonogonus</i> (Lem.) A.Berger ex A.W.Hill	Pr				XS, G	CD	R. Bárcenas 154 (MEXU, IEB)
87	<i>Stenocactus dichroacanthus</i> (Mart. ex Pfeiff.) A.Berger ex Backeb. & F.M.Knuth					CAOF, TDF, XS, G	CD, SMOr	J. Rzedowski 50656 (MEXU)
88	<i>Stenocactus lamellosus</i> (A.Dietr.) A.Berger ex A.W.Hill					CAOF, XS	CD, SMOr	S. Arias & D. Aquino 2259 (MEXU)
89	<i>Stenocactus ochoterenanus</i> Tiegel					CAOF, XS	CD, SMOr	D. Aquino <i>et al.</i> 360 (MEXU)
90	<i>Stenocactus pentacanthus</i> (Lem.) A.Berger ex A.W.Hill					CAOF, XS, G	CD, SMOr	L. Scheinvar & C. Orozco 3198 (MEXU)
91	<i>Stenocactus phyllacanthus</i> (Mart. ex A.Dietr. & Otto) A.Berger ex A.W.Hill					XS	CD	G. Navarro 92 (MEXU)
92	<i>Stenocactus sulphureus</i> (A.Dietr.) Bravo	Pr			ε	XS	CD	V. Huerta 1235 (MEXU)
93	<i>Stenocactus x irregularis</i> Gonz.-Zam., D.Aquino & Dan. Sánchez+					XS	CD	D. Aquino <i>et al.</i> 366 (MEXU)
94	<i>Stenocactus wippermannii</i> (Muehlenpf.) A.Berger					CAOF, XS	CD, SMOr	<a href="https://mexico.inaturalist.org/observations/22721563">https://mexico.inaturalist.org/observations/22721563</a>
95	<i>Stenocactus zacatecasensis</i> (Britton & Rose) A.Berger ex A.W.Hill					CAOF, TDF, G	CD	R. Bárcenas & C. Gómez-Hinostrosa 785 (MEXU)
96	<i>Stenocereus huastecorum</i> Alvarado-Sizzo, Arreola-Nava & Terrazas					CAOF, TDF, XS	CD, SMOr	S. Arias & S. Gama 716 (MEXU)
97	<i>Stenocereus queretaroensis</i> (F.A.C.Weber) Buxb.					CAOF, TF, TDF, XS	CD	S. Arias & S. Gama 716A (MEXU)
98	<i>Strombocactus corregidorae</i> S.Arias & E.Sánchez				ε	XS	SMOr	S. Zamudio 14107 (IEB)
99	<i>Strombocactus disciformis</i> (DC.) Britton & Rose							
99a	<i>Strombocactus disciformis</i> subsp. <i>disciformis</i>	A		I		CAOF, XS	CD, SMOr	U. Guzmán 3317 (IEB)

