Biodivers Conserv
DOI 10.1007/s10531-007-9303-2

ORIGINAL PAPER

Cactus species turnover and diversity along a latitudinal transect in the Chihuahuan Desert Region

Héctor M. Hernández · Bárbara Goettsch ·
Carlos Gómez-Hinostrosa · Héctor T. Arita

Received: 7 February 2007 / Accepted: 4 December 2007

Abstract A standardized sampling method was used to evaluate turnover (β diversity) among cactus species assemblages along a 798 km long latitudinal megatransect across the Chihuahuan Desert Region, from north-central Mexico to southern Texas. A total of 71 cactus species were found along the megatransect, 66.2% of which appeared at low frequencies, mostly as a consequence of their highly discontinuous distribution pattern. At the scale the study was conducted, there was always species turnover among cactus assemblages. The rate of turnover among contiguous sites primarily fluctuated from low to medium, but when all site combinations were considered (contiguous and non-contiguous), medium β diversity values were predominant ($\beta = 0.331–0.66$); however, 25.4% of the site pair combinations registered high values ($\beta = 0.661–1.0$). Our results showed that turnover among cactus species assemblages in the CDR does not consist for the most part of a process of species succession in the geographic space. Instead, we concluded that the continuous spatial changes in cactus species composition are primarily explained by the commonly intermittent distribution patterns of the species, by the presence in the megatransect of species at the margin of their distribution range, and, to a lesser extent, by the existence of narrowly endemic species.

Keywords Beta diversity · *Cactaceae* · Chihuahuan Desert · Mexico · Texas

---

H. M. Hernández (✉) · B. Goettsch · C. Gómez-Hinostrosa
Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México,
Apartado Postal 70-233, Ciudad Universitaria, 04510 Mexico City, Mexico
e-mail: hmhm@ibiologia.unam.mx

Present Address:
B. Goettsch
Biodiversity and Macroecology Group, Department of Animal and Plant Sciences,
University of Sheffield, Sheffield S10 2TN, UK

H. T. Arita
Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275,
04510 Mexico City, Mexico

Introduction

There is a broad agreement that biodiversity can be conceptualised as the conjunction of three components: local species richness or alpha (α diversity), species turnover or community differentiation (β diversity), and regional diversity (γ diversity). Beta diversity has been considered as an important factor determining diversity at regional scales (Harrison et al. 1992). From the conservation perspective, β diversity is as important as alpha diversity because species turnover influences diversity at large scales (Condit et al. 2002). In fact, it has been predicted that spatial patterns of species distributions may determine where protected areas should be located, and that regions with high β diversity would require more, or alternatively larger, reserves than regions with low β diversity (Wiersma and Urban 2005).

Recent studies on the *Cactaceae* in the Chihuahuan Desert Region (CDR) have revealed general patterns of diversity and spatial arrangement of members of this plant family at regional (Hernández and Bárcenas 1995, 1996; Hernández et al. 2004; Hernández and Gómez-Hinostrosa 2005) and local scales (Gómez-Hinostrosa and Hernández 2000; Hernández et al. 2001). These studies have demonstrated that the CDR is the world's most important centre of cactus diversity, that much of this diversity is either regionally or locally endemic, and that the areas of maximum concentration of cactus species, including the rarest and most endangered ones, are centered towards the south-eastern segments of the region. According to a recently published checklist (Hernández et al. 2004), the CDR shelters the world's richest assemblage of cactus genera (39 gen.) and species (329 spp.). Of these, 17 genera (or 43.6% of the generic diversity in the region) and 229 species (69.6%) are strictly endemic to the region. The genera *Mammillaria, Opuntia* sensu stricto, *Coryphantha*, and *Echinocereus*, with 79, 46, 36, and 30 species respectively, account for 58% of the total cactus diversity in the region.

Although the high diversity of cactus species in Mexican desert areas has been reasonably well documented at different scales, the changes in species composition in the geographical space have only been started to be understood. In a recent paper, Goettsch and Hernández (2006) analysed the patterns of cactus species turnover (β diversity) along a 250 km long, longitudinal (east–west) megatransect, near the south-eastern end of the Main Sub-region of the CDR [for a definition of the CDR sub-regions see Hernández and Gómez-Hinostrosa (2005)]. The most important results of this study were that: (1) a substantial proportion of the species found in the megatransect had low frequencies, primarily as a consequence of their patchy distribution pattern; (2) frequent discontinuities in the geographical range of the species result in an intermittent pattern of geographical distribution; and (3) this biogeographic scenario produces continuous species turnover, usually expressed in moderate to high β diversity values. It was concluded that the relatively high rate of species turnover found along the megatransect may be explained for the most part by the intermittent pattern of spatial distribution of the species, "rather than a real species turnover". In other words, the predominantly moderate to high β diversity values found in the study area are caused predominantly by the highly discontinuous distribution pattern of many of the species, and not by the succession of different species in the geographic space. This study allowed us to understand at a fine level of resolution the pattern of cactus species in this part of the CDR; however, we still do not know whether the observed pattern persists in other parts of the region or if other biogeographic configurations occur.

In order to situate Goettsch's and Hernández' (2006) findings in a regional perspective, in this paper we aim at assessing cactus species turnover along a south-north latitudinal transect across the entire Main Sub-region of the CDR (Fig. 1). Specifically, the following

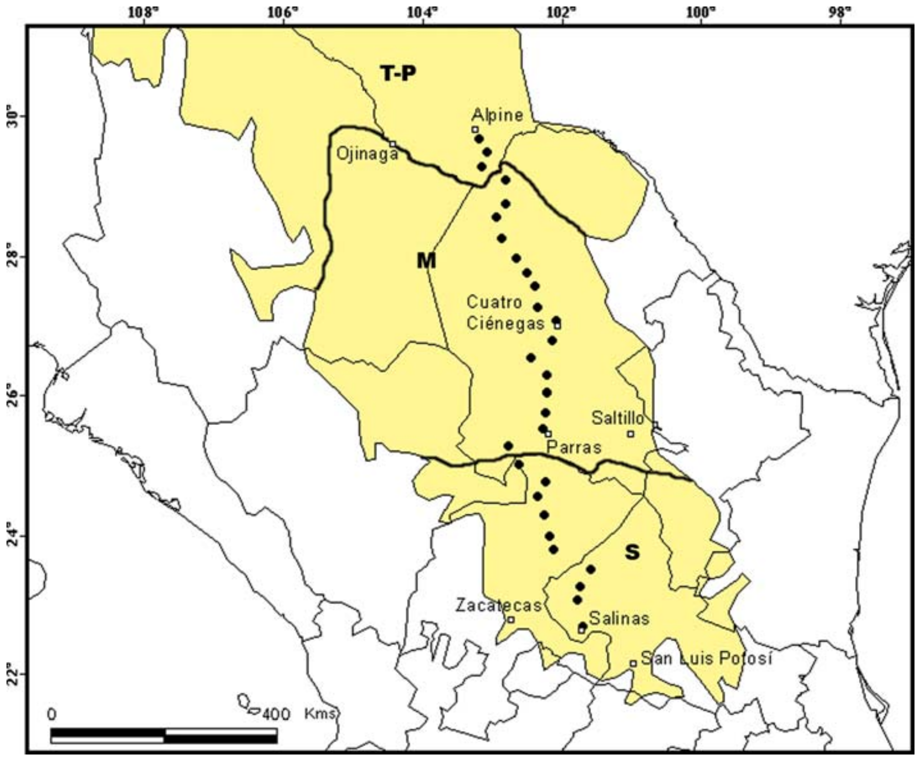


Fig. 1 Study area showing the sub-provinces of the Chihuahuan Desert after Morafka (1977); S = Saladan, M = Mapimian, and T-P = Trans-Pecos. The solid dots indicate the sampled sites (see also Appendix 1)

variables were evaluated: relative frequency and spatial patterns of individual species, as well as the variation in species richness, species turnover, and similarity among cactus assemblages. It is expected that this information, in conjunction with Goettsch's and Hernández' (2006) data, will help us to improve our understanding of the nature of cactus β diversity in the CDR and its potential use in conservation.

Study area and methods

Study area

The CDR extends from central Mexico, in the states of Guanajuato, Querétaro, and Hidalgo northwards to southern Texas, New Mexico, and a small area in Arizona (Hernández and Gómez-Hinostrosa 2005). To the west and east, the region is bordered by the Sierra Madre Occidental and the Sierra Madre Oriental, and it has an approximate extension of 507,000 km^2. Thanks to its relatively high biodiversity, numerous endemic species, and the existence of extensive well preserved areas, the CDR is considered among the three more outstanding deserts in the world (Dinerstein et al. 1999), and one of the 37 wilderness areas on the planet (Mittermeier et al. 2002).

