Nature (IUCN) (IUCN, 2003), and *ca*. 40 species are included in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Hunt, 1999; Lüthy, 2001). Likewise, over 200 species have been included in red lists of the Mexican environmental agency (Norma Oficial Mexicana; SEMARNAT, 2002). Due to the high number of threatened and endangered species, it has been suggested that it is crucial to obtain information on different biological and ecological aspects of cacti such as their geographical distribution patterns, levels of endemism, and endangerment, which could contribute to adequate management and conservation at a regional level (Ortega-Baes and Godínez-Alvarez, 2006).

Several studies have analyzed the geographical distribution patterns and levels of endemism and endangerment of Mexican cactus diversity. However, all of them were conducted in the Chihuahuan Desert only (Hernández and Bárcenas, 1995, 1996), or in particular localities within this region, *e.g.* Huizache (Hernández *et al*., 2001) and Mier y Noriega (Gómez-Hinostrosa and Hernández, 2000). Cactaceae are widely distributed in Mexico where they inhabit regions with arid climate like the Chihuahuan and Sonoran Deserts, in northern Mexico, or regions with more humid climate such as the Pacific coastal plain and the Yucatan Peninsula (Hernández and Godínez, 1994). Therefore, cactus diversity patterns should be influenced by environmental factors such as temperature and precipitation, which in turn could affect their presence in certain regions of the country. In this context, we believe that analyses of cactus diversity across Mexico are necessary to identify other areas with exceptional species richness and endemicity in the country. It is also necessary to analyze the relationship between species richness, endemism, and different environmental factors to determine which of these factors could explain cactus diversity. Various studies have shown that variability of some environmental factors such as temperature and precipitation could decrease the survival, growth, and reproduction of cacti, limiting their distribution and abundance patterns (Brum, 1973; Yeaton and Cody, 1979; Gibson and Nobel, 1986; Flores and Yeaton, 2003).

In this paper we analyze the diversity patterns of Cactaceae in Mexico to determine those federal states having high species richness, endemism, and endangerment, which could be important for the conservation of these plants. In addition, we analyze the relationships between species richness, endemism, temperature, and precipitation. These analyses were made considering states, instead of biogeographic or physiographic regions, since decisions to implement conservation actions frequently rely on state and federal governments. Several conservation strategies of different groups of plants such as Asteraceae (Villaseñor *et al*., 1998), Cucurbitaceae (Lira *et al*., 2002), and Poaceae (Dávila-Aranda *et al*., 2004) have been proposed by analyzing their diversity patterns at the state level. We address the following questions: (1) What are the states with the highest species richness, endemic species, and endangered species?, (2) Are species richness, endemic species, and endangered species related?, (3) Is there a relationship between temperature, precipitation, species richness, and endemism?, and (4) What are the most relevant states for cactus preservation?

Materials and methods

Species richness, endemism, and endangerment. Data used in this study were obtained from the *Catálogo de Cactáceas Mexicanas* (Guzmán *et al*., 2003). We recorded for each species its scientific name and federal states where it has been recorded, and whether it has been listed as threatened or endangered species in national (SEMARNAT, 2002) and international red lists (Hunt, 1999; Lüthy, 2001; IUCN, 2003). Cultivated species and species with incomplete data were excluded from the analysis.

Based on these data a presence-absence matrix was constructed to determine: (1) Species richness: the total number of species found in each state; (2) Endemism: the number of endemic species to Mexico found in each state, and (3) Endangerment: the number of endangered species found in each state. The total number of species along with the number of endemic and endangered species of Mexico may vary depending on the classification system used and the sampling effort conducted in the country. The *Catálogo de Cactáceas Mexicanas*, which is based mainly on the taxonomic proposal of the CITES Cactaceae Checklist (Hunt, 1999), is the most complete review of the taxonomy and distribution of Mexican cactus species that has been published to date by the organization responsible for the analysis of diversity in Mexico (i.e., Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, CONABIO).

Regression analyses between species richness and endemic species, as well as between species richness and endangered species, were conducted to determine whether these variables were significantly related. In addition, regression analyses with species richness and endemic species as dependent variables and total state area as independent variables were conducted to determine whether cactus diversity tends to increase with state extent. Total area of each state was obtained from Instituto Nacional de Estadística, Geografía e Informática (INEGI, 2005). Confidence intervals (95%) were calculated for fitted regression lines to identify those states having the highest species richness and endemism. States above confidence intervals were considered as having a higher number of species than expected according to their total area (Ortega-Baes and Godínez-Alvarez, 2006). Data were log-transformed to meet the assumptions of normality of the statistical test and analyzed with the statistical package JMP version 3.1 (SAS Institute, 1995).

