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Biogeographic analysis of endemic cacti of the Sierra Madre Oriental, Mexico

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The distribution of cacti species that inhabit the Sierra Madre Oriental (SMO) was analysed. Grid-cells were analysed using parsimony analysis of endemicity (PAE) and endemism indices. Areas characterized by their diagnostic species were determined, aiming to propose areas for the conservation of threatened cacti. Distributional data were obtained from 1936 herbarium specimens, electronic information, and from field collections. Eight areas of endemism and three main clades were obtained from the grid-cell analysis. Areas obtained from the endemism indices are very similar to those obtained with the PAE, but differ in the association of grid-cells. PAE showed endemism patterns indicating that southern and central sections of the SMO province are the areas richest in geographically-restricted species. The results obtained with different endemism indices detected more or less the same areas, although the importance level is different. The corrected weighted endemism index can be considered as a reliable measure of endemism because it is unrelated to species richness. A regionalization of the SMO in three subprovinces is suggested, supported by characteristic cacti taxa and the existence of natural barriers.

ADDITIONAL KEYWORDS: Cactaceae – corrected weighted endemism – grid-cell analysis – parsimony analysis of endemicity.

INTRODUCTION

Mexico is considered as the main centre of diversification of the family Cactaceae (Goettsch & Hernández, 2006; Ortega-Baes & Godínez-Álvarez, 2006). Sixty-three genera and 669 species occur in the country, of which 40% of the genera and 78% of the species are endemic (Guzmán, Arias & Dávila-Aranda, 2003; Ortega-Baes & Godínez-Álvarez, 2006). These plants are distributed mainly in arid and semi-arid vegetation types, which cover approximately 49% of the Mexican territory and comprise 20% of the country's flora (Goettsch & Hernández, 2006).

Mexican Cactaceae are important because: (1) they are components of the American flora, with the greatest diversity of genera and species found in Mexico; (2) they are economically important because the fruits and cladodes of many species are important human and animal food sources, as 'tunas' and 'nopales'; (3) the family includes many threatened taxa; and (4) their beauty and rarity have provoked their exploitation as ornamentals, which is particularly detrimental because many cactus populations are composed of few individuals. Studies on the geographic distribution of Cactaceae in Mexico are imperative (Godínez-Álvarez & Ortega-Baes, 2007) not only theoretically, but also practically, especially for those groups with great economic value such as *Opuntia*, *Echinocactus*, *Stenocereus*, and *Myrtillocactus*, among others, and threatened taxa such as

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Astrophytum, *Cephalocereus*, *Mammillaria*, and *Disocactus*, among many others. A total of 267 species belonging to 39 genera of Cactaceae have been included in some risk category by the Mexican government (SEMARNAT, 2002).

To determine endemism, we used the corrected weighted endemism index proposed and applied by Crisp *et al.* (2001) and Linder (2001) to Australian and African floras, respectively. The use of equal-area grids has also been considered as an important tool for studying biogeographic patterns in biological diversity (McAllister *et al.*, 1994). In Mexico, this index has been applied to the geographic distribution of seed plants, such as Ternstroemiaceae (Luna, Alcántara & Contreras-Medina, 2004a) and gymnosperms (Contreras-Medina & Luna, 2007).

Parsimony analysis of endemicity (PAE) was developed by Rosen (1988) and Rosen & Smith (1988) to address the shortcomings of phenetic approaches used to assess area relationships of fossil or recent assemblages from different areas (Porzecanski & Cracraft, 2005). As a starting point, PAE takes the presence/absence data for a set of sample localities and selected taxa (Rosen & Smith, 1988). With this information, a data matrix of areas versus taxa is constructed and analysed (Luna *et al.*, 1999). Shared presences of taxa group areas according to the most parsimonious cladogram, which represents nested sets of areas (Morrone & Crisci, 1995).

In Mexico, PAE has been applied to different geographic units, such as hydrological basins (Aguilar-Aguilar, Contreras-Medina & Salgado-Maldonado, 2003), grid-cells (Morrone & Escalante, 2002; Rojas-Soto *et al.*, 2003; Méndez-Larios *et al.*, 2005; Contreras-Medina, Luna & Morrone, 2007), biogeographic provinces (Morrone *et al.*, 1999; Dávila-Aranda *et al.*, 2002; Morrone & Escalante, 2002; Contreras-Medina *et al.*, 2007), and transects (García-Trejo & Navarro, 2004; León-Paniagua *et al.*, 2004; Navarro *et al.*, 2004). Grid-cells as unit areas have been applied to Mexican terrestrial mammals (Morrone & Escalante, 2002), birds of the Baja California Peninsula (Rojas-Soto, Alcántara & Navarro, 2003), and flowering plants of the Tehuacán-Cuicatlán Valley (Méndez-Larios *et al.*, 2005). Cacti species were included in this type of analysis in the latter study and in the study by Dávila-Aranda *et al.* (2002), but the Sierra Madre Oriental province was not included in either of these studies.

The aim of the present study was to detect areas of richness and endemism in the Sierra Madre Oriental province based on cacti species, applying a parsimony analysis of endemicity and endemism indices to grid-cells. These analyses should generate useful information on the geographical distribution of Cactaceae in this region, and assist in detecting and proposing areas that require conservation based on this family of flowering plants.

MATERIAL AND METHODS

Study area

The Sierra Madre Oriental province (SMO) is located in the northeastern part of Mexico, and comprises parts of the following states: Coahuila, Nuevo León, Tamaulipas, Durango, Zacatecas, San Luis Potosí, Veracruz, Guanajuato, Querétaro, Hidalgo, and Puebla (Cervantes-Zamora *et al.*, 1990). This province extends to the east to the Gulf of Mexico, in the south to the Transmexican Volcanic Belt, in the west to the Mexican Plateau, and in the north to the northern part of the state of Coahuila, western part of the state of Nuevo León and the southern part of the USA (Fig. 1).

The SMO province is a mountain chain underlain mainly by the Late Cretaceous and early Tertiary Laramide fold and thrust belt. This mountain chain may represent a generally non-extended backarc to the continental arc of the Sierra Madre Occidental (Ortega-Gutiérrez *et al.*, 1994). Climate in this province is variable and most of the main climatic types of the country are represented in the region. Climatic diversity is due to its complex physiographic heterogeneity and meteorological phenomena, among others factors (Hernández-Cerda & Carrasco-Anaya, 2004).

Different and diverse vegetation types occur in the SMO province, but oak and cloud forests are characteristic, with adequate abiotic conditions for their development (Luna, Morrone & Espinosa, 2004b). Although the SMO is a montane area with a prevalence of temperate forests, arid environments are represented in several places, mainly in the lowlands near the Mexican Plateau, where cacti species are well represented (Ruiz, Alcántara & Luna, 2004). In almost 60% of the SMO, dry climate types are present; this condition is influenced by the orographic shadow promoted by the mountain range. Annual average precipitation is lower than 600 mm, and an irregular rainfall season results in dry periods of 6–10 months. Nevertheless, in the Gulf of Mexico area and southeastern portions of the SMO, precipitation is greater than 1200 mm, reaching 4000 mm in the state of Puebla, with dry periods for only 2 months of the year. Maximum annual temperature is in the range 26–30 °C in this region with the exception of the highest areas, whereas the minimum annual temperature is less than 12 °C (Hernández-Cerda & Carrasco-Anaya, 2004).

Several studies have been carried out in this region, including some biogeographic analyses with different taxa, such as vascular plants (Luna *et al.*, 1999, 2000;