The study area corresponds to the Main Sub-region of the CDR proposed by Hernández and Gómez-Hinostrosa (2005). The climatic, ecological, biogeographic, and vegetational characteristics of the CDR have been described elsewhere by numerous authors (Shreve 1942; Johnston 1977; Schmidt 1979; Medellín-Leal 1982; Henrickson and Johnston 1986; Hernández and Gómez-Hinostrosa 2005; Hernández 2006, and others).

Morafka (1977) recognized the existence of three distinct subdivisions or sub-provinces within the Chihuahuan Desert: the Saladan, the Mapimian, and the Trans-Pecos. These are based on the general distribution and endemism patterns of the region's herpetofauna, and are delineated in Fig. 1. In particular, the existence of the Saladan and Mapimian subdivisions has been corroborated by Johnston (1974) and Hernández et al. (2001), through the analysis of plant distributions. These two segments of the CDR are divided by the transverse Sierra de Parras at about 25°15′ N latitude, resulting in a certain degree of biotic differentiation.

Sampling

In order to assess changes in the cactus species composition, we followed with minor modifications the method described by Goettsch and Hernández (2006). We sampled the cactus species in 29 localities along a south–north megatransect across the CDR (Fig. 1), in parts of the states of San Luis Potosí, Zacatecas, Coahuila (Mexico), and Texas (United States of America). The approximate linear distance of the megatransect was 798 km, and the sampling sites were located at nearly 15-min (roughly 28 km) intervals, starting in western San Luis Potosí and concluding in the Big Bend area in Texas. Whenever possible the sampling localities were located away of highways, main roads, and towns, where vegetation was found to be in a reasonably good state of conservation. The exact location of the sites (Appendix 1) was established using a Global Positioning System (GPS).

Fieldwork was conducted between April 2001 and March 2003. In each of the 29 localities we used the same sampling method, which consisted of recording all cactus species within eyesight along a three-kilometre line transect. These line transects, which were searched afoot by two or three observers, were measured with a GPS. For each cactus species in every locality, herbarium samples were obtained to be deposited in the National Herbarium of Mexico (MEXU). It has to be taken into consideration that, despite the relatively high altitudinal variation along the megatransect (altitudinal range = 908–2,160 m), all samplings were made in environmentally similar desert planes and nearby hills, where ecological conditions induce the development of typical Chihuahuan Desert plant communities (e.g., *Larrea* desert scrub, *Agave lechuguilla-Hechtia* desert scrub, *Yucca* or *Dasylirion* woodland, etc.). In contrast, higher altitude sites, such as high mountaintops, where desert scrub gives transition to mesic plant communities (Henrickson and Johnston 1986), were excluded from the samplings. In these high altitude areas there is an obvious decline in cactus diversity and clear divergences in species composition.

Data analysis

The relative frequency (f) of each one of the species was calculated as the number of sites in which a given species was found, in proportion to the total number of sampled sites (29).

In order to measure changes in cactus species composition between site pairs (species turnover or β diversity), we used Wilson and Shmida's (1984) formula: $\beta = (b + c)/2a + b + c$, where β = beta diversity, a = total number of species that occur in both sites, b = number of species that occur in the neighbouring site but not in the focal one, and c = number of species that occur in the focal site but not in the neighbouring one.

In addition to the *β* diversity analysis, we calculated Jaccard's index of floristic similarity among all sampled sites (Mueller-Dombois and Ellenberg 1974). The Numerical Taxonomy and Multivariate System version 2.10p of Exeter Software (serial number UH3071IX) was used. The similarity values were obtained by means of the formula $IS_J = a/a + b + c$, where IS_J = index of similarity; the rest of the components (*a*, *b* and *c*) are the same as in the *β* diversity formula.

To assess the statistical significance of richness patterns, we performed a null-model analysis. We constructed 1,000 null sites in which each species had a probability of occurrence equal to its occupancy (number of occupied sites) proportional to the total number of sites. With the resulting 1,000 assemblages, we determined the upper and lower 95% confidence limits for species richness in a given site. We found such limits to be 9 and 22 species. In other words, any site with 9 or less species would have a lower species richness than expected by chance ($P < 0.025$), and any site with 22 or more species would be significantly richer than expected by chance.

Results and discussion

Species richness

A total of 71 cactus species were found in the megatransect (Appendix 2). These correspond to 21.6% of the total cactus diversity in the entire CDR (Hernández et al. 2004). A considerable number of species (43 spp.), constituting 60.6% of species richness, are endemic to the CDR (Hernández et al. 2004). Four genera *Coryphantha* (11 spp.), *Opuntia* (10 spp.), *Echinocereus* (8 spp.), and *Mammillaria* (7 spp.) comprise the largest number of recorded species, whereas several other genera (*Acharagma*, *Ariocarpus*, *Astrophytum*, *Epithelantha*, *Escobaria*, *Leuchtenbergia*, etc.) were represented by only one or two species. This scheme of taxonomic distribution in the megatransect resembles significantly that of the whole region (Hernández et al. 2004). Species richness varied considerably among localities (Fig. 2 and Appendix 1), ranging from ten species in two localities within the municipality of Ocampo, Coahuila (sites 19 and 21) to 24 species in Cuatro Ciénegas, Coahuila (site 17). Species richness of this site in particular is outstanding according to the null model ($P < 0.003$). In average, species richness per sampling site was 15.07 species (S.D. = ±3.12).

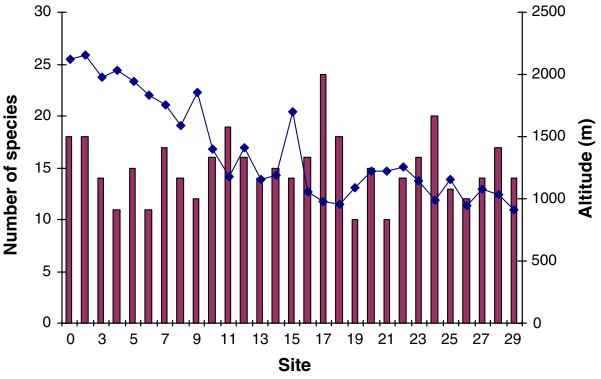


Fig. 2 Cactus species richness per site (bars) and altitude variation along the megatransect. The values of species richness and altitudes are also indicated in Appendix 1

Table 1 is a comparison between the longitudinal megatransect studied by Goettsch and Hernández (2006) and the latitudinal observations reported here. The slight variation in cactus species richness between the two megatransects (61 vs. 71 spp.) may be explained by differences in their length. Moreover, the small increment in the average number of species per site in the longitudinal megatransect (17.26 vs. 15.07 spp.) may be attributable to the fact that Goettsch´s and Hernández' megatransect intercepts the south-eastern portion of the CDR, identified as the area containing the highest concentration of cactus species in the continent (Gómez-Hinostrosa and Hernández 2000; Hernández et al. 2001).

Another aspect worth considering is the possible correlation between altitude and cactus species richness. There is a gradual decrease in altitude from the southern extreme of the megatransect northwards (see Fig. 2 and Appendix 1). The lowest areas in the CDR [e.g., Big Bend (minimum altitude = 600 m), Cuatro Ciénegas (740 m) and Mapimí (1075 m)] register the highest mean temperatures and lowest precipitation. As elevation increases from these areas, there is an increase in precipitation and mean temperatures decrease (Hernández and Gómez-Hinostrosa 2005). Our data shows no correlation between species richness and altitude ($r = 0.023$, $n = 29$, $P = 0.42$).

Relative frequency and spatial patterns

Appendix 2 shows the relative frequency (f) of each one of the species found along the megatransect. As shown in Fig. 3, the majority of the recorded species (66.2% or 47 spp.) had frequencies below the mean value ($f = 21.2\%$), and 52.1% of them (37 spp.) were found in three or fewer sites ($f = < 10.3\%$). Moreover, 17 species (23.9%) were found in a single site ($f = 3.4\%$), out of the 29 locations sampled (see also Table 1). It is worth noticing that, even though our latitudinal megatransect was considerably larger than Goettsch´s and Hernández' (2006) longitudinal study, the mean values of the frequencies, as well as

Table 1 Comparison of the main characteristics and results between the longitudinal study of Goettsch and Hernández (2006) and the present study

	Longitudinal megatransect (Goettsch and Hernández 2006)	Latitudinal megatransect (This paper)
Length of megatransect (km)	250	798
Sampled sites	23	29
Species richness	61	71
Species endemic to CDR	35 (57.4%)	43 (60.1%)
Range of number of species per site	10–30	10–24
Average number of species per site (±SD)	17.26 (±4.31)	15.07 (±3.12)
Mean value of the frequencies	28.3%	21.2%
Species with frequencies below mean value	34 (55.7%)	47 (66.2%)
Species present in three sites or less	32 (52.5%)	37 (52.1%)
Species present in only one site	19 (31.2%)	17 (23.9%)
β diversity (max. value)	0.93	1.00
β diversity (max. value between contiguous sites)	0.56	0.69
β diversity (average value among all sites)	0.52	0.58
Percent of site pairs with low β diversity values ($\beta = 0$–0.33)	11.9%	6.6%
Percent of site pairs with medium β diversity values ($\beta = 0.331$–0.66)	64%	68%
Percent of site pairs with high β diversity values ($\beta = 0.661$–1)	24.1%	25.4%