Cactus diversity and environmental factors. Multiple linear regressions between species richness or endemic species and various environmental factors were conducted to determine whether significant relationships exist among them. The environmental factors analyzed were: (1) mean altitude of each state (Alt), (2) mean annual precipitation (P_{mean}), (3) difference between average maximum and minimum monthly precipitation (P_{rang}), (4) sum of average precipitation falling from June to September (P_{sum}), (5) mean annual temperature (T_{mean}), (6) difference between average maximum and minimum monthly temperature (T_{rang}), and (7) aridity of each state or proportion of each state area with arid climates (Arid). These arid climates include the subtypes *BW* and *BS* proposed by García (2004). These environmental factors were chosen to evaluate the effects of temperature and precipitation on cactus diversity. Altitude and proportion of each state area with arid climates were directly obtained from the web page of the Instituto Nacional de Estadística, Geografía e Informática (INEGI, 2005). Precipitation and temperature data were obtained from the web site of the Comisión Nacional del Agua (CNA, 2005).

Regressions were conducted through generalized linear models with Poisson errors using the statistical package GLIM ver. 3.77 (Crawley, 1993). These models were preferred instead of models with normal errors because they consider species numbers as discrete variables whose variances increase with the mean. Models were fitted following an additive stepwise approach, in which the most significant variables according to *G*-statistics were included into the model at each step. In case of data overdispersion, the variance was multiplied by a scale parameter and the model was refitted (Crawley, 1993).

Table 1. Number of genera and species of cacti in each federal state of Mexico. Percentages of endemic and endangered species were calculated considering the number of species for each state.

States	Genera	Species	Endemic species (%)	Endangered species (%)
San Luis Potosí	33	151	115 (76)	69 (46)
Coahuila	24	126	71 (56)	53 (42)
Nuevo León	30	119	71 (60)	61 (51)
Oaxaca	32	118	97 (82)	29 (25)
Zacatecas	26	112	86 (77)	37 (33)
Tamaulipas	31	105	57 (54)	47 (45)
Sonora	21	100	42 (42)	24 (24)
Durango	22	97	65 (67)	29 (30)
Querétaro	29	96	82 (85)	31 (32)
Jalisco	25	93	81 (87)	20 (22)
Guanajuato	21	88	76 (86)	29 (33)
Chihuahua	21	85	30 (35)	25 (29)
Hidalgo	23	82	72 (88)	26 (32)
Puebla	25	80	71 (89)	22 (28)
Michoacán	20	62	57 (92)	14 (23)
Guerrero	21	61	53 (87)	15 (25)
Sinaloa	15	60	46 (77)	12 (20)
Baja California Sur	13	57	47 (82)	20 (35)
Baja California	13	56	31 (55)	16 (29)
Chiapas	19	49	18 (37)	9 (18)
Veracruz	21	49	31 (63)	13 (27)
México	18	45	40 (89)	10 (22)
Aguascalientes	14	37	31 (84)	9 (24)
Morelos	12	28	23 (82)	6 (21)
Nayarit	11	26	23 (88)	2 (8)
Colima	14	24	21 (88)	6 (25)
Tlaxcala	6	18	17 (94)	2 (11)
Distrito Federal	7	15	12 (80)	4 (27)
Yucatán	9	14	4 (29)	5 (36)
Tabasco	7	13	5 (38)	3 (23)
Quintana Roo	6	8	4 (50)	3 (38)
Campeche	5	7	1 (14)	1 (14)