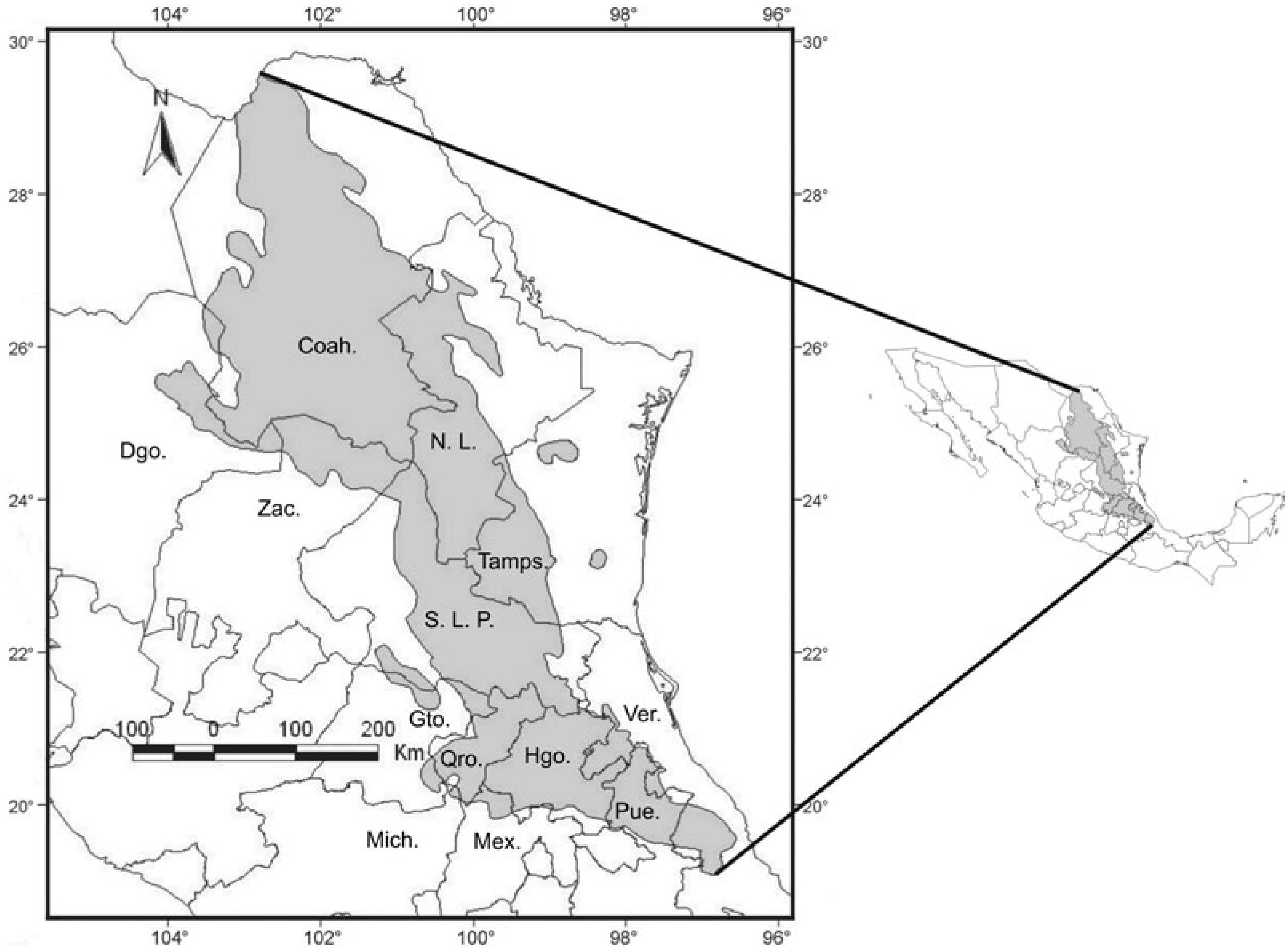

Figure 1. Study area. The grey area shows the localization and limits of the Sierra Madre Oriental (SMO) in Mexico. Coah., Coahuila; Dgo., Durango; Gto., Guanajuato; Hgo., Hidalgo; Mex., Estado de México; Mich., Michoacán; N.L., Nuevo León; Pue., Puebla; Qro., Querétaro; S.L.P., San Luis Potosí; Tamps., Tamaulipas; Ver., Veracruz; Zac., Zacatecas.

González-Zamora *et al.*, 2007), macromycetes (Cifuentes *et al.*, 2004), birds (Navarro *et al.*, 2004), mammals (León-Paniagua *et al.*, 2004), herpetofauna (Canseco-Márquez, Mendoza-Quijano & Gutiérrez-Mayén, 2004), and beetles (Márquez & Morrone, 2004). In these previous studies, the SMO province was divided into two or three subregions.

Distributional data

We included 88 species belonging to 25 genera of the subfamily Cactoideae, most of them included in some risk category of the Norma Oficial Mexicana 059 (NOM-059-ECOL-2001, SEMARNAT, 2002). In addition, 29 of them are recorded in the IUCN (2008) Red Data List of Threatened Species, whereas 22 species are registered in the Appendix I of CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora; http://www.cites.org/) (Table 1). Distributional data for the cacti species were obtained from the revision of 1936 herbarium specimens deposited in the following collections: National Herbarium of the Instituto de Biología, UNAM (MEXU); Herbarium of the Escuela Nacional de Ciencias Biológicas, IPN (ENCB); Herbarium of the Instituto de Ecología A.C. in Pátzcuaro City (IEB); Herbarium of the Facultad de Ciencias, UNAM (FCME); and Herbario Nacional Forestal (INIF). In addition, we obtained some records from the Red Mundial de Información Biótica (REMIB). Finally, five field expeditions to collect, take photographies, and make observations of natural populations of some cacti species were carried out between March 2003 and August 2004 in the Mexican states of Hidalgo, Querétaro, Guanajuato, and Veracruz. Cactus herbarium vouchers were deposited at the FCME. Specimens were georeferenced with the aid of a Global Positioning System.

With the above information, geographic distribution maps of each species were created using ArcView GIS

Table 1. Data matrix (grid-cells of 1° versus cacti species) for the parsimony analysis of endemicity

Areas	*Acharagma roseana*	*Aporocactus flagelliformis*	*Ariocarpus agavoides*	*Ariocarpus kotschoubeyanus*	*Ariocarpus retusus*	*Astrophytum capricorne*	*Astrophytum myriostigma*	*Astrophytum ornatum*	*Aztekium hintonii*	*Aztekium ritteri*	*Cephalocereus senilis*	*Coryphantha durangensis*	*Coryphantha glanduligera*	*Coryphantha maiz-tablasensis*	*Coryphantha nickelsiae*	*Coryphantha poselgeriana*	*Coryphantha pulleineana*	*Coryphantha wohlschlageri*	*Cumarinia odorata*	*Disocactus phyllanthoides*	*Echinocactus grusonii*	*Echinocereus knippelianus*
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Cimarrón	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Ocampo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Santa Rosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cuatrociénegas	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
La Paila	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Torreón	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Parras	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
General Cepeda	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Saltillo	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Los Indios	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Concepción del Oro	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galeana	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
La Ascensión	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mier y Noriega	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1
Ciudad Victoria	0	0	1	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Guadalcázar	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0
Ciudad del Maíz	0	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Xichú	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jalpan	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pisaflores	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Querétaro	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zimapán	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Metztitlán	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Teziutlán	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Jalapa	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Risk categories																						
NOM-059	Pr	Pr	Pr	Pr	Pr	A	A	A	Pr	A	A	Pr	A	A	A	A	Pr	Pr	Pr	A	P	A
IUCN			VU	NT										EN					VU		CR	
CITES			I	I	I					I												

Areas	*Echinocereus longisetus*	*Echinocereus nivosus*	*Echinocereus reichenbachii*	*Escobaria laredoi*	*Escobaria missouriensis*	*Geohintonia mexicana*	*Glandulicactus crassihamathus*	*Leuchtenbergia principis*	*Lophophora difusa*	*Mammillaria albicoma*	*Mammillaria albiflora*	*Mammillaria aurihamata*	*Mammillaria baumii*	*Mammillaria bocasana*	*Mammillaria carmenae*	*Mammillaria coahuilensis*	*Mammillaria decipiens*	*Mammillaria duwei*	*Mammillaria erythrosperma*	*Mammillaria grusonii*	*Mammillaria hahniana*	*Mammillaria herrerae*
	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
Cimarrón	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ocampo	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Santa Rosa	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cuatrociénegas	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
La Paila	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Torreón	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parras	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
General Cepeda	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Saltillo	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Los Indios	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Concepción del Oro	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Galeana	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
La Ascensión	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mier y Noriega	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Ciudad Victoria	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0
Guadalcázar	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0
Ciudad del Maíz	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Xichú	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	1	1	0	1	1
Jalpan	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Pisaflores	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Querétaro	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0
Zimapán	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1
Metztitlán	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Teziutlán	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jalapa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Risk categories																						
NOM-059	A	Pr	A	Pr	A	Pr	A	A	A	Pr		Pr	Pr	Pr	P	A	Pr	Pr	A	Pr	A	P
IUCN									VU	EN	CR	R						EN				CR
CITES																						

Table 1. *Continued*

TAXA

Areas	*Mammillaria humboldtii*	*Mammillaria klissingiana*	*Mammillaria laui*	*Mammillaria lenta*	*Mammillaria longimamma*	*Mammillaria mathildae*	*Mammillaria melaleuca*	*Mammillaria microhelia*	*Mammillaria nana*	*Mammillaria orcuttii*	*Mammillaria parkinsonii*	*Mammillaria pilispina*	*Mammillaria plumosa*	*Mammillaria roseoalba*	*Mammillaria schiedeana*	*Mammillaria stella-de-tacubaya*	*Mammillaria surculosa*	*Mammillaria weingartiana*	*Mammillaria zeilmanniana*	*Mammilloydia candida*	*Obregonia denegrii*
	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
Cimarrón	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ocampo	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Santa Rosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cuatrociénegas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
La Paila	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Torreón	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parras	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
General Cepeda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Saltillo	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Los Indios	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Concepción del Oro	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galeana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
La Ascensión	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Mier y Noriega	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0
Ciudad Victoria	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	1	1
Guadalcázar	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	1	0	0	1	0
Ciudad del Maíz	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Xichú	0	1	0	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	0
Jalpan	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0
Pisaflores	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Querétaro	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Zimapán	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
Metztitlán	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Teziutlán	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jalapa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Risk categories																					
NOM-059	A	A	P	A	A	P	A	Pr	Pr	Pr	Pr	Pr	A	Pr	Pr	Pr	Pr	A	Pr	A	A
IUCN						VU		VU								VU		VU	EN		VU
CITES																					I

Areas	*Pelecyphora aselliformis*	*Pelecyphora strobiliformis*	*Pilosocereus cometes*	*Stenocactus sulphureus*	*Strombocactus disciformis*	*Thelocactus hastifer*	*Thelocactus leucacanthus*	*Thelocactus rinconensis*	*Thelocactus tulensis*	*Turbinicarpus alonsoi*	*Turbinicarpus beguinii*	*Turbinicarpus booleanus*	*Turbinicarpus gielsdorfianus*	*Turbinicarpus horripilus*	*Turbinicarpus laui*	*Turbinicarpus pseudomacrochele*	*Turbinicarpus pseudopectinatus*	*Turbinicarpus saueri*	*Turbinicarpus schmiedickeanus*	*Turbinicarpus subterraneus*	*Turbinicarpus valdezianus*	*Turbinicarpus viereckii*	*Turbinicarpus zaragozae*
	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87
Cimarrón	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ocampo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Santa Rosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cuatrociénegas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
La Paila	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Torreón	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parras	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
General Cepeda	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Saltillo	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Los Indios	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Concepción del Oro	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galeana	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
La Ascensión	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Mier y Noriega	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	1	0
Ciudad Victoria	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	1	0	0	1	1
Guadalcázar	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0
Ciudad del Maíz	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Xichú	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Jalpan	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Pisaflores	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Querétaro	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zimapán	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Metztitlán	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Teziutlán	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jalapa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Risk categories																							
NOM-059	Pr	A	Pr	Pr	A	Pr	Pr	A	A		Pr		P		Pr	P	Pr			A	Pr		
IUCN						VU				CR		CR	CR	VU	VU	VU	VU			VU	VU	NT	VU
CITES	I	I			I					I	I	I	I	I	I	I	I	I	I	I	I	I	I

Species list and risk categories of NOM-059, IUCN and CITES for the cacti studied. Risk categories: NOM-059-ECOL-2001: P, endangered; A, threatened; Pr, with special protection. IUCN: CR, critically endangered; EN, endangered; NT, near threatened; R, rare; VU, vulnerable. CITES: I, Appendix I, list of species that are the most endangered among CITES-listed animals and plants.