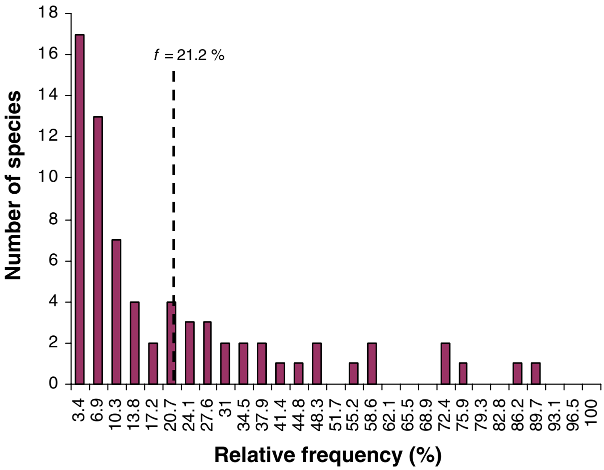


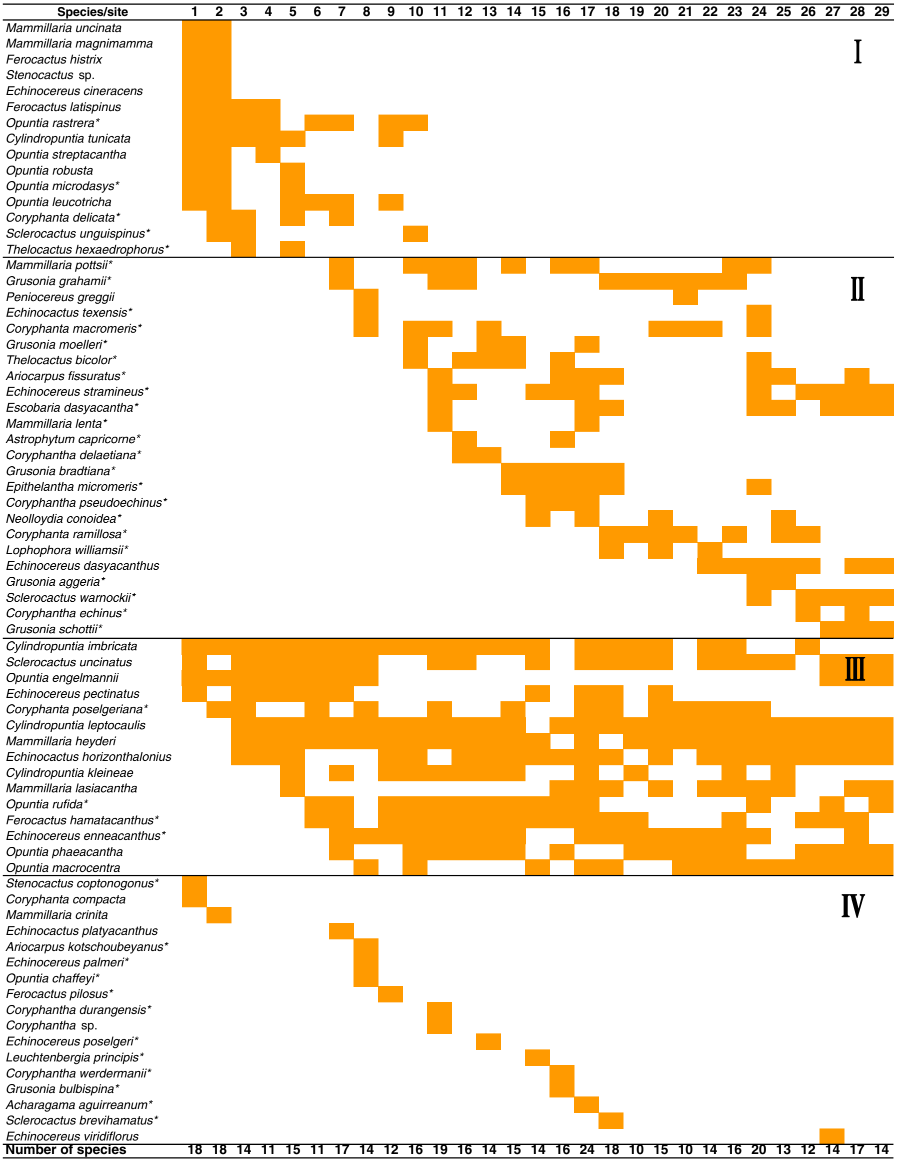
Fig. 3 Frequency distribution of the species in the megatransect. The dotted line indicates the mean value of the frequencies

the proportions of low frequency species were similar (Table 1). These results show that cactus species in the CDR tend to be highly infrequent.

Figure 4 help us to visualize the individual pattern of the cactus species registered along the megatransect. The figure was divided into four sections (I, II, III and IV), corresponding to four distinct distribution patterns. The first pattern comprises 15 species whose distribution area is restricted to the southern section of the megatransect. These plants, which were found exclusively in the ten southernmost sites, are relatively common and sometimes wide-ranging in the southern segment of the CDR and elsewhere. In fact, several of these species extend their ranges way beyond the southern limits of the CDR, into the Basin of Mexico (e. g., *Mammillaria magnimamma*, *Echinocereus cinerascens*, and *Opuntia streptacantha*), and even the Tehuacán Valley, Puebla (e. g., *Ferocactus latispinus*).

The second pattern includes the highest number of the recorded species in the megatransect (24 spp.). Species in this group are primarily distributed in the central part of the megatransect, extending their range northwards. The group includes a number of species occurring in large portions of the CDR (e. g., *Mammillaria pottsii*, *Grusonia grahamii*, *Ariocarpus fissuratus*, *Lophophora williamsii*, *Neolloydia conoidea*, and several others), but also species with narrower distributions (e. g., *Mammillaria lenta*, *Astrophytum capricorne*, and *Grusonia bradtiana*). With the exception of *Peniocereus greggii* and *Echinocereus dasyacanthus*, all of the species in this group are strictly endemic to the CDR. The frequency values registered in the megatransect by most of these species are relatively low, ranging from 6.9 to 34.5%, never exceeding the frequencies of the species in the third group. The low frequencies of these species may be explained by the fact that their distribution is highly discontinuous geographically (Fig. 4). However, a few of the species have a low frequency ($f = 6.9\%$) as a direct consequence of their relatively narrow distribution range (i. e., *Mammillaria lenta* and *Astrophytum capricorne*).

The third pattern comprises a group of 15 species that registered the highest frequency values in the megatransect ($f = 34.5–89.7\%$). Some of the most geographically and ecologically common species in the CDR are included in this group, among which *Cylindropuntia leptocaulis, Mammillaria heyderi, C. imbricata, Sclerocactus uncinatus*, and *Echinocactus horizonthalonius* are outstanding for their high frequency in the megatransect ($f = 89.7$,