No.	Taxon	NOM	UICN	CITES	Endemic	Vegetation	Province	Voucher (herbarium or iNaturalistMX)
99b	<i>Strombocactus disciformis</i> subsp. <i>esperanzae</i> Glass & S.Arias			I	ε	CAOF, XS	SMOr	D. Aquino <i>et al.</i> 524 (MEXU)
100	<i>Thelocactus hastifer</i> (Werderm. & Boed.) F.M.Knuth	Pr	VU			XS	CD	S. Arias & D. Aquino 2263 (MEXU)
101	<i>Thelocactus leucacanthus</i> (Zucc. ex Pfeiff.) Britton & Rose					CAOF, XS, G	CD, SMOr	S. Arias & T. Terrazas 1678 (MEXU)
102	<i>Turbinicarpus alonsoi</i> Glass & S.Arias		CR	I	ε	XS	SMOr	E. Pérez-Calix 3339 (IEB)
SUBFAMILIA Opuntioideae								
103	<i>Cylindropuntia imbricata</i> (Haw.) F.M.Knuth					CAOF, TF, TDF, XS, G	CD, SMOr	M. A. Baker 12842 (ASU)
104	<i>Cylindropuntia kleiniae</i> (DC.) F.M.Knuth					XS, G	CD, SMOr	J. Rzedowski 51023 (MEXU)
105	<i>Cylindropuntia leptocaulis</i> (DC.) F.M.Knuth					CAOF, XS	CD, SMOr	E. Sánchez <i>et al.</i> 206 (MEXU, IEB)
106	<i>Cylindropuntia tunicata</i> (Lehm.) F.M.Knuth					XS	CD	G. Navarro 37 (MEXU)
107	<i>Opuntia decumbens</i> Salm-Dyck					CAOF, TDF, XS	SMOr	C. Gómez-Hinostrosa 2136 (MEXU)
108	<i>Opuntia dejecta</i> Salm-Dyck					CAOF, TDF, XS	SMOr	U. Guzmán 3560 (IEB)
109	<i>Opuntia elizondoana</i> E.Sánchez & Villaseñor				ε	XS	CD	S. Arias <i>et al.</i> 1502 (MEXU)
110	<i>Opuntia engelmannii</i> Salm-Dyck							
110a	<i>Opuntia engelmannii</i> subsp. <i>cuija</i> (Griffiths & Hare) M.H.J.van der Meer					CAOF, TDF, XS, G	CD, SMOr	O. Rubio 501 (QMEX)
110b	<i>Opuntia engelmannii</i> subsp. <i>lindheimeri</i> (Engelm.) U. Guzmán & Mandujano					CAOF, TDF, XS, G	CD, SMOr	E. García & L. Scheinvar 42 (MEXU)
111	<i>Opuntia fuliginosa</i> Griffiths					TF, TDF	CD	L. Scheinvar & S. Arias 1601 (MEXU)
112	<i>Opuntia hyptiacantha</i> F.A.C.Weber					CAOF, TDF, XS, G	CD, TVB, SMOr	R. Bárcenas & C. Gómez Hinostrosa 770 (MEXU)
113	<i>Opuntia joconostle</i> F. A.C.Weber ex Diguet					TF, TDF, XS	CD, SMOr	R. Bárcenas & M. Meade 1480 (MEXU)
114	<i>Opuntia karwinskiana</i> Salm-Dyck					TDF	CD	A. Martínez 82 (MEXU)
115	<i>Opuntia lasiacantha</i> Pfeiff.					CAOF, TF, TDF, XS, G	CD, TVB, SMOr	L. Scheinvar <i>et al.</i> 3767 (MEXU)

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No.	Taxon	NOM	UICN	CITES	Endemic	Vegetation	Province	Voucher (herbarium or iNaturalistMX)
116	<i>Opuntia leucotricha</i> DC.					CAOF, TF, TDF, XS, G	CD, SMOr	G. Navarro 10-24 (MEXU)
117	<i>Opuntia microdasys</i> (Lehm.) Pfeiff.					XS	SMOr	E. Sánchez 208 (IEB, QMEX)
118	<i>Opuntia pachyrrhiza</i> H.M.Hern., C.Gómez-Hinostrosa & Bárcenas					XS	SMOr	R. Puente-Martínez 1260 (ASU, DES, SLPM)
119	<i>Opuntia pubescens</i> H.L.Wendl. ex Pfeiff.					CAOF, TF, TDF, XS	CD, TVB, SMOr	S. Arias <i>et al.</i> 1503 (MEXU)
120	<i>Opuntia robusta</i> H. L. Wendl. ex Pfeiff.					CAOF, TF, TDF, XS, G	CD, SMOr	S. Arias & T. Terrazas 1685 (MEXU)
121	<i>Opuntia stenopetala</i> Engelm.					CAOF, XS	CD, SMOr	S. Arias <i>et al.</i> 1504 (MEXU)
122	<i>Opuntia streptacantha</i> Lem.					CAOF, TF, TDF, XS, G	CD, TVB, SMOr	C. Gómez-Hinostrosa <i>et al.</i> 1617 (MEXU, MO)
123	<i>Opuntia tomentosa</i> Salm-Dyck					CAOF, TF, TDF, XS, G	CD, TVB, SMOr	A. Cabrera 5737 (QMEX)
124	<i>Opuntia velutina</i> F. A. C. Weber					CAOF, TF, TDF, G	CD, TVB	R. Bárcenas & M. Meade 187 (MEXU)
125	<i>Pereskiaopsis diguetii</i> (F.A.C.Weber) Britton & Rose					CAOF, TF, TDF, XS	CD, TVB	L. Hernández 4682 (IEB, QMEX)