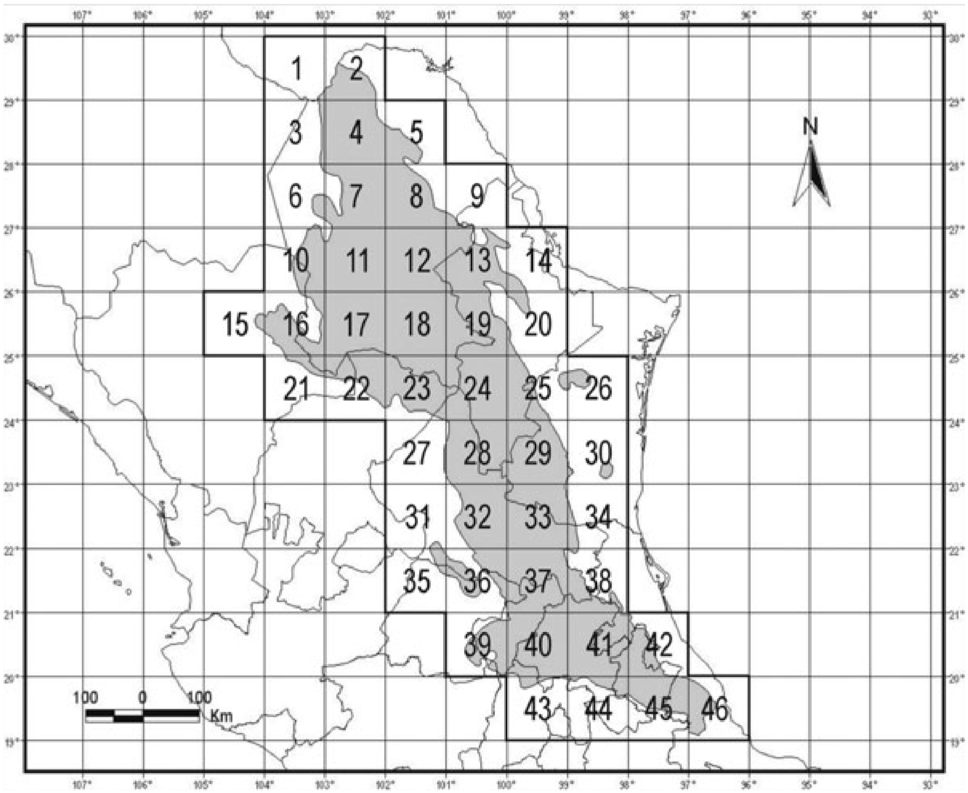

Figure 2. Grid-cells employed in the present study overlayed on a map of the Sierra Madre Oriental.

(ESRI 1999; data not shown). Most of the cacti studied herein are geographically restricted to the SMO province, but some are shared with the Mexican Plateau or occur in the USA. The map of known distribution of each species was projected on a grid map of the SMO divided into cells of one degree per side.

Data analysis

PAE method

We divided the SMO province in 46 grid-cells of 1° latitude × 1° longitude, which were used as units of analysis to run PAE, but cacti species were only recorded in 25 of the cells (Fig. 2). Consequently, we used 88 species (columns) and 25 grid-cells (rows) to construct the data matrix (Table 1). The matrix included one row coded with all zeros to root the area cladogram. The data matrix analysis was carried out using NONA (Goloboff, 1999) through WINCLADA (Nixon, 2002), applying multiple tree bisection-reconnection, searching on 100 000 initial trees (mult*100), and holding 30 trees per replication (*h*/10). When more than one parsimonious cladogram resulted from the analysis, a strict consensus cladogram was constructed.

Morrone (1994) proposed PAE as a tool to detect areas of endemism, using grid-cells as units based on their shared species, where a group of grid-cells defined by at least two taxa represents an area of endemism. We drew the grid-cells on a map of Mexico, including only those where at least one species was recorded. With this information, we constructed the data matrix described above and performed a parsimony analysis. The resultant cladogram grouped those grid-cells with shared species, and those groups were superimposed onto the map of grid-cells, delimiting the areas of endemism.

Endemism indices

We chose grid-cells of one geographical degree per side, partially to facilitate the data manipulation and to reduce the effect of sampling artefacts, such as mapping errors and unsampled grids in sparsely inhabited areas (Crisp *et al.*, 2001). This scale size was also chosen because it was tested in previous studies on areography and diversity of different groups of Mexican flora (Kohlmann & Sánchez, 1984; García-Mendoza, 1995; Dávila-Aranda, Lira & Valdés-Reyna, 2004; Contreras-Medina & Luna, 2007). We applied richness and endemism indices proposed by Crisp *et al.* (2001) and Linder (2001) to these grid-cells, aiming to detect centres of species richness and endemism of Cactaceae.

Species richness also known as 'unweighted species richness' was measured as the total count of species within each grid-cell (Linder, 2001). A first index termed 'weighted endemism' comprises several steps (Crisp *et al.*, 2001). The first step consisted of dividing each grid-occurrence by the total number of grids in which one species occurs. Thus, a species restricted to a single grid was scored as '1' for that grid, and '0' for all other grids, and a species found in five grids, was scored as '0.2' for each of the five grids, and '0' for all remaining grids; then the sum of all score species values for each grid was obtained. A second index termed 'corrected weighted endemism' (Crisp *et al.*, 2001), consisted of dividing the weighted endemism index by the total count of species in each grid cell. Those grid-cells with the highest scores in the first index were considered as centres of richness and for the second index as centres of endemism (Crisp *et al.*, 2001; Linder, 2001). Grid-cells with none or one species recorded were excluded from the analysis of corrected weighted endemism and are not shown in the resultant map because these cells do not include overlapping distributions, which represent a basic characteristic of the area of endemism concept. Grid-cell values obtained for weighted endemism (WE) and corrected weighted endemism (CWE) indices were scaled from 1 to 10, considering those values above the mean as centres of richness or centres of endemism depending of the index employed. These centres are composed of sets of neighbouring grid-cells or isolated grid-cells with high values in each index. Each species was scored as present in a grid-cell independently of whether it was recorded once or numerous times in that grid-cell (Linder, 2001).

We also carried out a regression analysis to evaluate the correlation between WE and CWE, in relation to species richness to detect important areas with endemic species independent of their species richness because Linder (2001) considered that WE is a measure sensitive to diversity, whereas CWE is not significantly correlated with grid diversity.

RESULTS AND DISCUSSION

Grid-cells analysis

The Sierra Madre Oriental province was divided in 46 grid-cells, 25 of them including at least one record; these were used as units of analysis. For the present study, we included 1223 occurrence records for 88 species of cacti. The mean and median numbers of occurrences are two grid-cells, and the mode a single cell (43 species). The taxa found in the greatest number of grid-cells were *Ariocarpus retusus* and *Astrophytum capricorne*, recorded each in ten grid-cells. Other well-represented taxa were *Ariocarpus kotschoubeyanus* and *Coryphantha poselgeriana*, recorded in eight and seven grid-cells, respectively.

Cacti species in the SMO are mainly distributed in arid scrub and tropical deciduous forest; however, some species inhabit other types of vegetation that receive more rainfall, such as oak forest, pine-oak forest, and cloud forest. Notwithstanding, the distributional patterns obtained in the present study are mainly defined by arid landscapes.

Two previous studies (Gómez-Hinostrosa & Hernández, 2000; Hernández, Gómez-Hinostrosa & Bárcenas, 2001) carried out systematic strategies for sampling Cactaceae at the central part of the SMO and found elevated diversity levels and species richness concentrated in two grid-cells (Mier y Noriega and Guadalcázar). These rich grid-cells contrast with other areas of the SMO, where collections are few or absent (Fig. 3). Some areas have been investigated over several years and by different botanists, with more or less intensive specimen collection, such as Cd. Victoria and Jaumave in the state of Tamaulipas (Martínez-Ávalos & Jiménez, 1993; Hernández, 1998), the states of Coahuila (Pinkava, 1984; Wehbe & Elizondo, 1986), and Querétaro (Scheinvar, 2004). All these previous studies contribute herbarium specimens that were recorded and used in the present study.

Richness values and the number of endemic species to each grid-cell are presented in Table 2. Grid-cells richest in species were concentrated in different areas (Fig. 3), mainly located in the states of Hidalgo, Nuevo León, Querétaro, San Luis Potosí, and Tamaulipas. The Cd. Victoria grid-cell, located in the state of Tamaulipas, is the richest (Fig. 3), followed by Guadalcázar and Mier y Noriega grid-cells, San Luis Potosí, and Nuevo León (Table 2). Our results are congruent with those of Hernández *et al.* (2001) in that the Guadalcázar grid-cell is an exceptionally rich area, including both geographically-restricted and widespread cacti species. In comparison with other Mexican areas, and also with other American areas, this grid-cell has an extraordinary richness of cacti species, despite its small size (Hernández *et al.*, 2001). Furthermore, Godínez-Álvarez & Ortega-Baes (2007) detected that San Luis Potosí, Coahuila, and Nuevo León represent the Mexican states with high species richness in the country, which are included in the SMO. Similarly, Martínez-Ávalos & Jurado (2005) detected some grid-cells in the state of Tamaulipas with high cacti diversity within the SMO.