	Species/site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
I	*Mammillaria uncinata*	■	■																											
	Mammillaria magnimamma	■	■																											
	Ferocactus histrix	■	■																											
	Stenocactus sp.	■	■																											
	Echinocereus cineracens	■	■																											
	Ferocactus latispinus	■	■	■	■																									
	*Opuntia rastrera**	■	■	■	■		■	■		■	■																			
	Cylindropuntia tunicata	■	■	■	■	■				■																				
	Opuntia streptacantha	■	■		■																									
	Opuntia robusta	■	■			■																								
	*Opuntia microdasys**	■	■			■																								
	Opuntia leucotricha	■	■			■	■	■		■																				
	*Coryphanta delicata**		■	■		■		■																						
	*Sclerocactus unguispinus**		■	■							■																			
	*Thelocactus hexaedrophorus**			■		■																								
II	*Mammillaria pottsii**							■			■	■	■		■		■	■						■	■					
	*Grusonia grahamii**							■				■	■						■	■	■	■	■	■						
	Peniocereus greggii								■													■								
	*Echinocactus texensis**								■																■					
	*Coryphanta macromeris**								■		■	■		■							■	■	■		■					
	*Grusonia moelleri**										■			■	■			■												
	*Thelocactus bicolor**										■		■	■	■		■								■					
	*Ariocarpus fissuratus**											■					■	■	■						■	■			■	
	*Echinocereus stramineus**											■	■			■	■	■							■		■	■	■	■
	*Escobaria dasyacantha**											■						■	■						■	■		■	■	■
	*Mammillaria lenta**											■						■												
	*Astrophytum capricorne**												■				■													
	*Coryphantha delaetiana**												■	■																
	*Grusonia bradtiana**														■	■	■	■	■											
	*Epithelantha micromeris**														■	■	■	■	■						■					
	*Coryphantha pseudoechinus**															■	■	■												
	*Neolloydia conoidea**															■		■			■					■				
	*Coryphanta ramillosa**																		■	■	■	■		■		■	■			
	*Lophophora williamsii**																		■		■		■							
	Echinocereus dasyacanthus																						■	■	■	■	■		■	■
	*Grusonia aggeria**																								■	■				
	*Sclerocactus warnockii**																								■		■	■	■	■
	*Coryphantha echinus**																										■		■	
	*Grusonia schottii**																											■	■	■
III	*Cylindropuntia imbricata*	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■		■	■	■	■		■	■			■			
	Sclerocactus uncinatus	■		■	■	■	■	■	■			■	■			■		■	■	■	■		■	■	■	■		■	■	■
	Opuntia engelmannii	■	■	■	■	■	■	■	■																			■	■	■
	Echinocereus pectinatus	■		■	■	■	■	■								■		■	■		■									
	*Coryphanta poselgeriana**		■	■			■		■			■			■			■	■		■	■	■	■	■					
	Cylindropuntia leptocaulis			■	■	■	■	■	■	■	■	■	■	■	■		■	■	■	■	■	■	■	■	■	■	■	■	■	■
	Mammillaria heyderi			■	■	■	■	■	■	■	■	■	■	■	■	■		■		■	■	■	■	■	■	■	■	■	■	■
	Echinocactus horizonthalonius			■	■	■				■	■		■	■	■	■	■	■	■		■		■	■	■	■	■	■	■	■
	Cylindropuntia kleineae					■		■		■	■	■	■	■	■			■		■				■		■				
	Mammillaria lasiacantha					■											■	■	■		■		■	■	■	■			■	■
	*Opuntia rufida**						■	■		■	■	■	■	■	■	■	■	■							■			■		■
	*Ferocactus hamatacanthus**						■	■		■	■	■	■	■	■	■	■	■	■	■				■			■	■	■	
	*Echinocereus enneacanthus**							■	■	■	■	■	■	■	■			■	■	■	■	■	■	■	■				■	
	Opuntia phaeacantha							■			■	■	■	■	■		■			■	■	■	■	■			■	■	■	■
	Opuntia macrocentra								■		■					■		■	■			■	■	■	■	■	■	■	■	■
IV	*Stenocactus coptonogonus**	■																												
	Coryphanta compacta	■																												
	Mammillaria crinita		■																											
	Echinocactus platyacanthus							■																						
	*Ariocarpus kotschoubeyanus**								■																					
	*Echinocereus palmeri**								■																					
	*Opuntia chaffeyi**								■																					
	*Ferocactus pilosus**									■																				
	*Coryphantha durangensis**											■																		
	Coryphantha sp.											■																		
	*Echinocereus poselgeri**													■																
	*Leuchtenbergia principis**															■														
	*Coryphantha werdermanii**																■													
	*Grusonia bulbispina**																■													
	*Acharagama aguirreanum**																	■												
	*Sclerocactus brevihamatus**																		■											
	Echinocereus viridiflorus																											■		
	Number of species	18	18	14	11	15	11	17	14	12	16	19	16	14	15	14	16	24	18	10	15	10	14	16	20	13	12	14	17	14

Fig. 4 Presence (shaded squares) and absence patterns of cactus species in the megatransect. The numbers at the top of the figure are site numbers. The species with an asterisk are Chihuahuan Desert endemics according to Hernández et al. (2004)

86.2, 75.9, 72.4, and 72.4% respectively). This group is dominated by wide-ranging, mostly non-endemic species to the CDR that very often extend their ranges beyond this region. Interestingly, several of these species are characterised by having large, showy, fleshy, bird or mammal dispersed fruits, as it is the case of prickly pears (*Opuntia* spp.), chollas and tasajos (*Cylindropuntia* spp.), barrel cacti (*Ferocactus hamatacanthus*), and pitayas (*Echinocereus enneacanthus*, *E. pectinatus*). As earlier suggested by Goettsch and

Table 2 Beta diversity values among sampling sites

Site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1		0.22	0.56	0.45	0.52	0.59	0.66	0.81	0.73	0.88	0.89	0.88	0.94	0.94	0.81	1.00	0.86	0.83	0.86	0.82	1.00	0.88	0.88	0.95	0.94	0.93	0.88	0.89	0.88
2			0.5	0.59	0.58	0.66	0.71	0.81	0.73	0.82	0.89	0.94	0.94	0.88	0.94	1.00	0.90	0.89	0.93	0.88	0.93	0.88	0.88	0.95	1.00	0.93	0.88	0.94	0.94
3				0.2	0.31	0.36	0.48	0.57	0.54	0.60	0.70	0.67	0.71	0.66	0.64	0.87	0.63	0.63	0.67	0.52	0.75	0.57	0.60	0.71	0.70	0.69	0.64	0.68	0.64
4					0.38	0.36	0.50	0.50	0.48	0.63	0.73	0.63	0.68	0.69	0.60	0.85	0.66	0.66	0.62	0.54	0.81	0.60	0.63	0.74	0.67	0.65	0.60	0.64	0.60
5						0.46	0.44	0.66	0.48	0.68	0.71	0.61	0.66	0.67	0.66	0.81	0.59	0.64	0.60	0.53	0.84	0.59	0.55	0.71	0.57	0.70	0.66	0.63	0.59
6							0.29	0.52	0.39	0.56	0.53	0.56	0.60	0.54	0.52	0.78	0.54	0.59	0.52	0.54	0.71	0.60	0.56	0.68	0.75	0.65	0.52	0.64	0.60
7								0.61	0.38	0.39	0.39	0.33	0.48	0.44	0.61	0.70	0.51	0.60	0.33	0.50	0.63	0.55	0.39	0.68	0.73	0.66	0.55	0.59	0.61
8									0.69	0.60	0.58	0.67	0.64	0.66	0.71	0.93	0.63	0.63	0.58	0.52	0.42	0.43	0.53	0.53	0.70	0.69	0.64	0.61	0.64
9										0.36	0.55	0.43	0.38	0.41	0.62	0.71	0.56	0.67	0.45	0.63	0.73	0.62	0.50	0.69	0.68	0.58	0.62	0.66	0.69
10											0.43	0.31	0.20	0.23	0.60	0.56	0.45	0.65	0.46	0.55	0.54	0.47	0.38	0.50	0.66	0.50	0.53	0.58	0.60
11												0.31	0.45	0.41	0.64	0.60	0.35	0.51	0.38	0.47	0.52	0.45	0.37	0.44	0.63	0.61	0.52	0.50	0.58
12													0.30	0.29	0.53	0.44	0.45	0.59	0.31	0.48	0.62	0.47	0.31	0.50	0.66	0.50	0.47	0.52	0.53
13														0.24	0.64	0.60	0.53	0.69	0.42	0.52	0.58	0.50	0.47	0.59	0.70	0.54	0.57	0.61	0.64
14															0.52	0.42	0.33	0.52	0.44	0.53	0.60	0.52	0.35	0.49	0.71	0.56	0.59	0.63	0.66
15																0.53	0.32	0.50	0.67	0.59	0.83	0.64	0.60	0.59	0.63	0.54	0.50	0.61	0.57
16																	0.45	0.59	0.77	0.74	0.85	0.73	0.63	0.50	0.72	0.64	0.60	0.58	0.60
17																		0.33	0.59	0.49	0.71	0.53	0.40	0.36	0.46	0.61	0.53	0.46	0.53
18																			0.50	0.33	0.57	0.38	0.35	0.47	0.48	0.60	0.63	0.49	0.63
19																				0.36	0.40	0.42	0.23	0.73	0.57	0.45	0.58	0.56	0.67
20																					0.36	0.17	0.29	0.54	0.50	0.56	0.66	0.56	0.59
21																						0.33	0.38	0.60	0.65	0.55	0.67	0.63	0.67
22																							0.20	0.41	0.48	0.46	0.57	0.42	0.43
23																								0.44	0.38	0.36	0.53	0.39	0.47
24																									0.39	0.56	0.47	0.35	0.35
25																										0.52	0.56	0.40	0.41
26																											0.38	0.31	0.38
27																												0.23	0.14
28																													0.16
29	**S**										**M**																**T-P**		

The high β diversity values ($\beta = >0.661$) are dark shaded, whereas the low β diversity values ($\beta = <0.33$) are light shaded (see text). The vertical lines indicate the limits among the Saladan (S), Mapimian (M), and Transpecos (T-P) sub-provinces of Morafka (1977)

Hernández (2006), it is likely that these fruit characteristics confer these plants a high dispersal potential; however, this hypothesis has yet to be demonstrated.