*Endemism analysis.* The distribution of endemic species was related to the distribution of species richness in the region. These species were concentrated to the northeast of the Flora of Bajío area, on the borders of the Chihuahuan Desert and the Sierra Madre Oriental, and decreased toward the southern region on the borders with the Trans-Mexican Volcanic Belt. The xerophilous scrub was the type of vegetation with the greatest number of endemisms, with 24 species (Tables 1 and 2). On the other hand, the Chihuahuan Desert and the Sierra Madre Oriental included 18 and 16 endemic species, respectively.

At the municipal level, Cadereyta de Montes hosted the greatest number of endemic species, with seven species, followed by Peñamiller, with four species. A second center of endemism was San Luis de la Paz, with four species, while the neighboring municipalities, *i.e.*, Victoria and Xichú, each hosted 2 endemic species (Figure 5). The municipalities of El Marqués and Querétaro hosted 3 and 2 species, respectively. Finally, the municipalities of San Juan del Río, Tequisquiapan, Colón, Pinal de Amoles, San Miguel de Allende, Dolores Hidalgo, Guanajuato and San Felipe, hosted only one endemic species within their perimeters (Figure 5).

On the other hand, the analysis of endemism by cell revealed that four of the cells presented high WE values (Figure 6A), which were located in the same region observed in the richness analysis. Moreover, the CWE analysis revealed only two cells with high values (Figure 6B) at the northeast and northwest ends of the Bajío Flora area. A cell in the far north is surrounded by others with a WE value of >1.86. It is likely that there are no endemic taxa for that cell. The CWE corroborates this assertion because, despite being a species-rich area (Figure 4B), there are no restricted species for that cell.

## Discussion

This work recognizes the Flora of Bajío area as a region with an important diversity of cacti, with 30 genera and 125 species distributed over an area of 60,171.42 km<sup>2</sup> (Suárez-Mota *et al.* 2015, [Figures 6](#) and [7](#)). This value is higher than that of other regions with high diversity, such as the Tehuacán-Cuicatlán Valley, which has 28 genera and 87 species distributed over an area of 10,000 km<sup>2</sup> (Valiente-Banuet *et al.* 2000, Arias *et al.* 2012, Tristan *et al.* 2018). In turn, it is comparable to the richness of a State such as Tamaulipas, where 33 genera and 157 species are currently known, with an area of 80,249 km<sup>2</sup> (García-Morales *et al.* 2022).

The number of genera of Cactoideae recorded by Arias & Aquino (2019) for the Flora of Bajío differs from the present work, since recent phylogenetic analysis allows the recognition of *Kadenicarpus* Doweld (Vázquez-Sánchez *et al.* 2019) and *Kroenleinia* Lodé (Vargas-Luna *et al.* 2018) as independent genera, which are included here (27 correspond to Cactoideae and three to Opuntioideae), thus adding up to 30 genera. On the other hand, studies focused on the delimitation of species in *Stenocactus* allow us to confirm that the individuals previously identified as *Stenocactus obvallatus* (DC.) A.Berger ex A.W.Hill corresponds to *S. pentacanthus* (Lem.) A.Berger ex A.W.Hill and *S. dichroacanthus* (Mart. ex Pfeiff.) A.Berger ex Backeb. & F.M.Knuth (Franco 2020). Likewise, field observations allow us to rule out the presence of *Mammillaria fittkaui* Glass & R.A.Foster for the study area and that, such records correspond to *M. mathildae* Kraehenb. & Krainz, so its distribution previously known only for Querétaro now includes Guanajuato. iNaturalistMX (2023) allow us to corroborate the presence in Guanajuato of *Disocactus speciosus* (Cav.) Barthlott and *Opuntia pachyrrhiza* H.M.Hern., C. Gómez-Hinostrosa & Bárcenas, previously known for the northern part of Michoacán and northeast of Querétaro, respectively. On the other hand, we confirm the presence of *Echinocereus weinbergii*, *Mammillaria bombycina*, *Selenicereus ocamponis* and *Stenocactus wippermannii* as new records for the study area ([Table 1](#)). Additionally, owing to recent exploration work, three new taxa in the study area are described: *Stenocactus* × *irregularis* Gonz.-Zam., D.Aquino & Dan.Sánchez (González-Zamora *et al.* 2023a), *Mammillaria monochrysantha* (González-Zamora *et al.* 2023b) and *M. ariasii* U.Guzmán & D.Aquino (Aquino *et al.* 2024), so new discoveries in the future should not be ruled out.