In relation to endemism, those grid-cells containing more geographically-restricted species are mainly concentrated in the states of Hidalgo, Guanajuato, Nuevo León, San Luis Potosí, and Tamaulipas. The area richest in endemic species is also the Cd. Victoria grid-cell (Table 2) with eight endemic species, fol-

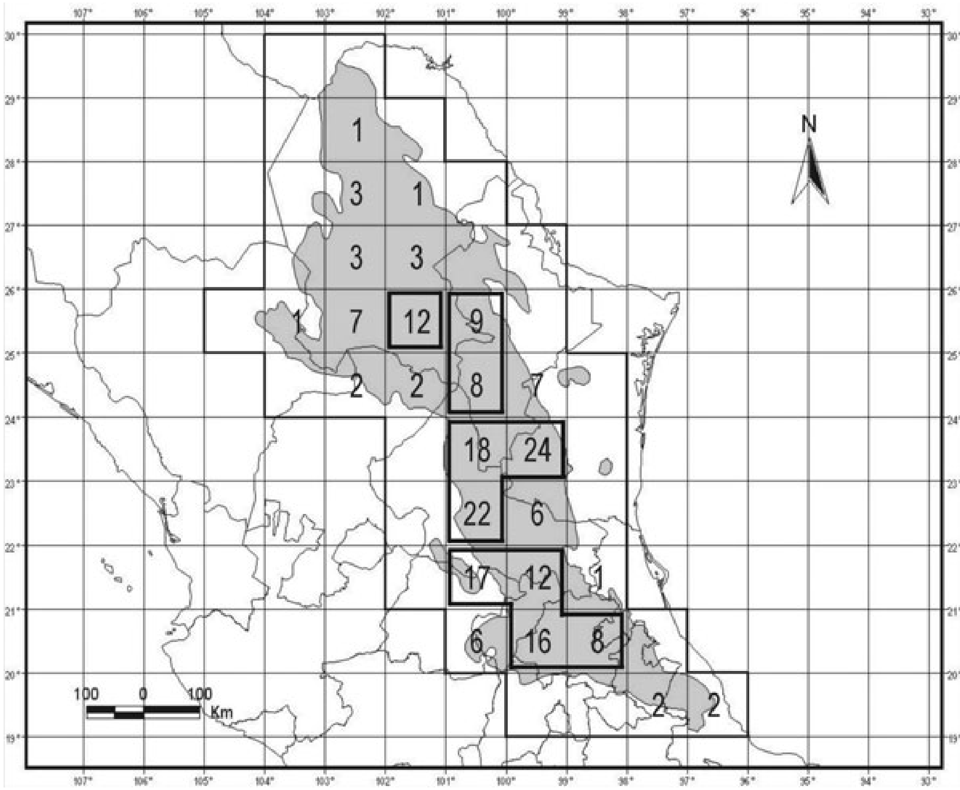

Figure 3. Grid-cells richest in species of Cactaceae in the Sierra Madre Oriental. Numbers are species recorded in each grid-cell.

lowed by Guadalcázar, Xichú and Zimapán grid-cells with four species each. A high proportion of the cacti species studied are geographically restricted to the SMO and some genera are distributed exclusively in this province (monotypic or stenoendemic *sensu* Gómez-Hinostrosa & Hernández, 2000), such as *Strombocactus*, *Geohintonia*, and *Obregonia*, among others. Some species are also distributed in the Mexican Plateau (e.g. *Ariocarpus retusus* and *Mammillaria bocasana*), whereas others are also distributed in the USA (e.g. *Echinocereus reichenbachii* and *Escobaria missouriensis*).

Geographic distribution of cacti species that inhabit the SMO are limited by geographic barriers, which have influenced the distribution of the cactological flora of this province. In general, the main area in the SMO where cacti species are distributed is located from the central portion of the state of Hidalgo throughout the northwestern part of the Sierra, reaching the vicinities of the Sierra de la Paila in the state of Coahuila, and maybe as far as the Cuatrociénegas basin. The more elevated portions of this province are located in the eastern portion of the SMO, with oak, pine, and cloud forests; cacti species occur in this area but are not as diverse as in the lower parts of the Sierra. The SMO runs from the northern portion of the state of Puebla through the northwestern reaching the Saltillo-Monterrey region; in its southern portion, it contacts the Transmexican Volcanic Belt, which represents a barrier for many cacti species; however, some of them continue their distribution along the other side of this chain in southern Puebla, mainly in the Tehuacán-Cuicatlán Valley (e.g. *Echinocactus platyacanthus* and *Myrtillocactus geometrizans*). To the west, the SMO neighbours the Mexican Plateau, which also acts as barrier; the relatively extreme climatic conditions of this arid region represent a limiting factor that prevents expansion of several cacti species into this region. Finally, climatic conditions in the northern portion of the SMO are similar to those found in the Mexican Plateau, where a clear reduction of species richness is evident. Many species that are distributed in the northern portion of the SMO are also distributed in the Mexican Plateau, such as *Ariocarpus fissuratus*, *Echinocereus poselgeri*, *Epithelantha micromeris*, *Escobaria dasyacantha*, *Glandulicactus uncinatus*, *Lophophora williamsii*, and *Thelocactus bicolor*.

PAE

The data matrix including 88 species and 25 grid-cells is shown in Table 1. PAE produced 171 most parsi-

Table 2. Species richness, endemism and range values of grid-cells obtained for weighted endemism (WE) and corrected weighted endemism (CWE)

Grid-cell number	Grid-cell name	Richness (number of species)	Endemics (number of species)	WE	Class	CWE	Class
29	Cd. Victoria	24	8	13.122	10	0.546	9
32	Guadalcázar	22	4	9.572	8	0.435	7
36	Xichú	17	4	8.448	7	0.496	8
40	Zimapán	16	4	7.907	7	0.494	8
28	Mier y Noriega	18	1	6.789	6	0.377	6
18	General Cepeda	12	3	5.699	5	0.474	8
24	Galeana	8	3	4.599	4	0.574	9
37	Jalpan	12	1	4.398	4	0.366	6
19	Saltillo	9	1	4.266	4	0.474	8
41	Metztitlán	8	3	4.199	4	0.524	9
39	Querétaro	6	3	3.916	3	0.652	10
17	Parras	7	2	3.341	3	0.477	8
33	Cd. del Maíz	6	2	2.591	2	0.431	7
25	La Ascención	7	1	2.257	2	0.322	5
12	La Paila	3	1	1.242	1	0.414	7
23	Concepción del Oro	2	1	1.100	1	0.555	9
7	Ocampo	3	0	0.975	1	0.325	5
11	Cuatrociéneagas	3	0	0.641	1	0.213	4
46	Jalapa	2	0	0.499	1	0.249	4
45	Teziutlán	2	0	0.499	1	0.249	4
22	Los Indios	2	0	0.267	1	0.133	3

Indices values were in the range 1–10, considering those values above the mean value (mean = 4.111 in WE and mean = 0.418 in CWE) as centres of richness for WE and centres of endemism for CWE; these centres are composed by sets of neighbouring grid-cells with high values for each index.

monious cladograms of 86 steps, a consistency index of 0.52, and a retention index of 0.60. The strict consensus cladogram (Fig. 4), with 92 steps, consistency index of 0.48, and retention index of 0.55, showed a polytomy composed of eight grid-cells and three main components. The first component is comprised by Cuatrociénegas, Parras, and General Cepeda grid-cells at the northern part of the province (state of Coahuila); the second component by Saltillo, Galeana, La Ascención, Ciudad del Maíz, Guadalcázar, Mier y Noriega, and Cd. Victoria at the central part of the province (states of Coahuila, Nuevo León, Tamaulipas, and San Luis Potosí), and the third component includes Pisaflores, Teziutlán, Jalapa, Metztitlán, Xichú, Jalpan, and Zimapán grid-cells (states of Hidalgo, Guanajuato, Querétaro, Veracruz, and Puebla), located at the southern part of the Sierra.

In the northern component, there are two areas of endemism (Fig. 5). Parras is characterized by *Mammillaria grusonii* and *Mammillaria stella-de-tacubaya* and General Cepeda is supported by *Acharagma roseana*, *Echinocereus nivosus*, and *Escobaria laredoi*.

The second and central component is divided in two clades (Fig. 5); one consists of two grid-cells and forms an area of endemism (Saltillo-Galeana), which is characterized by *Aztekium ritterii* and *Turbinicarpus subterraneus*; *Mammillaria plumosa* is endemic to the Saltillo, whereas *Aztekium hintonii*, *Geohintonia mexicana*, and *Turbinicarpus booleanus* are geographically restricted to Galeana. A second clade comprised three areas of endemism; the first was Cd. del Maíz, supported by *Coryphantha maiz-tablasensis* and *Turbinicarpus gielsdorfianus*; the second was Guadalcázar, supported by *Coryphantha pulleineana*, *Coryphantha wohlschlageri*, *Pelecyphora aselliformis*, and *Turbinicarpus laui*; the third area consited of Mier y Noriega and Cd. Victoria grid-cells and is characterized by the restricted distributions of *Mammillaria albicoma*, *Pelecyphora strobiliformis*, and *Turbinicarpus viereckii*, whereas *Ariocarpus agavoides*, *Mammillaria baumii*, *Mammillaria carmenae*, *Mammillaria laui*, *Mammillaria melaleuca*, *Mammillaria roseoalba*, *Obregonia denegrii*, and *Turbinicarpus zaragozae* are geographically restricted to Cd. Victoria (Fig. 5). This area represents the grid-cell richest in geographically-restricted species.