Finally, the fourth pattern comprises 17 infrequent species ($f = 3.4\%$), all of which were only found in one site, in different parts of the megatransect. This group includes some taxa with overall narrow distribution ranges (e. g., *Echinocereus palmeri* subsp. *mazapil*, *Opuntia chaffeyi*, *Coryphantha werdermanii*, and *Acharagma aguirreanum*), or species with larger, but highly discontinuous distributions (e. g., *Stenocactus coptonogonus*, *Ariocarpus kotschoubeyanus*, and *Leuchtenbergia principis*). Species within this group also include highly conspicuous and relatively common species in the CDR, such as the barrel cacti *Echinocactus platyacanthus* and *Ferocactus pilosus*; these species are widely distributed in the south-eastern part of this region, becoming rather infrequent westwards, just in the area where the sampling was conducted.

Beta diversity

The β diversity values for all pairs of contiguous and non-contiguous sites are shown in Table 2. All values were higher than zero, which means that all sampling sites differ to each other in their cactus species composition. In other words, there is always turnover among cactus assemblages at the scale used in our study. The reported values ranged from $\beta = 0.14$, corresponding to site pair 27–29 which differed by only two species (*Echinocereus dasyacanthus* and *Mammillaria lasiacantha*), to $\beta = 1.0$ in site pairs 16–1, 16–2, 21–1, and 25–2, where total species turnover was registered.

As expected, most of the lowest β diversity values were registered in the neighbouring site pairs (Table 2). In fact, the average value among contiguous sites ($\beta = 0.38$) was much lower than the average value calculated for all contiguous and non-contiguous sites ($\beta = 0.58$). The correlation between diversity and physical distance among sampling sites was highly significant ($r = 0.57$, $n = 406$ pairs, $P < 0.0001$, Fig. 5). The probability value

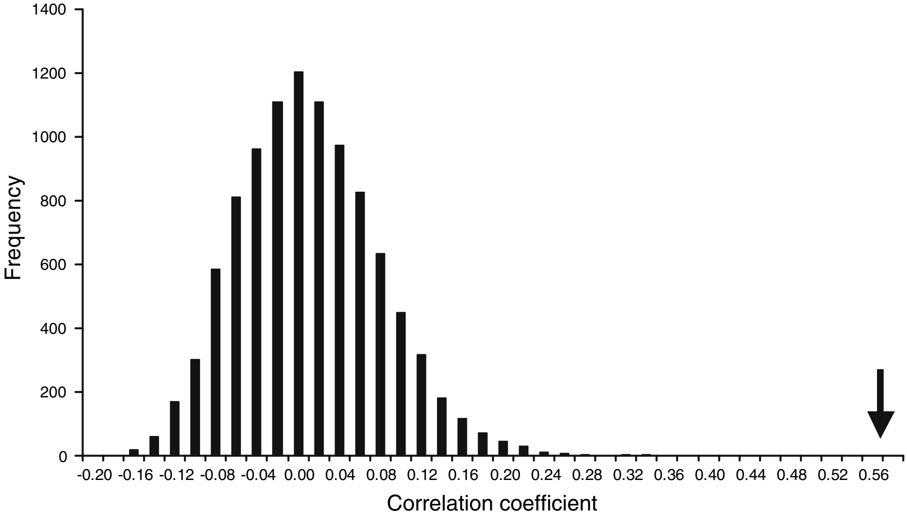


Fig. 5 Mantel test comparing the β diversity and distance matrices. The plot shows the frequency distribution of correlation coefficients generated from 10,000 permutations, and the location of the observed value

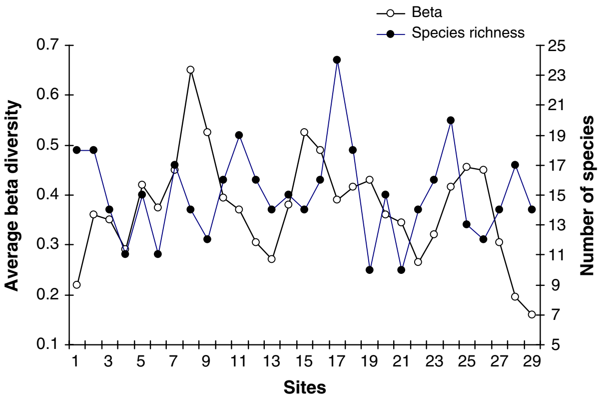


Fig. 6 Patterns of β diversity and species richness along the megatransect

corresponds to a one-tailed Mantel test with 10,000 permutations comparing the β diversity and distance matrices (Mantel 1967; Manly 1997).

There was no correlation between species richness and β diversity ($r = 0.086$, $P > 0.05$). Figure 6 shows the relationship between the patterns of β diversity and species richness among all sites. In this graph, the β diversity values are average figures calculated for each site and their contiguous sites, with the exception of sites 1 and 29. Sites 8, 9, and 15 registered the highest average β diversity values ($\beta = 0.65$, 0.52, and 0.52, respectively). However, all of these sites had below-average species richness. In the same way, site 17 had the highest species richness (24 spp.), but a low average β diversity value ($\beta = 0.39$).

As mentioned above, site 8 registered the highest average β diversity value in the megatransect. The relatively high species turnover in this site is attributable to its atypical species composition. Here, we recorded three taxa (*Ariocarpus kotschoubeyanus,* *Echinocereus palmeri* subsp. *mazapil*, and *Opuntia chaffeyi*) not found in any of the other sampling sites; in addition, several relatively common species present in the adjacent sites (e. g., *Opuntia rastrera, O. leucotricha, Cylindropuntia tunicata*, etc.) are absent here. The unusual combination of cactus species found in this site responds to its contrasting ecological characteristics. Site 8 differs from the other sites by the widespread occurrence of extensive silty dry lake deposits and the scarcity of low rocky hills typical of the CDR. These peculiar edaphic conditions induce the occurrence of a specific repertoire of cactus species, and our observations in the CDR indicate that the three geographically rare taxa mentioned above (*Ariocarpus kotschoubeyanus, Echinocereus palmeri* subsp. *mazapil*, and *Opuntia chaffeyi*) are edaphic specialists, being adapted to grow in silty dry lake deposits, and not occurring in other soil types (Hernández and Gómez-Hinostrosa 2004).

As far as β diversity values and eco-regional boundaries is concerned, there is a weak coincidence between high species turnover and the edges of the Morafka's (1977) sub-provinces (Fig. 1). That is, the areas where high turnover was registered not necessarily match with the borders of the Saladan, Mapimian, and Trans-Pecos sub-provinces (Table 2 and Fig. 6).

Mourelle and Ezcurra (1997), in their study on Argentinean cactus species turnover, suggested the grouping of the β diversity values into three categories: high for values ranging from 0.661 to 1.0, medium for $\beta = 0.331–0.66$, and low for $\beta = 0–0.33$. If we accept this scheme, which was followed by Goettsch and Hernández (2006), more than two thirds (68%) of the β diversity values reported in Table 2 fall in the medium category (276 of the 406 pair wise combinations), whereas a smaller proportion of them fall in the high (25.4%) and low categories (6.6%). In the same way, if we consider the average values by site of Fig. 6, 20 of the sites (69%) fall in the medium category, whereas the remaining nine (31%) correspond to the low category, with no sites falling in the high category. The average value of all site combinations ($\beta = 0.58$) falls in the medium category.

The previous paragraphs lead us to consider the nature of species turnover in the CDR. From the analysis of our data, three major causes producing an increase in β diversity may be inferred, the most obvious and probably most important one being the patchy distribution pattern exhibited by most cactus species in Mexico. This phenomenon, previously discussed by Goettsch and Hernández (2006), consist of the existence of numerous discontinuities along the distribution range of the species at various scales. Figure 4 shows that most of the species registered along the megatransect exhibit an intermittent pattern of distribution at a regional scale. This alternating presence/absence pattern of the species along their range is probably a consequence of the heterogeneous ecological conditions throughout the CDR (Hernández 2006). The basin and range topography prevailing in the CDR results in a mosaic of edaphic conditions promoting patchy distribution patterns at varied scales. Also, increased aridity since the last glacial period (11,000 y. b. p.) has probably stimulated population fragmentation and speciation. Moreover, it is likely that small and/or highly discontinuous distributions may also be a result of the poor seed dispersal ability of many of the species.

The second promoter of β diversity is the fact that a number of species were registered in or near the margin of their geographic range, explaining their low frequency in the megatransect. For instance, several of the species that were found in sites 1 and 2 are by no means geographically rare species, although they were infrequent in our study. This is the case of *Echinocereus cinerascens*, *Ferocactus histrix*, *F. latispinus*, *Mammillaria magnimamma*, *M. uncinata*, *Opuntia robusta*, *O. streptacantha*, and other species that are rather common and have a wide distribution range in the periphery of the CDR and elsewhere. These species were highly infrequent in our study ($f = <13.8$) not because they are geographically restricted, but because the sampling was initiated at the northern edge of their distribution range.