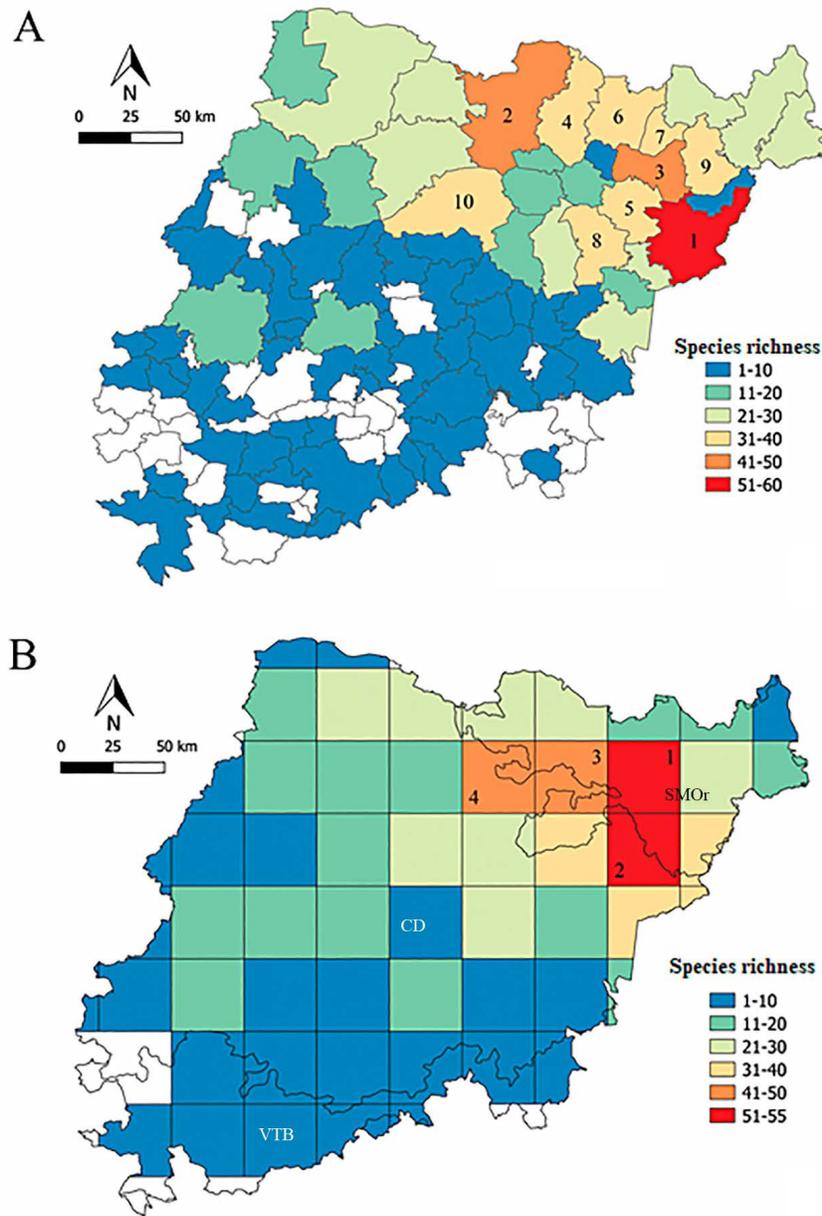
*Species richness.* The sites that host the greatest number of species occur in the eastern region of the Flora of Bajío area, with Cadereyta de Montes in Querétaro being the municipality with the highest concentration of species. In contrast, toward the south, in the municipalities of Guanajuato that border Michoacán, the richness decreases noticeably. In the case of Asteraceae of Flora del Bajío, Villaseñor & Ortiz (2012) reported that the greatest number of species is concentrated at the southern end of the study area, while the eastern region occupies second place in terms of species