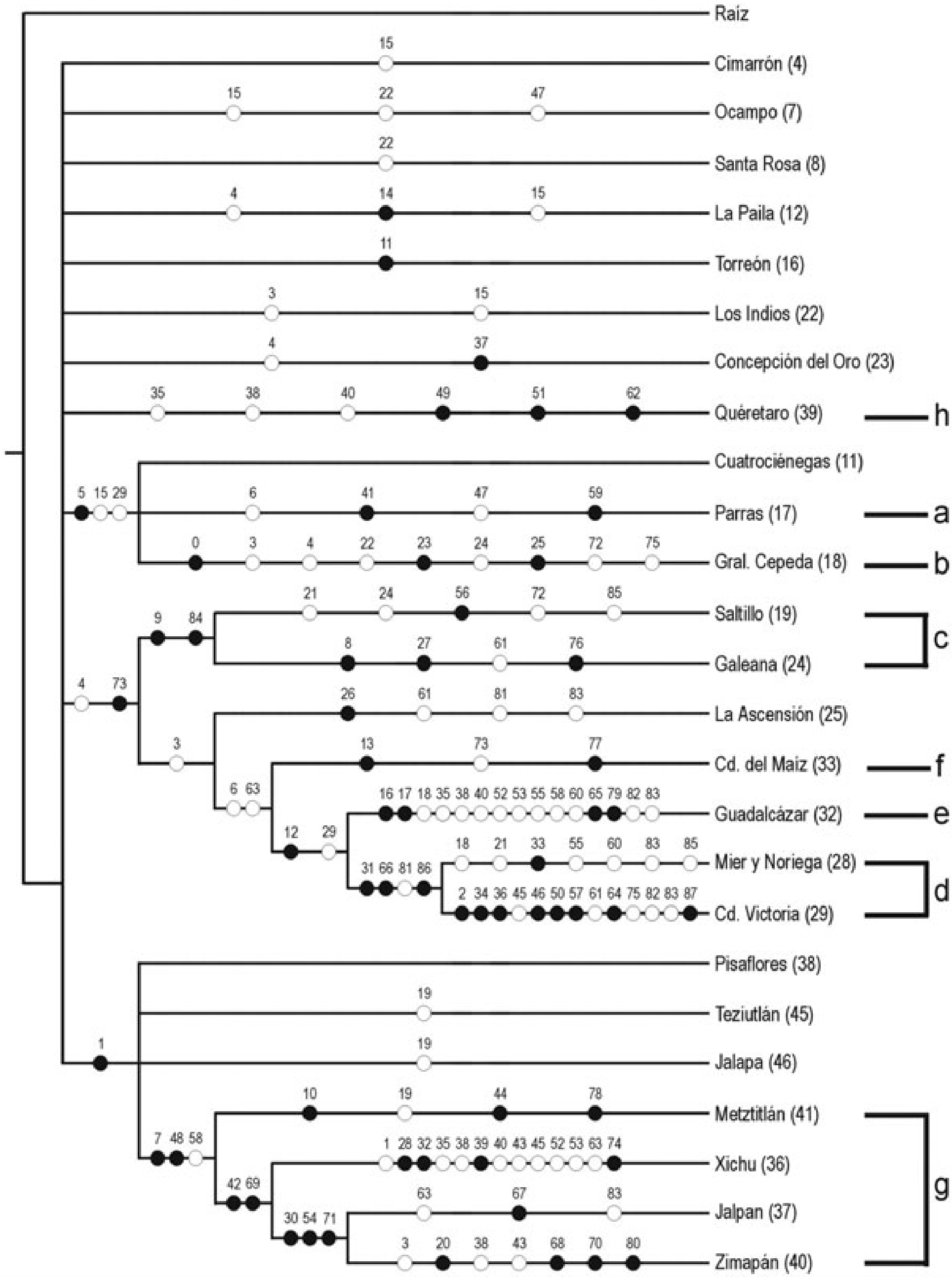

Figure 4. Strict consensus cladogram obtained with grid-cell analysis. The numbers after the name of grid-cell corresponds to the numbers shown in Fig. 2. Numbers above branches represent the number of species shown in Table 1. Black circles, synapomorphies; white circles, homoplasies.

The third and southern component (Fig. 5) is composed of four grid-cells (Xichú, Jalpan, Zimapán, and Metztitlán), forming an area of endemism supported by *Astrophytum ornatum* and *Mammillaria longimamma*. These grid-cells contain one or more geographically-restricted species: *Cephalocereus senilis*, *Mammillaria humboldtii*, and *Turbinicarpus horripilus* are restricted to Metztitlán, *Glandulicactus crassihamathus*, *Mammillaria albiflora*, *Mammillaria duwei*, and *Turbinicarpus alonsoi* are restricted to Xichú, and *Pilosocereus cometes* is restricted to Jalpan; finally *Echinocactus grusonii*, *Stenocactus sulphureus*, and *Turbinicarpus pseudomacrochele* are restricted to Zimapán.

Consensus cladogram shows a polytomy, which includes eight grid-cells, four of which contain at least

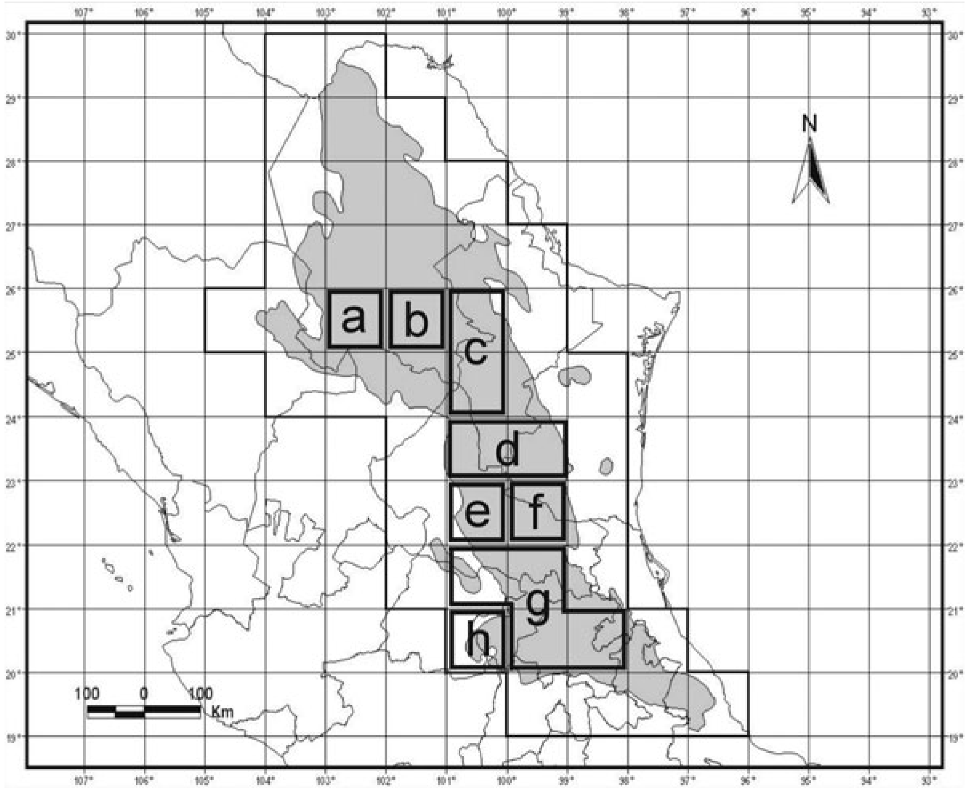

Figure 5. Areas of endemism obtained with the parsimony analysis of endemicity method. a, Parras (17); b, General Cepeda (18); c, Saltillo-Galeana (19 and 24); d, Mier y Noriega-Cd. Victoria (28 and 29); e, Guadalcázar (32); f, Cd. del Maíz (33); g, Xichú-Jalpan-Zimapán-Metztitlán (36, 37, 40 and 41); h, Querétaro (39). Numbers after names of grid-cells are as indicated in Fig. 2.

one geographically-restricted species; these grid-cells are La Paila, Torreón, Concepción del Oro and Querétaro. Only the latter was considered as an area of endemism because, in this grid-cell, *Mammillaria mathildae*, *Mammillaria microhelia*, and *Mammillaria zeilmanniana* occur exclusively (Fig. 5).

In summary, the results obtained in the present study suggest that the SMO province is composed by three sections: a meridional and a central one, which includes many endemic taxa, and one septentrional, which is mainly related with the Mexican Plateau province. These three sections are separated by two geographic features: the Pánuco Basin, which represents a natural barrier and divides the meridional from the central section, and a second feature, which comprises the Saltillo-Monterrey montane system, consisting of faults and deformations located between the states of Nuevo León and Coahuila, and end in the state of Zacatecas, which divides the central from the septentrional section. The area northeast of this montane system is small and includes two areas of endemism. The inclusion of this septentrional area in the SMO is controversial because many taxa and some grid-cells of the polytomy show strong relationships with the Mexican Plateau, so the analysis including cacti species distributed in both provinces (SMO and Mexican Plateau) could clarify and resolve problems in the delimitation of these two provinces. The central region includes four areas of endemism; the Pánuco basin divides the central section from the meridional one. This southern portion represents an area of endemism that mainly coincides with the Sierra Gorda in the state of Querétaro and with the Metztitlán gorge in the state of Hidalgo.

The Saltillo-Monterrey montane system was previously recognized by González-Zamora *et al.* (2007) as an important geographic feature in the biogeography of Asteraceae, dividing a central section from a septentrional one. In a study of the vascular plants of cloud forests, the Pánuco basin represented a barrier that separates the SMO in two sections (Luna *et al.*, 1999).