Finally, the third major factor explaining the observed species turnover was the presence in particular sites of infrequent, geographically restricted species. In our megatransect we detected several taxa with extremely to moderately narrow overall distribution ranges, such as *Acharagma aguirreanum*, *Astrophytum capricorne*, *Coryphantha pseudoechinus*, *C. werdermanii*, *Echinocereus palmeri*, *Grusonia bradtiana*, *G. bulbispina*, *Mammillaria lenta*, *Opuntia chaffeyi*, and *Sclerocactus unguispinus*. This phenomenon is especially obvious in site 16, where several of these narrow endemics concur.

In sum, it can be concluded that the continuous spatial changes in cactus species composition expressed in Table 2 are primarily explained by the commonly intermittent distribution patterns of the species and the presence in the megatransect of species at the margin of their range. On the other hand, the contribution of narrow endemics to β diversity is less important, as it involves a relatively low number of species. We estimate that out of the 71 species recorded in the megatransect, only ten have relatively small overall geographic ranges (Hernández, unpublished data).

An additional aspect that merits special consideration refers to how the β diversity patterns reported here compare to those found by Goettsch and Hernández (2006) in their longitudinal megatransect. In the previous section we emphasized the striking similarities between the two studies regarding species frequencies and spatial patters. The β diversity patterns in the two studies were also extremely similar, in cases almost identical (Table 1). It is interesting to notice that the maximum and average values, as well as the proportions of low, medium and high β diversity values were comparable (Table 1). Consequently, it can be concluded that the striking similarity between the results of the present study and those of Goettsch and Hernández (2006) suggest that the observed β diversity pattern is consistent throughout the whole CDR. However, it is likely that different scenarios (i.e., higher β diversity values) are found in particular areas within the region, where there is a increased proportion of rare species. This is particularly true in the south-eastern extreme of the CDR, where numerous narrow endemic species are concentrated in relatively small areas (Hernández and Bárcenas 1995; Hernández et al. 2001; Hernández and Gómez-Hinostrosa 2005). In these areas, we would expect abrupt increases in β diversity values.

Biogeographic affinities

The subdivision of the CDR proposed by Morafka (1977) described in the introduction (Fig. 1) provides a suitable scenario for discussing the biogeographic affinities among the cactus assemblages recorded in the present study. Figure 7 is a phenogram generated with the values of floristic similarity among the sites. Taking the index of similarity of $IS_j = 0.33$ as a baseline, five distinct clusters are distinguished (see Roman numbers in Fig. 7), which harmonize well with Morafka's subdivisions. Cluster I is formed by sites 1 and 2, that are transitional between the CDR and the southern localities, and diverge from the remaining sampled localities by the presence of several species widely distributed in the southern extreme of the CDR and southwards. The second cluster, comprising sites 3 to 7 and 9, is also defined by several species with southern biogeographic affinities within the main body of the CDR. All sites in clusters I and II are located south of the Sierra de Parras, and correspond to the Saladan sub-province (see vertical bars in Fig. 7). Cluster III groups ten sites (sites 10–14 and 19–23) that, with the exception of site 10, are all located within the Mapimian sub-province, north of the Sierra de Parras (Fig. 7). Site 10 is the northernmost of the localities situated south of this mountain range; the placement of this Saladan site within this cluster may be a

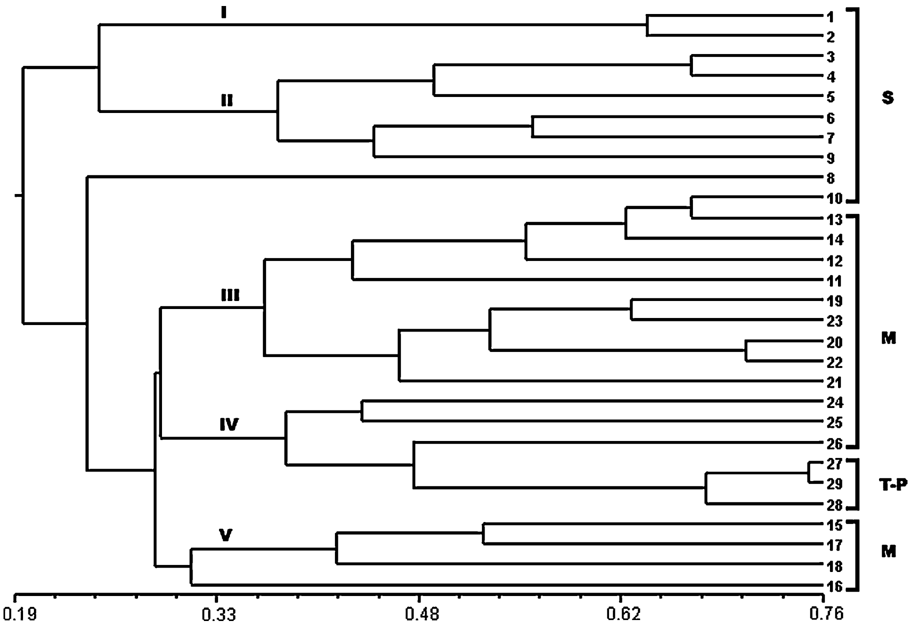


Fig. 7 Phenogram derived from the Jaccard's similarity values among the sampling sites ($r = 0.74165$). The Roman numbers on the left portion of the figure indicate the identified clusters; the numbers on the right are the site numbers indicated in Appendix 1; and the bars show the localization of the sites in concordance with Morafka's (1977) Chihuahuan Desert sub-provinces: S = Saladan, M = Mapimian, and T-P = Trans-Pecos

consequence of its transitional nature. Within the general geographical area of this cluster lies a group of three sites (15, 17, and 18) constituting a divergent cluster (Cluster V). These three sites, located at the Bolsón of Cuatro Ciénegas, Coahuila and neighbouring areas (Cuates de Australia), share a number of species with their adjacent areas, but diverge by the presence of some infrequent species, such as *Grusonia bradtiana*, *Leuchtenbergia principis*, *Acharagma aguirreanum*, and *Sclerocactus brevihamathus*.

Finally, sites 24–29, located in the northernmost fragment of the Mapimian subprovince and in the Trans-Pecos, are grouped in a discrete cluster (Cluster IV). This portion of the CDR is home to some characteristic species, such as *Sclerocactus warnockii, Coryphantha echinus*, and *Grusonia schottii.*

The phenogram also reveals that sites 8 and 16 are highly divergent due to their distinctive cactus species composition. In fact, it is precisely in site 8, and to a lesser extent site 16, where the highest β diversity values among contiguous sites were registered (Fig. 6 and Table 2). In the previous section we described how site 8 (Estación Camacho, Mazapil, Zacatecas) differs from the other sampling localities by the presence of three edaphically specialised taxa (*Ariocarpus kotschoubeyanus*, *Echinocereus palmeri* subsp. *mazapil*, and *Opuntia chaffeyi*) and by the absence of several relatively common species present in the adjacent sites. As for site 16, located at the centre of the Bolsón of Cuatro Ciénegas, two rare species were recorded here. However, it becomes apparent that the distinctiveness of this site is explained with a greater emphasis by the absence of several common species present in the contiguous and nearby sites. For reasons that we cannot explain at this moment, several common species (e. g., *Cylindropuntia imbricata*, *C. kleiniae*, *Sclerocactus uncinatus*, *Echinocereus pectinatus*, *E. enneacanthus*, *Mammillaria heyderi*, and *Opuntia macrocentra*) present in the adjoining sites, and that are widespread in the CDR, were not recorded here (see also Fig. 4).

Final considerations

There is no doubt that local cactus assemblages change continuously across the Chihuahuan Desert landscape. In fact, our study showed that, at the scale we chosen, there is always at least a minimum degree of species turnover, and very often changes are considerable. The rate of cactus species turnover among contiguous sites primarily fluctuated from low to medium, but if all site combinations are considered (contiguous and non-contiguous), medium values are predominant ($\beta = 0.331–0.66$). Moreover, it is outstanding that a quarter of the β diversity values fall in the high category ($\beta = 0.661–1.0$).

In a region such as the Chihuahuan Desert, where 69.8% of the 329 cactus species occurring in the area are regionally or locally endemic (Hernández et al. 2004), it can be easily presumed that the contribution of narrow endemics to β diversity is prominent. However, the evidence offered in this study, in conjunction with the data provided by Goettsch and Hernández (2006), does not support such assumption. Species turnover among cactus species assemblages in the CDR does not consist for the most part of a real process of species substitution, but rather corresponds to changes between adjacent sites resulting from intermittent distributions of widespread taxa. Nonetheless, we have to be cautious not to minimize the contribution of the narrowly endemic species to β diversity. Scattered throughout this region, there is a significant number of cactus species with small geographic ranges (see Fig. 13.6 in Hernández and Gómez-Hinostrosa 2005). In fact, Hernández and Navarro (2007) reported several species that restrict their ranges to areas below 500 km^2, and as small as 6 km^2. However, we currently do not know the proportion of narrowly endemics in the region's cactus flora. An investigation aimed at estimating the geographic range size of many cactus species occurring in the CDR is in progress. Undoubtedly, the contribution of microendemic species to β diversity is significant, although they are less numerous than the common, widespread species. In addition, due to their small ranges, these rare species are more difficult to detect in a vast area such as the CDR.