**Table 2.** Species richness by vegetation type (Rzedowski 2006).

Vegetation type	Richness
Coniferous and <i>Quercus</i> forest	74
Thorn forest	19
Tropical deciduous forest	46
Xerophilous scrub	112
Grassland	46

**Table 3.** Species richness by biogeographic province (Morrone *et al.* 2017).

Biogeographic province	Richness
Chihuahuan Desert	97
Trans-Mexican Volcanic Belt	9
Sierra Madre Oriental	88

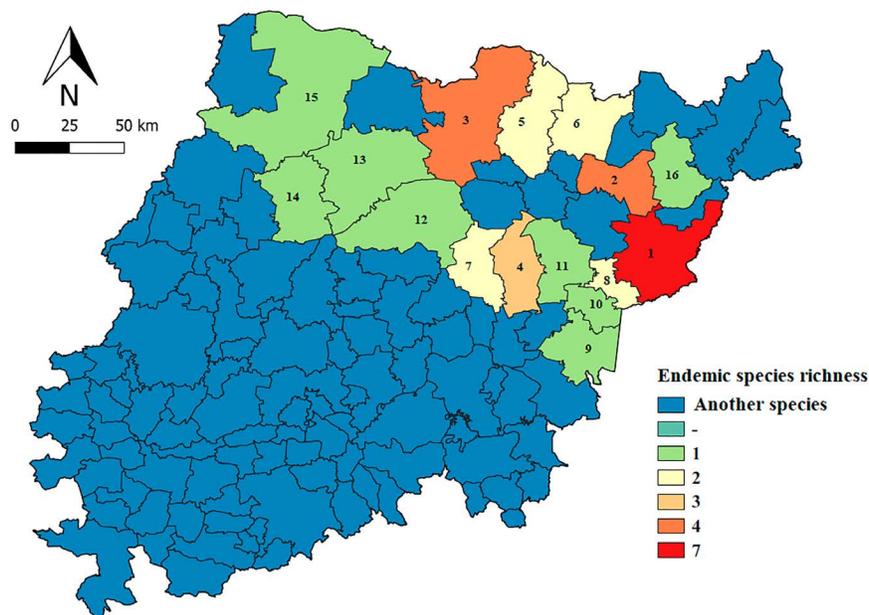


**Figure 4.** Richness of cactus species in the Bajío and adjacent regions. A. Municipal political division. 1: Cadereyta de Montes; 2: San Luis de la Paz; 3: Peñamiller; 4: Victoria; 5: Tolimán; 6: Xichú; 7: Atarjea; 8: Colón; 9: Pinal de Amoles; 10: San Miguel de Allende. B. Species richness by cell; the regions delimited within the study area represent the VTB, CD and SMOr.

richness. On the other hand, our results for the Flora of Bajío Cactaceae agree with those reported by Hernández-Oria *et al.* (2007) for central Querétaro, since quadrants 1 and 2 of our results (Figure 4B) coincide with the “Tolimán” quadrant, where the areas corresponding to Cadereyta de Montes and a sector bordering Hidalgo are recognized as areas of high species richness. The high incidence of species can be explained by the fact that it is a transition zone between the canyons of the Estórax and Moctezuma River basins and the mountainous areas of the El Doctor massif (Hernández-Magaña *et al.* 2012). Bárcenas (1999) reported a high number of species in the central-eastern and north-eastern regions of Guanajuato. This area corresponds to the municipalities of San Luis de la Paz, Victoria, Xichú, Atarjea and San Miguel de Allende (Figure 1A) in quadrants 3 and 4 (Figure 4B). This richness is probably related to