Several earlier studies that examined the relationships among the different sections of the Sierra Madre Oriental show partial agreement with our results, in that the division of this mountain range in three regions agrees with prior results based in mammals (León-Paniagua *et al.*, 2004), birds (Navarro *et al.*,

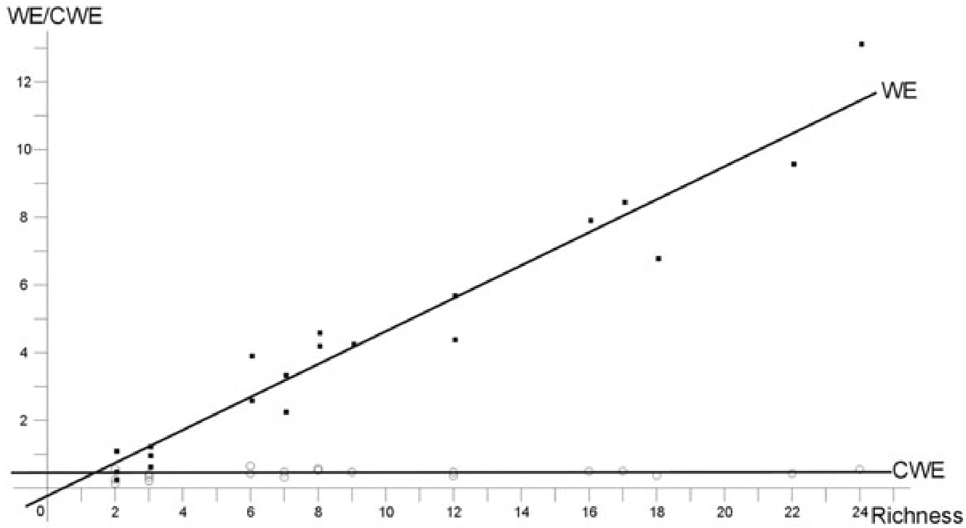

Figure 6. Correlation between grid-cell diversity and endemism indices. Weighted endemism (WE): $r = 0.974 \geq r$ ($\upsilon = 23$, $\alpha = 0.01$) = 0.396; corrected weighted endemism (CWE): $r = 0.242 \leq r$ ($\upsilon = 23$, $\alpha = 0.01$) = 0.396.

2004), and Asteraceae (González-Zamora *et al.*, 2007). In this sense, distribution of Cactaceae supports this biogeographic regionalization.

Indices analysis

Ranges values of grid-cells obtained from the WE and CWE indices of Cactaceae species are shown in Table 2, including the rank class of each grid-cell. With the values of WE (which counts all the species in an inverse proportion to their range), we produced a map that resembles the pattern of species richness represented in Figure 3. This is an expected result because Crisp *et al.* (2001) suggested that there is a high correlation between WE and species richness. Correlation between the WE and CWE in relation to species richness show that the values of WE are correlated with richness at 99% of confidence level, whereas CWE values are not significant at the same confidence level (Fig. 6). The regression analysis showed that WE index presents a positive relation with richness.

The ten grid-cells with the highest WE index values in relation to an arithmetic mean are very similar to those obtained for species richness (Fig. 7).

The map representing the values of CWE (Fig. 8) showed a remarkable correspondence with those areas obtained with PAE. This index emphasizes such areas that are not necessarily high in species richness, but have a high proportion of geographically-restricted species. This is the case of the Cd. Victoria grid-cell.

Table 2 shows grid-cell values obtained with CWE, including some grid-cells not considered in the WE index, such as Querétaro and Concepción del Oro. Furthermore, Galeana and Metztitlán, with low values of the WE index, have high values for the CWE index. For the CWE index, Guadalcázar and Mier y Noriega grid-cells have low values, despite having high richness values.

When we compare those grid-cells with higher values in relation to the arithmetic mean, a different result is obtained with the CWE index because four areas of endemism are included. In the CWE index the septentrional area is composed of four rather than two grid-cells (WE and PAE), by the addition of La Paila and Concepción del Oro.

The Saltillo and Galeana grid-cells represent an interesting area because it appears in both analyses (CWE and PAE).

At the central part of the SMO, an area composed by Cd. Victoria, Guadalcázar and Cd. del Maíz grid-cells have the highest values of CWE, and, for this reason, deserves special attention because these grid-cells contains several species that are geographically restricted to the SMO.

The meridional area of SMO is composed of four grid-cells (Querétaro, Metztitlán, Xichú, and Zimapán); the first had the highest value of CWE, and the remaining three had similar values. Cd. del Maíz and Querétaro grid-cells had high CWE values due to their high proportion of endemic species, independent of their species richness; however, values of these grid-cells would change if we considered other species inhabiting the SMO and shared with other Mexican provinces. This is common in other grid-cells with high CWE index values, mainly those located in the northern and western portions of the state of Coahuila, because they are transitional between the

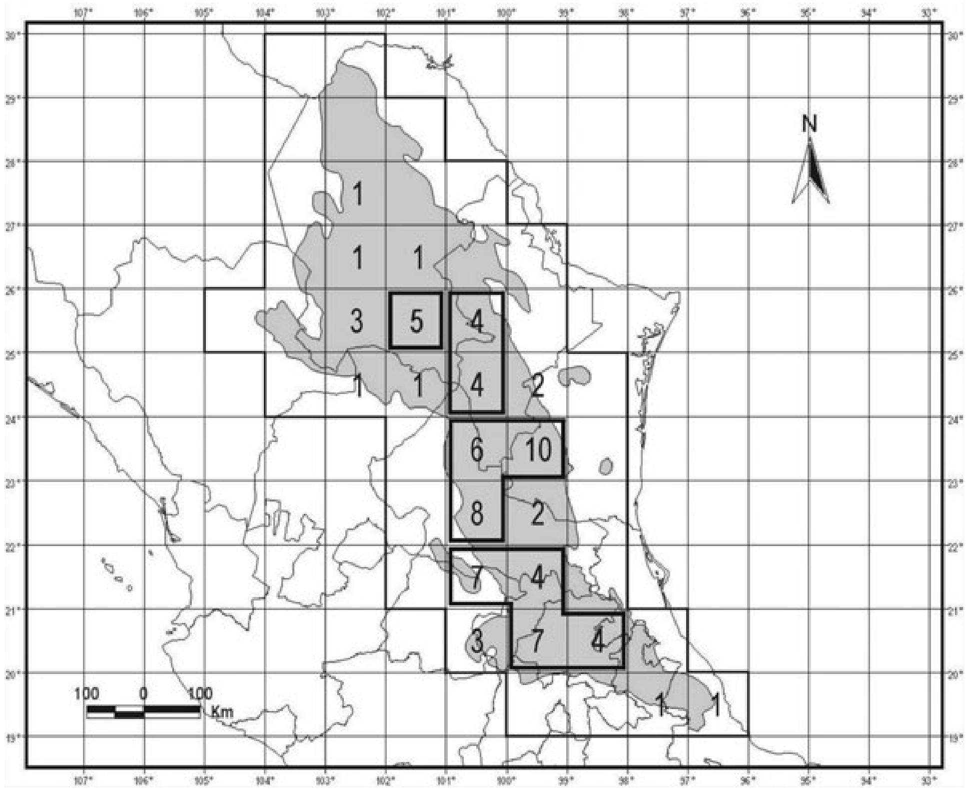

Figure 7. Weighted endemism of endemic cacti of the Sierra Madre Oriental. The number in each grid-cell represents the sum of weights for all species occurring in each grid-cell (range 1–10).

Mexican Plateau and the southern part of the USA. Future studies in the zone are necessary to establish their relationships. Some SMO areas could benefit from future analyses that include more cacti species, especially those located along the boundary with the Chihuahuan Desert. These diffuse limits do not occur in the eastern and southern portions of the SMO, where natural barriers (SMO cliffs in east and Transmexican Volcanic Belt in the south) limit the geographic distribution of cacti species investigated in the present study.

The present study includes those cacti species endemic or almost geographically restricted to the SMO province. As a result, peripheral grid-cells present unexpected values in both indices. This pattern is also evident in the studies of Linder (2001) and Crisp *et al.* (2001), where a clear diminution of species richness is noted in grid-cells outside the study area (edge effect).

Conclusions

Because Cactaceae is an American endemic with the exception of some species of *Rhipsalis*, we propose the use of this framework for the other richest sites in the American Continent, such as southeastern USA, northeastern Brazil, north of Argentina, and some sites of Bolivia and Peru (Hernández & Godínez, 1994); notwithstanding, the biogeographical methodology used in the present study can be tested with other sets of organisms, environments, and places. Many countries in Central and South America with a high diversity of Cactaceae have not performed conservation actions (Boyle & Anderson, 2002); thus, there are no rules to insure their conservation. As Ortega-Baes & Godínez-Álvarez (2006) suggested, there is an urgent need to focus conservation efforts in the establishment of priority areas based on desert ecosystems, where a high diversity of cactus exist.