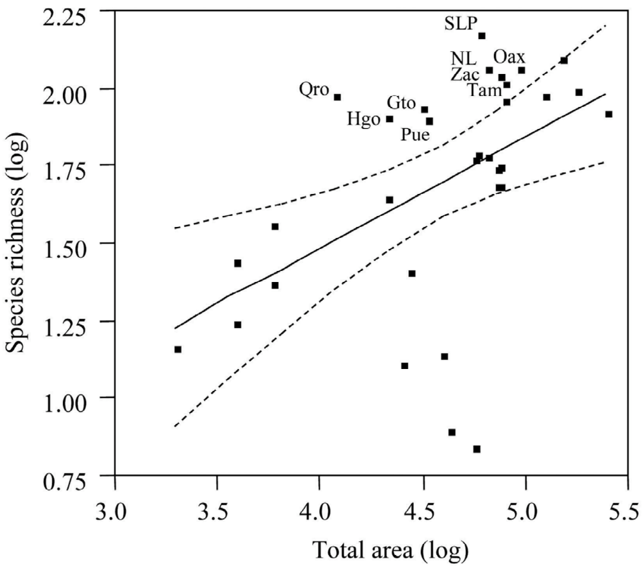

Figure 1. Relationship between species richness and total area for federal states of Mexico. Continuous line and dotted line refer to fitted line and 95% confidence interval, respectively. States with higher diversity than expected according to their area are: Guanajuato (Gto), Hidalgo (Hgo), Nuevo León (NL), Oaxaca (Oax), Puebla (Pue), Querétaro (Qro), San Luis Potosí (SLP), Tamaulipas (Tam), and Zacatecas (Zac).

Complementarity analysis. A complementarity analysis was conducted to determine the relative importance of each state in the conservation of Mexican cacti. This analysis was carried out using an algorithm in which states were selected according to their total number of species. The procedures used were as follows: (1) the state with the highest number of species was selected first and their taxa were dropped from the analysis; (2) the state with the highest number of species that had not been selected yet (*i.e.*, the state with the highest complementarity) was chosen from the remaining states. This procedure was repeated until all species were selected.

Results

Species richness, endemism, and endangerment. San Luis Potosí and Coahuila had the highest species richness (> 125) followed by Nuevo León, Oaxaca, Zacatecas, Tamaulipas, and Sonora, with total number of species ranging between 100 and 120 (table 1). In turn, San Luis Potosí, Oaxaca, and Zacatecas had the highest number of endemic species. In all cases, Quintana Roo and Campeche had the lowest species richness and endemism. States with the highest number of endangered species were San Luis Potosí, Nuevo León, and Coahuila (> 50), whereas Campeche, Nayarit, and Tlaxcala had the lowest numbers (2; table 1).

There was a significant relationship between species richness and endemism ($F_{1, 30}$ = 201.0, P < 0.00001, R^2 = 0.89). Species richness and endangered species were also significantly related ($F_{1, 30}$ = 255.4, P < 0.00001, R^2 = 0.9).

The relationship between species richness and state area was statistically significant ($F_{1, 30}$ = 10.1, P = 0.0035, R^2 = 0.25), indicating that the largest states had the highest number of species. However there were some states such as Guanajuato, Hidalgo, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Tamaulipas, and Zacatecas, which had higher number of species than expected according to their area (figure 1). There was no significant relationship between number of endemic species and state area ($F_{1, 30}$ = 1.9, P = 0.18, R^2 = 0.06).

Cactus diversity and environmental factors. The aridity of each state explained significant fractions of total variance in species richness (R^2 = 0.40, P = 0.0002) and endemism (R^2 = 0.23, P = 0.005; table 2). The most arid states generally tended to have high species richness and endemic species. It is worth mentioning, however, that Oaxaca had a low proportion of arid climates (5%), but high species richness (118) and endemic species (97; figure 2).

Other environmental factors such as mean annual temperature and difference between the average maximum and minimum monthly precipitation also explained significant proportions of variance in the number of endemic species. However, these proportions were lower than the proportion explained by aridity of each state (T_{mean}: R^2 = 0.17, P = 0.02; P_{rang}: R^2 = 0.12, P = 0.04). There was a significant negative correlation between aridity of each state and difference between average maximum and minimum monthly precipitation (R = -0.4, P = 0.02), which could decrease the explanatory power of these environmental factors (table 3).

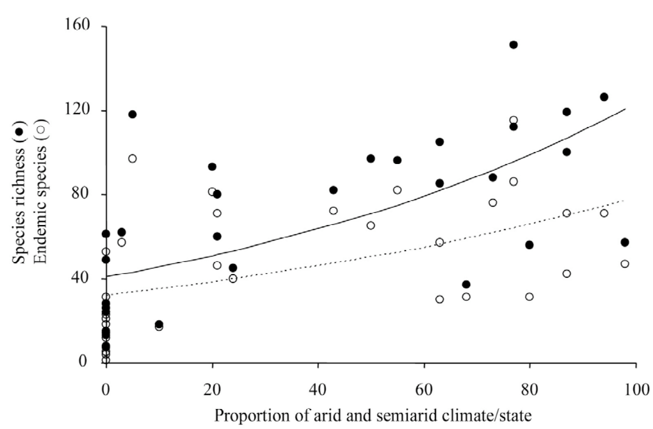

Figure 2. Relationship between species richness and endemic species of cactus, and aridity of each federal state of Mexico. Continuous line (species richness) and dotted line (endemic species) refer to regression lines predicted by the log-linear models.