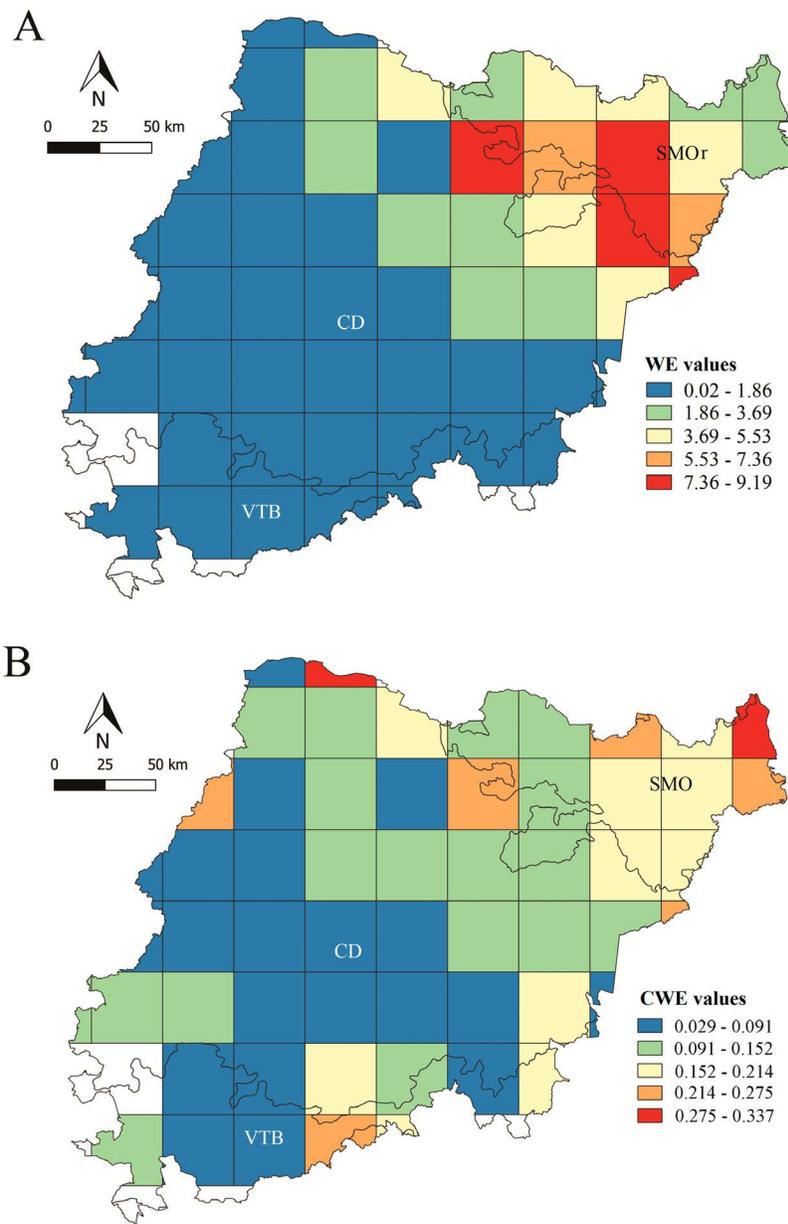
its condition as a climatic refuge during the Pleistocene and to the wide diversity of soil types of presents (Hernández & Bárcenas 1995). Additionally, Sierra Gorda (including the Querétaro sector) presents a diverse relief that supports different types of vegetation such as the *Quercus* Forest and xerophilous scrubs (Rzedowski *et al.* 2012), so lineages were isolated and diversified in this mountain range, which is reflected in the WE and CWE values which are significant (Figure 6). There are no previous investigations of the northeastern part of Michoacán; however, based on our results, the low level of taxon richness is relevant, and only widely distributed species such as *Disocactus speciosus* and *Opuntia streptacantha* are recorded in the area. Based on the presence of members of Asteraceae, Villaseñor & Ortiz (2012) consider the southern sector of the Flora of Bajío to be relevant, as it hosts a significant number of species belonging to this family. However, many species of Asteraceae tend to be synanthropogenic, which is why they withstand severe disturbance events (Ruiz-Acevedo *et al.* 2024). In contrast, members of the Cactaceae are affected by severe disturbances (Figure 3D). With the notable exception of *Cylindropuntia* (Engelm.) F.M.Knuth, *Opuntia*, and *Pereskiaopsis* Britton & Rose, they can be synanthropic, having the ability to establish themselves on roadsides or persist through *in situ* management (Bravo-Hollis & Sánchez-Mejorada 1991, Arias *et al.* 2024).