Our study revealed the complexity of the distribution patterns of *Cactaceae* in the CDR. These patterns are determined by the prevalence of infrequent species (Fig. 3) and conspicuous discontinuities in their range (Fig. 4), which cause constant changes in the species composition of cactus assemblages (Table 2). This biogeographic scenario makes actions to conserve these plants a difficult task. However, we need to address the issue about whether β diversity in itself is a good indicator of conservation value.

Theoretically, it can be predicted that an area where abrupt increases in β diversity (or extremely low similarity values) are detected should be a candidate for conservation action, such as the establishment of protected areas (Wiersma and Urban 2005). The analysis of our data indicates that this assertion is correct, at least partially. For instance, the highest average β diversity values in our megatransect were registered in sites 8, 9, 15, and 16 (Fig. 6) and a prerequisite for an area with high β diversity to be susceptible of conservation actions is that turnover is caused, at least partially, by species with narrow overall distribution ranges. This is the case of sites 8 and 16, where several of these narrow endemics concur. In other words, these two sites, that registered higher-than-average β diversity values, have a high conservation value because turnover is linked to the presence of species that have been confirmed as geographically rare.

The detection of areas where rare species coincide spatially is relatively easy when reliable information on their range is available. Published data, however, suggest that a substantial proportion of narrow endemic cactus species occur scattered in isolated patches of the CDR (see Fig. 13.6 in Hernández and Gómez-Hinostrosa 2005), away from known areas of high concentration of these species (e. g., Huizache, Jaumave, Tolimán, etc.). In view of this scenario, the network of small protected areas suggested by Hernández and Bárcenas (1996) to shelter the highly priced, rarest, and most endangered cactus species in the CDR is still valid today.

Acknowledgments We would like to thank Exequiel Ezcurra for constructive criticisms to the manuscript, Rolando Bárcenas for identifying some of the species of *Grusonia*, Raul Puente for assisting us and making the arrangements for fieldwork in the Big Bend area, and Alfredo Wong for support in the analysis of similarity. We also thank the officials at the Big Bend National Park for allowing us to conduct fieldwork in the area. Fieldwork associated to this project was carried out under collecting permits FLOR-0004 and FLOR-0094, provided by Secretaría del Medio Ambiente, Recursos Naturales y Pesca, Mexico.

Appendices

Appendix 1 Number, localization, altitude, and number of cactus species found in the sampling sites

Site	State, municipality/county	Locality	Coordinates	Altitude (m)	Number of species
1	SLP, Salinas	5 km N of Salinas	22°40′34″ N 101°41′35″ W	2,117	18
2	SLP, Santo Domingo	50 km N of Salinas	23°03′18″ N 101°45′46″ W	2,160	18
3	SLP, Santo Domingo	26 km N of La Herradura	23°14′54″ N 101°43′31″ W	1,980	14
4	SLP, Santo Domingo	18 km NE of the Santo Domingo-Charcas road, towards El Bozal	23°29′14″ N 101°34′51″ W	2,030	11
5	Zac, El Rucio	31.7 km N of the Concepción del Oro-Zacatecas road, towards Nuevo Mercurio	23°46′26″ N 102°07′33″ W	1,949	15
6	Zac, Mazapil	28 km S of Nuevo Mercurio	23°58′32″ N 102°10′27″ W	1,830	11
7	Zac, Mazapil	21 km S of Estación Camacho	24°16′38″ N 102°14′52″ W	1,760	17
8	Zac, Mazapil	12 km N of Estación Camacho	24°31′57″ N 100°20′29″ W	1,590	14
9	Zac, Mazapil	Ca. 5 km SE of Apizolaya	24°44′56″ N 102°14′31″ W	1,857	12
10	Zac, Mazapil	Ca. 3 km SE of San Juan de los Charcos	25°00′04″ N 102°36′51″ W	1,403	16
11	Coah, Viesca	Ca. 10 km SE of Viesca	25°16′18″ N 102°45′51″ W	1,176	19
12	Coah, Parras	11.5 km NW of Parras	25°30′39″ N 102°15′48″ W	1,409	16
13	Coah, Parras	10.3 km N of the Saltillo-Torreón road, towards San José de Mahoma	25°45′20″ N 102°13′32″ W	1,155	14
14	Coah, Parras	43 km N of the Saltillo-Torreón road, towards Estanque de León	26°02′17″ N 102°13′07″ W	1,185	15
15	Coah, San Pedro de las Colonias	72 km N of the Saltillo-Torreón road, towards Cuates de Australia	26°16′08″ N 102°12′39″ W	1,700	14
16	Coah, Cuatro Ciénegas	9.3 km SE of the Cuatro Ciénegas-Torreón road, towards Cuates de Australia	26°30′40″ N 102°26′16″ W	1,060	16
17	Coah, Cuatro Ciénegas	28 km SE of Cuatro Ciénegas	26°45′56″ N 102°08′33″ W	973	24

Appendix 1 continued

Site	State, municipality/county	Locality	Coordinates	Altitude (m)	Number of species
18	Coah, Cuatro Ciénegas	6 km N of Cuatro Ciénegas	27°03′11″ N 102°05′28″ W	960	18
19	Coah, Ocampo	41 km NW of Cuatro Ciénegas	27°15′01″ N 102°21′23″ W	1,090	10
20	Coah, Ocampo	24 km N of Ocampo	27°32′30″ N 102°22′35″ W	1,217	15
21	Coah, Ocampo	54 km N of Ocampo	27°44′49″ N 102°29′53″ W	1,220	10
22	Coah, Ocampo	80 km N of Ocampo	27°57′16″ N 102°38′52″ W	1,252	14
23	Coah, Ocampo	125 km N of Ocampo	28°14′07″ N 102°51′29″ W	1,150	16
24	Coah, Ocampo	10 km S of San Miguel	28°32′44″ N 102°56′17″ W	984	20
25	Coah, Ocampo	17 km NE of San Miguel	28°43′30″ N 102°48′36″ W	1,153	13
26	Coah, Ocampo	20 km SE of Boquillas del Carmen	29°03′54″ N 102°47′39″ W	940	12
27	Tex, Brewster	Big Bend National Park. Base of Nuget Mountain	29°15′29″ N 103°09′46″ W	1,073	14
28	Tex, Brewster	Big Bend National Park. Nine km on main road to Dagger Flat	29°28′31″ N 103°04′34″ W	1,038	17
29	Tex, Brewster	Big Bend National Park. Near the main entrance to the park	29°40′18″ N 103°10′24″ W	908	14

State abbreviations: Coah = Coahuila, SLP = San Luis Potosí, Tex = Texas, and Zac = Zacatecas

Appendix 2 Relative frequencies of the cactus species found in the megatransect. All vouchers were deposited in the National Herbarium of Mexico (MEXU)

Taxon	Frequency (%)	Voucher
Acharagma aguirreanum (Glass et R. A. Foster) Glass	3.4	H - 3407
Ariocarpus fissuratus (Engelm.) K. Schum.	24.1	C - 1825
A. kotschoubeyanus (Lem.) K. Schum.	3.4	H - 3526
Astrophytum capricorne (Dietr.) Britton et Rose	6.9	C - 1822
Coryphantha compacta (Engelm.) Britton et Rose	3.4	H - 3462
C. delaetiana (Quehl) A. Berger	6.9	H - 3332
C. delicata (Quehl) A. Berger	13.8	H - 3681
C. durangensis (Quehl) A. Berger	3.4	C - 1839
C. echinus (Engelm.) Orcutt	6.9	H - 3666
C. macromeris (Engelm.) Lem.	27.6	C - 1891
C. poselgeriana (Dietr.) Britton et Rose	44.8	C - 1896
C. pseudoechinus Boed.	10.3	C - 1906
C. ramillosa Cutak	24.1	H - 3379
C. werdermanii Boed.	3.4	C - 1911
C. sp.	3.4	C - 1826
Cylindropuntia imbricata (Haw.) F. M. Knuth	75.9	H - 3600
C. kleiniae (DC.) F. M. Knuth	41.4	H - 3414
C. leptocaulis (DC.) F. M. Knuth	89.7	C - 1841
C. tunicata (Lehm.) F. M. Knuth	20.7	C - 1866
Echinocactus horizonthalonius Lem.	72.4	C - 1809