Repeatability of the methods applied in the present study can be carried out in some Latin American countries where endemism and a high percentage of threatened cacti species is notable, such as Chile, Ecuador, Brazil, and Cuba (Hernández & Godínez, 1994), as well as in other arid and semiarid regions of Mexico, in order to contribute to conservation plans of threatened species of Cactaceae. In some Latin American countries, it is necessary to carry out similar studies due to the high richness and endemism in relation to their geographic area, in order to formulate conservation plans of Cactaceae, such as Argentina and Peru, but these countries do not have

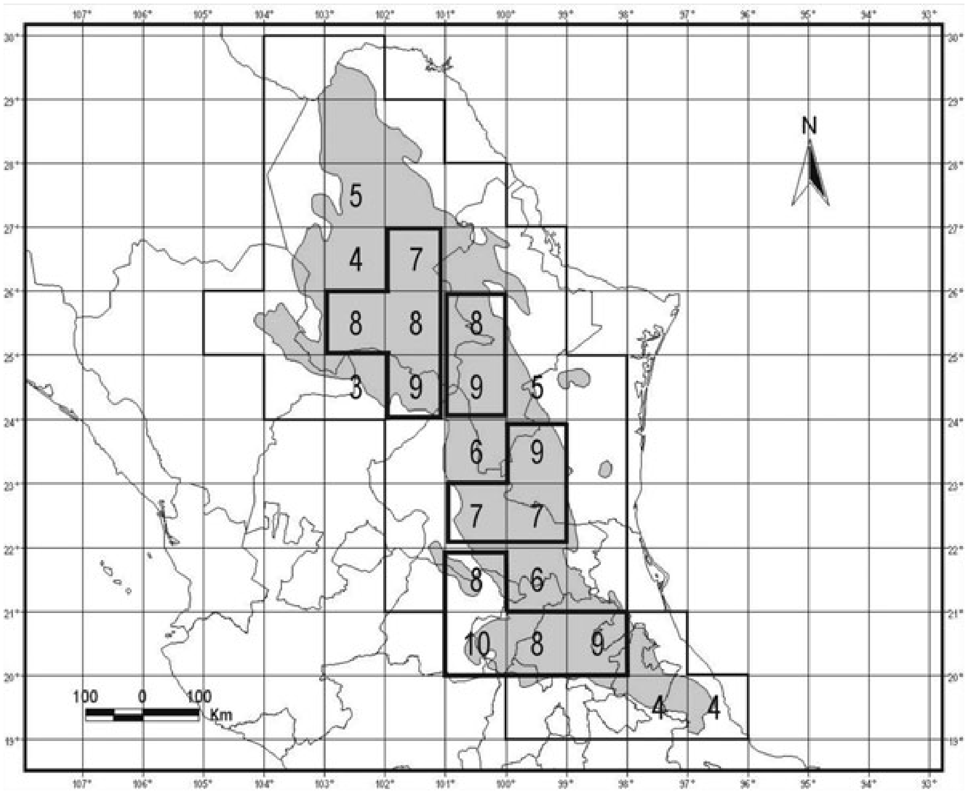

Figure 8. Corrected weighted endemism of endemic cacti of the Sierra Madre Oriental. The number in each grid-cell is the weighted endemism for that grid-cell, divided by the grid-cell diversity (range 1–10).

national red lists or demographic studies of threatened or endangered cacti, and, furthermore, they not have legislation to regulate the national and international trade of their native species of Cactaceae (Ortega-Baes & Godínez-Álvarez, 2006).

The recognition and localization of areas with potential value for the conservation of Mexican cacti represents an important step in conservation plans of this family of flowering plants because, as Hernández & Godínez (1994) suggest, there is an urgent need for the implementation of strategies for the conservation of Mexican cacti, mainly due to fragility caused by biological and intrinsic ecological factors, as well as anthropogenic pressures of natural populations (Hernández & Godínez, 1994).

As Hernández & Godínez (1994) noted when referring to Cactaceae, restricted taxa are potentially more endangered than those that are widespread; in this sense, Cactaceae with 78% of its species endemic to Mexico, constitute a plant group in need of urgent conservation; furthermore, Godínez-Álvarez & Ortega-Baes (2007) suggest that it is crucial to obtain information on different biological and ecological aspects of Cactaceae, such as their geographical distributions, endemism, and threatened species, because this contributes to adequate management and conservation at the regional level, which is the case with respect to the present contribution.

The present study is based on the distributional data for cacti species included in some risk category in the NOM-059-ECOL-2001 (SEMARNAT, 2002), IUCN (2008) Red Lists, and the Appendix I of CITES. These types of studies by themselves are fundamental for conservation. A network of scattered reserves partially located in the SMO province was previously suggested (Hernández & Bárcenas, 1995), and we propose that some of the grid-cells analysed in the present stusy must be included in a conservation plan of Cactaceae.

The present study represents an example of the value of specimen-based data, such as those held in museums and herbaria. Most of the distributional data of the species of Cactaceae used in the present study were obtained from an analysis of hundreds of specimens from Mexican herbaria. Data obtained from herbaria are of special value because permanently preserved specimens can be physically examined, and re-examined on subsequent occasions, and any comments about identification noted (Hall, 1994). Although such botanical collections harbour millions or thousands of specimens, these do not reflect the real or potential geographical distribution of species

(González-Zamora *et al.*, 2007), so we consider our results as an approximation of the most up to date general biogeographic scenario of Cactaceae in the SMO.

Distributional data from scientific collections are only useful if they are available (Crisp *et al.*, 2001). The 'Red Mexicana Sobre la Biodiversidad' (REMIB) hosted in the web page of the Comisión Nacional Para el Uso y Conocimiento de la Biodiversidad (CONABIO), located in Mexico City, has compiled data access on the available scientific collections in Mexico and represents a web-based flora and fauna information system developed by the cooperation of several American and Mexican scientific institutions (Contreras-Medina & Luna, 2007). Unfortunately, it only provides direct access to a fraction of the specimen-based data. Furthermore, distributional information of threatened and rare species is relevant for families such as Cactaceae and represents key data in analyses such as the one presented here. Finally, specimen determinations in scientific collections are not revised regularly (Contreras-Medina & Luna, 2007).

The results obtained in the present study agree with those obtained previously in studies of different taxa (Luna *et al.*, 2004b). Our results can be used in future analyses of arid and semiarid Mexican areas and can be contrasted with other biological groups (animals, fungi, and other plants). This study contributes to the proposal of Godínez-Álvarez & Ortega-Baes (2007), because these authors consider that is necessary to identify areas with richness and endemicity across Mexico and, accordingly, carried out analyses of cactus diversity in that country.

The conservation plans in Cactaceae not only insure the preservation of grid-cells with high species richness and endemic species, but also endangered ones (Godínez-Álvarez & Ortega-Baes, 2007), which is a special consideration because all the species used in the present study are included in some risk category under different national and international red lists (Table 1).

The areas of endemism obtained applying the CWE index represent sets of neighbour grid-cells with high values, and are not associated by shared or characteristic species; due to this fact, comparison with those results obtained using the PAE method is impossible methodologically because the cladogram obtained with PAE is based on shared species. Despite this, the areas proposed as a result of applying both methods show a strong congruence, indicating that regions in the SMO represent important centres of diversity and endemism of Cactaceae (e.g. Guadalcázar, Cd. Victoria, and Xichú).

The CWE index is not correlated to grid-cell richness, and shows discordant values for some of the main grid-cells; there is no intrinsic reason to expect that these two indices should retrieve the same patterns (Linder, 2001).

We consider that the CWE represents a reliable measure of endemism, due to its independence from species richness and because our study is mainly based on geographically-restricted species. We propose that those grid-cells with high values of CWE coinciding with those areas of endemism obtained in PAE should be considered as priority areas for further investigations oriented towards the conservation and management of Mexican species of Cactaceae.

The above methods can be combined in different stages of a biogeographical research. The initial step includes the documentation of taxa localities, expressed by their coordinates (latitude and longitude). As in the present study, it is preferable to begin with well-studied taxa (as Cactaceae) and then extend the investigation to other groups of organisms.

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REFERENCES

Aguilar-Aguilar R, Contreras-Medina R, Salgado-Maldonado G. 2003. Parsimony analysis of endemicity (PAE) of Mexican hydrological basins based on helminth parasites of freshwater fishes. *Journal of Biogeography* **30:** 1861–1872.

Boyle TH, Anderson E. 2002. Biodiversity and conservation. In: Nobel PS, ed. *Cacti. Biology and uses*. Los Angeles, CA: University of California Press, 125–141.

Canseco-Márquez L, Mendoza-Quijano F, Gutiérrez-Mayén MG. 2004. Análisis de la distribución de la herpetofauna. In: Luna I, Morrone JJ, Espinosa D, eds. *Biodiversidad de la Sierra Madre Oriental*. Mexico City: Las Prensas de Ciencias, Universidad Nacional Autónoma de México-CONABIO, 417–437.

Cervantes-Zamora Y, Cornejo-Olguín SL, Lucero-Márquez R, Espinoza-Rodríguez JM, Miranda-Viquez E, Pineda-Velázquez A. 1990. *Clasificación de regiones naturales de México II, IV.10.2. Atlas Nacional de México. vol. 2, Escala 1: 4 000000*. Mexico City: Instituto de Geografía, UNAM.

Cifuentes J, Villegas M, García-Sandoval R, Vidal-Gaona G, Sierra S, Valenzuela R, Pérez-Ramírez L, Morales-Torres E. 2004. Distribución de macromicetos: una aproximación al análisis de áreas de endemismos. In: Luna I, Morrone JJ, Espinosa D, eds. *Biodiversidad de la Sierra Madre Oriental*. Mexico City: Las Prensas de Ciencias, Universidad Nacional Autónoma de México-CONABIO, 355–374.

Contreras-Medina R, Luna I. 2007. Species richness, endemism and conservation of Mexican gymnosperms. *Biodiversity and Conservation* **16:** 1803–1821.

Contreras-Medina R, Luna I, Morrone JJ. 2007. Application of parsimony analysis of endemicity (PAE) to Mexican gymnosperm distributions: grid-cells, biogeographic provinces and track analysis. *Biological Journal of the Linnean Society* **92:** 405–417.

Crisp MD, Laffan S, Linder HP, Monro A. 2001. Endemism in the Australian flora. *Journal of Biogeography* **28:** 184–198.

Dávila-Aranda P, Arias-Montes S, Lira-Saade R, Villaseñor JL, Valiente-Banuet A. 2002. Phytogeography of the columnar cacti (tribe Pachycereeae) in Mexico: a cladistic approach. In: Fleming TH, Valiente-Banuet A, eds. *Columnar cacti and their mutualists: evolution, ecology, and conservation*. Tucson, AZ: The University of Arizona Press, 25–41.

Dávila-Aranda P, Lira R, Valdés-Reyna J. 2004. Endemic species of grasses in Mexico: a phytogeographic approach. *Biodiversity and Conservation* **13:** 1101–1121.

García-Mendoza A. 1995. Riqueza y endemismos de la familia Agavaceae en México. In: Linares E, Dávila P, Chiang F, Bye R, Elías T, eds. *Conservación de plantas en peligro de extinción: diferentes enfoques*. Mexico City: Instituto de Biología, UNAM, 51–75.