**Endemism and conservation areas.** The distribution of endemic species occurs toward the east of the study area, whereas toward the south, the level of endemism is very low. The strictly endemic species for the Flora of Bajío are concentrated between Cadereyta de Montes, Peñamiller and Ezequiel Montes (Figure 2). Some of the endemism presents are *Mammillaria herrerae* Werderm., *M. scheinvariana*, *M. occulta*, *Strombocactus corregidora* S.Arias & E.Sánchez and *Stenocactus sulphureus*, among others. It has been proposed that Cadereyta de Montes, Peñamiller and Tolimán be declared protected natural areas, since anthropogenic factors have been detected that negatively affect the diversity of the flora in general and the Cactaceae in particular (Sánchez-Martínez *et al.* 2006, Suárez-Mota *et al.* 2015). The second most important center of endemism is the municipality of San Luis de la Paz, with four species, followed by Victoria and Xichú, with two species each (Figure 3A). Some endemic species are *Ferocactus mathss-*



**Figure 5.** Richness of endemic cactus species in the Bajío and adjacent regions by municipal political division: 1) Cadereyta de Montes, Qro.; 2) Peñamiller, Qro.; 3) San Luis de la Paz, Gto.; 4) El Marqués, Qro.; 5) Victoria, Gto.; 6) Xichú, Gto.; 7) Querétaro, Qro.; 8) Ezequiel Montes, Qro.; 9) San Juan del Río, Qro.; 10) Tequisquiapan, Qro.; 11) Colón, Qro.; 12) San Miguel de Allende, Gto.; 13) Dolores Hidalgo, Gto.; 14) Guanajuato, Gto.; 15) San Felipe, Gto.; and 16) Pinal de Amoles, Qro.

## Cactaceae in the Flora of Bajío



**Figure 6.** Analysis of endemic cacti in Bajío and adjacent regions. A. Weighted Endemism (WE). B. Corrected weighted endemism (CWE). The inland boundaries correspond to the biogeographic provinces VTB, CD and SMOr.

*nii* (Berge ex K.Schum.) N.P.Taylor, *Mammillaria albiflora* (Werderm.) Backeb., *M. ariasii*, *M. duwei* Rogoz. & P.J.Braun, *M. monochrysacantha*, *M. multiamata* and *Turbinicarpus alonsoi* Glass & S.Arias.

The quadrant endemism analyses do not include information on the distribution of the taxon outside the study area, examples of which are *Kroenleinia grusonii* (Hildm.) Lodé, *Strombocactus disciformis* (DC.) Britton & Rose and *Thelocactus hastifer* (Werderm. & Boed.) F.M.Knuth, which are distributed in Cadereyta de Montes and in localities in the state of Hidalgo (unpublished data). The limits of the Chihuahuan Desert and its continuation to the north with the Sierra Madre Oriental are recognized as centers of endemism for Cactaceae (Figure 3A). The WE analysis does not consider subspecies; however, at the recovered center of endemism is distributed, *Strombocactus discifor-*