Appendix 2 continued

Taxon	Frequency (%)	Voucher
E. platyacanthus Link et Otto	3.4	H - 3514
E. texensis Hopffer	6.9	H - 3637
Echinocereus cinerascens (DC.) Lem.	6.9	H - 3457
E. dasyacanthus Engelm.	24.1	H - 3655
E. enneacanthus Engelm.	58.6	C - 1874
E. palmeri Britton et Rose	3.4	H - 3528
E. pectinatus (Scheidw.) Engelm.	34.5	H - 3364
E. poselgeri Lem.	3.4	H - 3329
E. stramineus (Engelm.) Seitz	34.5	C - 1912
E. viridiflorus Engelm.	3.4	RP - 2614
Epithelantha micromeris (Engelm.) F. A. C. Weber	20.7	C - 1910
Escobaria dasyacantha (Engelm.) Britton et Rose	27.6	C - 1838
Ferocactus hamatacanthus (Muehlenpf.) Britton et Rose	58.6	H - 3401
F. histrix (DC.) G. E. Linds.	6.9	H - 3448
F. latispinus (Haw.) Britton et Rose	13.8	H - 3473
F. pilosus (Galeotti ex Salm-Dyck) Werderm.	3.4	C - 1871
Grusonia aggeria (Ralston et Hilsenb.) E. F. Anderson	6.9	H - 3653
G. bradtiana (J. M. Coult.) Britton et Rose	17.2	C - 1901
G. bulbispina (Engelm.) H. Rob.	3.4	C - 1903
G. grahamii (Engelm.) H. Rob.	31.0	H - 3513
G. moelleri (A. Berger) E. F. Anderson	13.8	H - 3416
G. schottii (Engelm.) H. Rob.	10.3	RP - 2621
Leuchtenbergia principis Hook.	3.4	H - 3368
Lophophora williamsii (Lem. ex Salm-Dyck) J. M. Coult.	10.3	C - 1875
Mammillaria crinita DC.	3.4	H - 3440
M. heyderi Muehlenpf.	86.2	C - 1820
M. lasiacantha Engelm.	37.9	C - 1902
M. lenta K. Brandegee	6.9	C - 1830
M. magnimamma Haw.	6.9	H - 3445
M. pottsii Scheer ex Salm-Dyck	31.0	C - 1829
M. uncinata Zucc. ex Pfeiff.	6.9	H - 3429
Neolloydia conoidea (DC.) Britton et Rose	13.8	C - 1876
Opuntia chaffeyi Britton et Rose	3.4	H - 3525
O. engelmannii Salm-Dyck ex Engelm.	37.9	H - 3668
O. leucotricha DC.	20.7	H - 3509
O. macrocentra Engelm.	48.3	C - 1845
O. microdasys (Lehm.) Pfeiff.	10.3	H - 3670
O. phaeacantha Engelm.	55.2	H - 3334
O. rastrera F. A. C. Weber	27.6	H - 3506
O. robusta H. L. Wendl. ex Pfeiff.	10.3	H - 3432
O. rufida Engelm.	48.3	C - 1835
O. streptacantha Lem.	10.3	H - 3454
Peniocereus greggii (Engelm.) Britton et Rose	6.9	H - 3527
Sclerocactus brevihamatus (Engelm.) D. R. Hunt	3.4	H - 3384
S. uncinatus (Galeotti) N. P. Taylor	72.4	C - 1832
S. unguispinus (Engelm.) N. P. Taylor	10.3	H - 3471
S. warnockii (L. D. Benson) N. P. Taylor	17.2	H - 3631
S. coptonogonus (Lem.) A. Berger ex A. W. Hill	3.4	H - 3446
S. sp.	6.9	H - 3427
Thelocactus bicolor (Galeotti ex Pfeiff.) Britton et Rose	20.7	C - 1846
T. hexaedrophorus (Lem.) Britton et Rose	6.9	H - 3469

Vouchers collected by Carlos Gómez-Hinostrosa (C), Héctor M. Hernández (H), and Raul Puente (RP)

References

Condit R, Pitman N, Leigh EG Jr, Chave J, Terborgh J, Foster RB, Núñez P, Aguilar S, Valencia R, Villa G, Muller-Landau HC, Losos E, Hubbell SP (2002) Beta-diversity in tropical forest trees. Science 295:666–669

Dinerstein E, Olson D, Atchley J, Loucks C, Contreras-Balderas S, Abell R, Iñigo E, Enkerlin E, Williams CE, Castilleja G (eds) (1999) Ecoregion-based conservation in the Chihuahuan Desert: a biological assessment and biodiversity vision. WWF, CONABIO, PRONATURA and ITESM, Washington, DC, USA

Goettsch B, Hernández HM (2006) Beta diversity and similarity among cactus assemblages in the Chihuahuan Desert. J Arid Environ 65:513–528

Gómez-Hinostrosa C, Hernández HM (2000) Diversity, geographical distribution, and conservation of Cactaceae in the Mier y Noriega region, Mexico. Biodivers Conserv 9:403–418

Harrison S, Ross SJ, Lawton JH (1992) Beta diversity on geographical gradients in Britain. J Anim Ecol 61:151–158

Henrickson J, Johnston MC (1986) Vegetation and community types of the Chihuahuan Desert. In: Barlow JC, Powell AM, Timmermann B (eds) Second symposium on the resources of the Chihuahuan Desert Region, United States and Mexico. Chihuahuan Desert Research Institute and Sul Ross State University. Alpine, Texas, USA, pp 20–39

Hernández HM (2006) La vida en los desiertos mexicanos. Fondo de Cultura Económica, Mexico City, Mexico, 188 pp

Hernández HM, Bárcenas RT (1995) Endangered cacti in the Chihuahuan Desert. I. Distribution patterns. Conserv Biol 9:1176–1190

Hernández HM, Bárcenas RT (1996) Endangered cacti in the Chihuahuan Desert. II. Biogeography and conservation. Conserv Biol 10:1200–1209

Hernández HM, Gómez-Hinostrosa C (2004) Studies on Mexican Cactaceae. IV. A new subspecies of *Echinocereus palmeri* Britton & Rose, first record of the species in the Chihuahuan Desert. Bradleya 22:1–8

Hernández HM, Gómez-Hinostrosa C (2005) Cactus diversity and endemism in the Chihuahuan Desert Region. In: Cartron JL, Felger R, Ceballos G (eds) Biodiversity and conservation in Northern Mexico. Oxford University Press, New York, USA, pp 264–275

Hernández HM, Navarro M (2007) A new method to estimate areas of occupancy using herbarium data. Biodivers Conserv 16:2457–2470

Hernández HM, Gómez-Hinostrosa C, Bárcenas RT (2001) Diversity, spatial arrangement, and endemism of Cactaceae in the Huizache area, a hot-spot in the Chihuahuan Desert. Biodivers Conserv 10:1097–1112

Hernández HM, Gómez-Hinostrosa C, Goettsch B (2004) Checklist of Chihuahuan Desert Cactaceae. Harvard Papers Bot 9:51–68

Johnston MC (1977) Brief resume of botanical, including vegetational, features of the Chihuahuan Desert Region with special emphasis on their uniqueness. In: Wauer RH, Riskind DH (eds) Transactions of the symposium on the biological resources of the Chihuahuan Desert Region, United States and Mexico. National Park Service, Washington, DC, USA, pp 335–359

Manly BFJ (1997) Randomization, bootstrap and Monte Carlo methods in biology, 2nd edn. Chapman and Hall, London

Mantel N (1967) The detection of disease clustering and a generalize regression approach. Cancer Res 27:209–220

Medellín-Leal F (1982) The Chihuahuan Desert. In: Bender GL (ed) Reference handbook on the deserts of North America. Greenwood Press, Westport, CT, USA, pp 321–372

Mittermeier RA, Goettsch C, Robles-Gil P, Pilgrim J, Fonseca G, Konstant WR, Brooks T (eds) (2002) Wilderness: earth's last wild places. CEMEX, Mexico City, Mexico, 568 pp

Morafka DJ (1977) A biogeographical analysis of the Chihuahuan Desert through its herpetofauna. Biogeographica 9:1–313

Mourelle C, Ezcurra E (1997) Differentiation diversity of Argentine cacti and its relationship to environmental factors. J Veg Sci 8:547–558

Mueller-Dombois D, Ellenberg H (1974) Aims and methods of vegetation ecology. John Wiley and Sons, New York, USA, 547 pp

Schmidt RH Jr (1979) A climatic delineation of the "real" Chihuahuan Desert. J Arid Environ 2:243–250

Shreve F (1942) The desert vegetation of North America. Bot Rev 8:195–246

Wilson MV, Shmida A (1984) Measuring beta diversity with presence-absence data. J Ecol 72:1055–1064

Wiersma YF, Urban DL (2005) Beta diversity and nature reserve system design in the Yukon, Canada. Conserv Biol 19(4):1262–1272