Table 2. Significant predictors of the multiple log-linear regression models.

Dependent variable	Independent variable	*G*	*P*	r^2
Species richness	Arid	13.6	0.0002	0.40
Endemic species	Arid	7.9	0.005	0.23
	T_{mean}	5.7	0.02	0.17
	P_{rang}	4.2	0.04	0.12

Independent variables were: Arid-aridity of each state or proportion of each state area with arid climates (subtypes *BW* and *BS*, *sensu* García 2004), P_{rang}-difference between average maximum and minimum monthly precipitation, and T_{mean}-mean annual temperature.

Complementarity analysis. Twenty-three states were necessary to represent all cactus species of Mexico (figure 3). However, 80% of the total species may be preserved focusing conservation efforts on only eight states (Baja California Sur, Coahuila, Hidalgo, Jalisco, Nuevo León, Oaxaca, San Luis Potosí, and Sonora). According to our regression analyses, these states have high species richness as well as high number of endemic species and endangered species, because of the positive relationship among these attributes.

Discussion

The main goals of this study were to identify those federal states of Mexico that could be important for the conservation of Cactaceae, and to analyze the relationship between cactus diversity, temperature, precipitation, and aridity. The analysis of diversity patterns indicated that San Luis Potosí, Coahuila, Nuevo León, Oaxaca, Zacatecas, Tamaulipas, and Sonora had more than 100 cactus species. However, some of these states such as San Luis Potosí, Nuevo León, and Oaxaca stand out from this group, since they have higher species richness than expected according to their total area. The relative importance of these states for conservation of Mexican cacti is highlighted when the significant relationship between species richness and endemism, and between species richness and endangered species, are taken into account. These results mean that conservation actions carried out in the states with high species richness would not only insure the preservation of endemic species, but also of endangered ones.

In analyzing the flora of the Mexican regions with arid climates, several authors have found high levels of species richness and endemism, especially in the cactus family (Rzedowski, 1962; 1973; Villaseñor *et al.*, 1990). In this study we found that 78% of the total number of recorded species (512 out of 660) are endemic to Mexico, which is similar to figures previously reported by other authors (Hernández and Godínez, 1994; Ortega-Baes and Godínez-Alvarez 2006). Different factors could explain the high species richness and endemism of Cactaceae in Mexico. One of these factors could be the presence of regions with arid climates in this country since the early Tertiary. It has been suggested that the presence of arid regions for a long period of time might allow the origin and evolution of plant lineages (Rzedowski, 1962; 1973; 1991). Another factor that could also contribute to the high species richness and endemism is that some Mexican dry regions, particularly those located within the Chihuahuan Desert, might have acted as refuge areas during the last glacial period, leading to the isolation and allowing the diversification of several species of cactus (Hernández and Bárcenas, 1995).

The relationship between cactus diversity and arid climates is supported by the results of our multiple linear regressions. According to these results, the aridity of each state was the most significant environmental factor explaining variance in species richness and endemism. The most arid states generally had high number of cactus species. However, it is important to bear in mind that there was a significant correlation between aridity of each state and precipitation, which could decrease the explanatory power of these environmental factors. Different authors had suggested that certain states, regions, and smaller geographic units of Mexico with arid climates were important in terms of cactus species richness and endemism (Hernández and Godínez, 1994; Hernández and Bárcenas, 1995; Gómez-Hinostrosa and Hernández, 2000; Hernández *et al.*, 2001). For instance, in analyzing the distribution patterns of

Table 3. Correlation matrix of the environmental factors used in the multiple log-linear regression models. All values shown are significant ($P < 0.05$).

	Alt	Arid	P_{mean}	P_{rang}	P_{sum}	T_{mean}	T_{rang}
Alt	1.00						
Arid		1.00					
P_{mean}			1.00				
P_{rang}		-0.40	0.89	1.00			
P_{sum}		-0.46	0.87	0.97	1.00		
T_{mean}	-0.83					1.00	
T_{rang}							1.00

Environmental factors were: Alt-mean altitude of each state, Arid-aridity of each state or proportion of each state area with arid climates (subtype *BW* and *BS*, sensu García 2004), P_{mean}-mean annual precipitation, P_{rang}-difference between average maximum and minimum monthly precipitation, P_{sum}-sum of average precipitation falling from June to September, T_{mean}-mean annual temperature, and T_{rang}-difference between average maximum and minimum monthly temperature.