**Figure 7.** Some Cactaceae representative in the Bajío and adjacent regions. A. *Kadenicarpus pseudomacroechele* (D. Aquino & M. Vázquez-Sánchez 572 (MEXU)). B. *Kroenleinia grusonii* (R. Ortega s. n. (MEXU)). C. *Mammillaria monochrysacantha* (P. González-Zamora *et al.* 84 (IBUG, IEB)). D. *M. ariasii* (D. Aquino *et al.* 510 (MEXU, IBUG)). E. *Strombocactus disciformis* (D. Aquino & P. González-Zamora 547 (MEXU)). F. *Thelocactus hastifer* (S. Arias & D. Aquino 2263 (MEXU)). G. *Echinocereus schmollii* (D. Aquino & P. González-Zamora 550 (MEXU)). H. *Lophophora diffusa* (S. Arias & T. Terrazas 1698 (MEXU)). I. *M. scheinvariana* (D. Sánchez & A. Martínez-Poiré 884 (IBUG)). J. *Ferocactus mathssonii* (S. Arias & T. Terrazas 1688 (MEXU)). K. *M. albiflora* (D. Aquino *et al.* 506 (MEXU)). L. *Strombocactus disciformis* subsp. *esperanzae* (D. Aquino *et al.* 524 (MEXU)). M. *F. macrodiscus* subsp. *septentrionalis* (D. Aquino *et al.* 364 (MEXU)). N. *M. mathildae* (D. Aquino & P. González-Zamora 553 (MEXU)). Ñ. *M. hahniana* (D. Aquino *et al.* 522 (MEXU)). O. *Astrophytum ornatum* (D. Aquino *et al.* 517 (MEXU)). Photo D. Aquino (A-H, J-O), D. Sánchez (I).

*mis* subsp. *esperanzae* Glass & S.Arias, a very particular morphotype of the Sierra Gorda. Additionally, some species endemic to the Flora of Bajío (*Mammillaria schwarzii*, *M. zeilmanniana* Boed. and *Opuntia elizondoana* E.Sánchez & Villaseñor, among others) are distributed in areas with a low level of endemism. Similarly, *Mammillaria microhelia* Werderm. is distributed in the Sierra de Zamorano (municipality of Colón), which is also an area with a low level of endemism for Cactaceae (Figure 2); however, this region is relevant for other plant families (Suárez-Mota *et al.* 2015). Although the portion belonging to Guanajuato is recognized as a protected natural area (SMAOT 2024), it is necessary to include the portion of the Sierra de Zamorano corresponding to Querétaro, since it is a mountainous massif covered with temperate climate vegetation (*Abies* forest) surrounded by arid climate vegetation (xerophilous scrub), forming an ecological island, which favors the isolation of species (Rzedowski *et al.* 2012). A similar case occurs in the municipality of San Felipe, where *Mammillaria schwarzii* is found, although it is recognized as a relevant area for conservation (Suárez-Mota *et al.* 2015). The WE and CWE values indicate that they are low, however, in this quadrant the presence of endemism has been reported for other families such as Crassulaceae (Pérez-Calix 1997), so a floristic study is required to integrate other families to evaluate the presence of endemism in San Felipe.

The CWE shows cells with high values at the northern and southern ends of the study area because it recovers species that are found only in that cell and not in others; however, these taxa are common in regions outside the study polygon; for example, *Rhipsalis baccifera* (Sol.) Stearn and *Selenicereus spinulosus* (DC.) Britton & Rose at the northern end and *S. ocamponis* were distributed in a single quadrant at the southern end (Figure 3B).

Considering that species such as *Mammillaria monochrysacantha*, *M. microhelia* or *Lophophora diffusa* cover an area of less than 150 km<sup>2</sup> (Hernández *et al.* 2010, González-Zamora *et al.* 2023a), and that a set of species that are listed under the protection of national and international laws are distributed in Sierra Gorda (Santa-Anna-del-Conde *et al.* 2009), including species that are not endemic to the study area but are in vulnerable conditions, it is necessary to evaluate the direct and indirect impacts on these populations to propose *in situ* preservation strategies (Hernández-Oria *et al.* 2006, Záhora *et al.* 2017). Notably, the work carried out at the Regional Botanical Garden of Cadereyta's "Ing. Manuel González de Cosío", where propagation exercises have been carried out of an initial number of nine to 19 priority species (Sánchez-Martínez *et al.* 2006, Chávez *et al.* 2006). In addition, their research has contributed to the understanding of the biology of threatened species, such as *Echinocereus schmollii* (Weing.) N.P.Taylor (Hernández-Oria *et al.* 2006), as well as the discovery of a new species, namely, *Strombocactus corregidorae* (Arias & Sánchez-Martínez 2006).

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