García-Trejo EA, Navarro AG. 2004. Patrones biogeográficos de la riqueza de especies y el endemismo de la avifauna en el oeste de México. *Acta Zoológica Mexicana* **20:** 167–185.

Godínez-Álvarez H, Ortega-Baes P. 2007. Mexican cactus diversity: environmental correlates and conservation priorities. *Boletín de la Sociedad Botánica de México* **81:** 81–87.

Goettsch B, Hernández H. 2006. Beta diversity and similarity among cactus assemblages in the Chihuahuan Desert. *Journal of Arid Environments* **65:** 513–528.

Goloboff P. 1999. NONA*, Version 2.0 (for Windows)*. San Miguel de Tucumán. Published by the author.

Gómez-Hinostrosa C, Hernández H. 2000. Diversity, geographical distribution, and conservation of Cactaceae in the Mier y Noriega region, Mexico. *Biodiversity and Conservation* **9:** 403–418.

González-Zamora A, Luna I, Villaseñor JL, Ruiz-Jiménez CA. 2007. Distributional patterns and conservation of species of Asteraceae (asters etc.) endemic to eastern Mexico: a panbiogeographical approach. *Systematics and Biodiversity* **5:** 135–144.

Guzmán U, Arias S, Dávila-Aranda P. 2003. *Catálogo de cactáceas mexicanas*. Mexico City: Universidad Nacional Autónoma de México-CONABIO.

Hall JB. 1994. Mapping for monographs: baselines for resource development. In: Miller RI, ed. *Mapping the diversity of nature*. London: Chapman & Hall, 21–35.

Hernández H, Godínez H. 1994. Contribución al conocimiento de las cactáceas mexicanas amenazadas. *Acta Botánica Mexicana* **26:** 33–52.

Hernández H, Gómez-Hinostrosa C, Bárcenas R. 2001. Diversity, spatial arrangement, and endemism of Cactaceae in the Huizache area, a hotspot in the Chihuahuan Desert. *Biodiversity and Conservation* **10:** 1097–1112.

Hernández HM, Bárcenas RT. 1995. Endangered cacti in the Chihuahuan Desert: I. Distribution patterns. *Conservation Biology* **9:** 1176–1188.

Hernández JT. 1998. Cactáceas del municipio de Victoria, Tamaulipas. *Cactáceas y Suculentas Mexicanas* **43:** 17–23.

Hernández-Cerda M, Carrasco-Anaya G. 2004. Climatología. In: Luna I, Morrone JJ, Espinosa D, eds. *Biodiversidad de la Sierra Madre Oriental*. Mexico City: Las Prensas de Ciencias, Universidad Nacional Autónoma de México–CONABIO, 63–108.

ICUN. 2008. Red list of threatened species. Available at: http://www.iucnredlist.org.

Kohlmann B, Sánchez S. 1984. Estudio areográfico del género *Bursera* Jacq. ex L. (Burseraceae) en México: una síntesis de métodos. In: Ezcurra E, Kohlmann B, eds. *Métodos cuantitativos en la biogeografía*. Mexico City: Instituto de Ecología AC, 45–120.

León-Paniagua L, García E, Arroyo-Cabrales J, Castañeda-Rico S. 2004. Patrones biogeográficos de la mastofauna. In: Luna I, Morrone JJ, Espinosa D, eds. *Biodiversidad de la Sierra Madre Oriental*. Mexico City: Las Prensas de Ciencias, Universidad Nacional Autónoma de México-CONABIO, 469–486

Linder HP. 2001. Plant diversity and endemism in sub-Saharan tropical Africa. *Journal of Biogeography* **28:** 169–182.

Luna I, Alcántara O, Contreras-Medina R. 2004a. Patterns of diversity, endemism and conservation: an example with Mexican species of Ternstroemiaceae Mirb. ex DC. (Tricolpates: Ericales). *Biodiversity and Conservation* **13:** 2723–2739.

Luna I, Alcántara O, Espinosa D, Morrone JJ. 1999. Historical relationships of the Mexican cloud forests: a preliminary vicariance model applying parsimony analysis of endemicity to vascular plant taxa. *Journal of Biogeography* **26:** 1299–1305.

Luna I, Alcántara O, Epinosa D, Morrone JJ. 2000. Track analysis and conservation priorities in the cloud forests of Hidalgo, Mexico. *Diversity and Distributions* **6:** 137–143.

Luna I, Morrone JJ, Espinosa D, eds. 2004b. *Biodiversidad de la Sierra Madre Oriental*. Mexico City: Las Prensas de Ciencias, Universidad Nacional Autónoma de México–CONABIO.

McAllister DE, Schueler FW, Roberts CM, Hawkins JP. 1994. Mapping and GIS analysis of the global distribution of coral reef fishes on an equal-area grid. In: Miller RI, ed. *Mapping the diversity of nature*. London: Chapman & Hall, 155–175.

Márquez J, Morrone JJ. 2004. Relaciones biogeográficas basadas en la distribución de Coleoptera (Insecta). In: Luna I, Morrone JJ, Espinosa D, eds. *Biodiversidad de la Sierra Madre Oriental*. Mexico City: Las Prensas de Ciencias, Universidad Nacional Autónoma de México-CONABIO, 375–392.

Martínez-Ávalos J, Jiménez J. 1993. Las cactáceas del Valle de Jaumave, Tamaulipas. *Cactáceas y Suculentas Mexicanas* **38:** 75–81.

Martínez-Ávalos J, Jurado E. 2005. Geographic distribution and conservation of Cactaceae from Tamaulipas, Mexico. *Biodiversity and Conservation* **14:** 2483–2506.

Méndez-Larios I, Villaseñor JL, Lira R, Morrone JJ, Dávila-Aranda P, Ortiz E. 2005. Toward the identification of a core zone in the Tehuacán-Cuicatlán biosphere reserve, Mexico, based on Parsimony Analysis of Endemicity of flowering plant species. *Interciencia* **30:** 267–274.

Morrone JJ. 1994. On the identification of areas of endemism. *Systematic Biology* **43:** 438–441.

Morrone JJ, Crisci JV. 1995. Historical biogeography: introduction to methods. *Annual Review of Ecology and Systematics* **26:** 373–401.

Morrone JJ, Escalante T. 2002. Parsimony Analysis of Endemicity (PAE) of Mexican terrestrial mammals at different area units: when size matters. *Journal of Biogeography* **29:** 1095–1104.

Morrone JJ, Espinosa D, Aguilar C, Llorente J. 1999. Preliminary classification of the Mexican biogeographic provinces: a Parsimony Analysis of Endemicity based on plant, insect, and bird taxa. *The Southwestern Naturalist* **44:** 507–514.

Navarro AG, Garza-Torres H, López de Aquino S, Rojas-Soto O, Sánchez-González LA. 2004. Patrones biogeográficos de la avifauna. In: Luna I, Morrone JJ, Espinosa D, eds. *Biodiversidad de la Sierra Madre Oriental*. Mexico City: Las Prensas de Ciencias, Universidad Nacional Autónoma de México-CONABIO, 439–467.

Nixon KC. 2002. *WinClada,* Version 1.00.08. Ithaca, NY. Published by the author.

Ortega-Baes P, Godínez-Álvarez H. 2006. Global diversity and conservation priorities in the Cactaceae. *Biodiversity and Conservation* **15:** 817–827.

Ortega-Gutiérrez F, Sedlock RL, Speed RC. 1994. Phanerozoic tectonic evolution of Mexico. In: Speed RC, ed. *Phanerozoic evolution of North American continent-ocean transitions*. Boulder, CO: The Geological Society of America, 265–306.

Pinkava DJ. 1984. Vegetation and flora of the bolson of Cuatrociénegas region, Coahuila, Mexico: IV. Summary, endemism and corrected catalogue. *Journal of Arizona–Nevada Academy of Science* **19:** 23–47.

Porzecanski AL, Cracraft J. 2005. Cladistic analysis of distributions and endemism (CADE): using raw distributions of birds to unravel the biogeography of the South American aridlands. *Journal of Biogeography* **32:** 261–275.

Rojas-Soto O, Alcántara O, Navarro AG. 2003. Regionalization of the avifauna of the Baja California Peninsula, Mexico: a Parsimony Analysis of Endemicity and distributional modeling approach. *Journal of Biogeography* **30:** 449–461.

Rosen BR. 1988. From fossils to earth history: applied historical biogeography. In: Myers AA, Giller PS, eds. *Analytical biogeography: an integrated approach to the study of animal and plant distributions*. London: Chapman & Hall, 437–481.

Rosen BR, Smith AB. 1988. Tectonics from fossils? Analysis of reef-coral and sea-urchin distributions from late Cretaceous to Recent, using a new method. In: Audley-Charles MG, Hallam A, eds. Gondwana and Tethys. *Special Publications of the Geological Society of London* **37:** 275–306.

Ruiz C, Alcántara O, Luna I. 2004. Límites. In: Luna I, Morrone JJ, Espinosa D, eds. *Biodiversidad de la Sierra Madre Oriental*. Mexico City: Las Prensas de Ciencias, Universidad Nacional Autónoma de México-CONABIO, 7–24.

Scheinvar L. 2004. *Flora cactológica del estado de Querétaro: diversidad y riqueza*. Mexico City: Fondo de Cultura Económica.

SEMARNAT (Secretaría de Medio Ambiente y Recursos Naturales). 2002. *Norma Oficial Mexicana NOM-059-ECOL-2001, Protección ambiental-Especies nativas de México y de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-lista de especies en riesgo*. Mexico City: Diario Oficial de la Federación, 6 de marzo de 2001.

Wehbe JA, Elizondo JL. 1986. Estudio florístico de las cactáceas del municipio de Ramos Arizpe, Coahuila. *Cactáceas y Suculentas Mexicanas* **31:** 97–102.