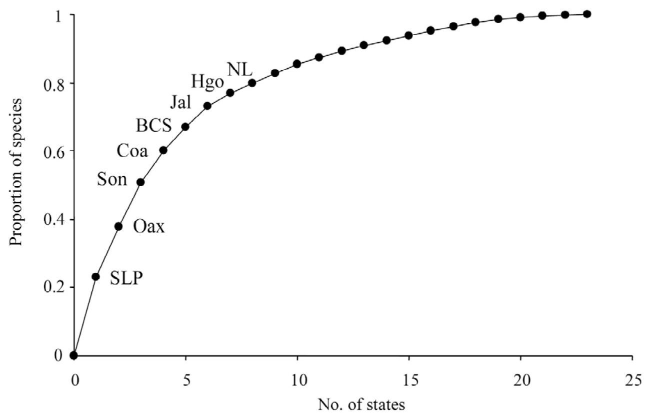

Figure 3. Complementarity analysis for the federal states of Mexico. The most important states for cactus preservation are: Baja California Sur (BCS), Coahuila (Coa), Hidalgo (Hgo), Jalisco (Jal), Nuevo León (NL), Oaxaca (Oax), San Luis Potosí (SLP), and Sonora (Son). The remaining states, whose names are not provided, contribute to the preservation of only 20% of the total number of cactus species.

endangered cacti in the Chihuahuan Desert, Hernández and Bárcenas (1995) indicated that the areas with high species richness were characterized by a *BS* subtype climate. However, neither of these authors analyzed the whole cactus diversity of Mexico nor used regression analyses to quantitatively test the relationship between cactus diversity and aridity. Hernández and Bárcenas (1995) also suggested that the areas with high cactus diversity within the Chihuahuan Desert had mean annual precipitation between 300-600 mm. In our study, we did not find a significant relationship between precipitation and species richness. This environmental factor was only significantly correlated with the number of endemic species, although it explained lower proportion of variance than aridity of each state. Temperature did not correlate with species richness or endemic species. Data used in this study were average values that broadly describe the climate of each state; therefore our results of the regression analyses should be interpreted cautiously and as a preliminary method to identify those factors that might explain cactus diversity at the country level. The analysis of the relationship between cactus diversity and environmental factors at smaller spatial scales will depend on gathering more detailed climatic data.

Based on the complementarity analysis, it was concluded that eight states are needed to preserve 80% of the total cactus species recorded in Mexico (Baja California Sur, Coahuila, Hidalgo, Jalisco, Nuevo León, Oaxaca, San Luis Potosí, and Sonora). All these states are part of the most important arid and semiarid regions of this country, except for Jalisco, which is located on the Pacific coast, in regions with tropical deciduous forests. Hernández and Godínez (1994) found that high proportions of endangered cactus species also tend to concentrate in these same states. Similarly, studies on Asteraceae, Cucurbitaceae, and Poaceae have shown that Coahuila, Jalisco, Oaxaca, and Sonora are also important for preserving these plants in Mexico (Villaseñor *et al.*, 1998; Lira *et al.*, 2002; Dávila-Aranda *et al.*, 2004). To define the entirety of these eight states as priority conservation areas would be prohibitive. However, the results of the complementarity analysis could be used to determine those states where conservation actions should be focused to preserve particular groups of cacti. Many species of the tribe Cacteae (subfamily Cactoidea) could be preserved in San Luis Potosí, Coahuila, and Nuevo León, while the species of the tribe Pachycereeae (subfamily Cactoidea) could be protected in Jalisco, Hidalgo, and Oaxaca. Other species of these tribes could also be preserved in Baja California Sur and Sonora. Likewise, the species of other subfamilies such as Pereskioidea and Opuntioidea could be preserved in most of the states selected by the complementarity analysis.

All states chosen by the complementarity analysis have priority regions for the preservation of biodiversity in Mexico (Arriaga *et al.*, 2000). Some of these states such as Baja California Sur, Coahuila, Hidalgo, Oaxaca, and Sonora currently have federal protected areas in which some conservation actions have been implemented (Arriaga *et al.*, 2000). However, reserves are scarce or nonexistent in other states with high cactus diversity such as San Luis Potosí and Nuevo León (Hernández and Bárcenas, 1995; Hernández *et al.*, 2001; Gómez-Hinostrosa and Hernández, 2000). The creation of new state and federal reserves and the implementation of other conservation actions in most of these states would contribute to protect cactus diversity, but also the diversity of other plant groups such as Asteraceae (Villaseñoer *et al.*, 1998), Cucurbitaceae (Lira *et al.*, 2002), and Poaceae (Dávila-Aranda *et al.*, 2004).

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