

Beta diversity and similarity among cactus assemblages in the Chihuahuan Desert

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Abstract

We sampled the cactus species in 23 localities along a longitudinal transect in the southeastern segment of the Chihuahuan Desert. Using Wilson and Shmida's formula we calculated beta diversity values among contiguous and non-contiguous sites. As a complement, Jaccard's index of similarity was also calculated among all sites. A total of 61 species were found along the transect, although most tended to be infrequent, and only 27 surpassed the mean value of the frequencies (mean $f = 28.3\%$). In most cases, relatively high to moderate β diversity values were obtained. The average value for all the site combinations was $\beta = 0.52$ (S.D. = ± 0.17 , range = 0.12–0.93). The highest similarity value was $JS_j = 0.79$, corresponding to two non-contiguous localities. The high diversity of cactus species in the study area may be explained, in part, by a relatively high to moderate level of turnover among the different species assemblages. However, β diversity is mainly a product of the intermittent pattern of spatial distribution of the cactus species in this region, rather than a real species turnover.

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1. Introduction

Mexico is considered the main center of diversification of the family Cactaceae. There are in this country some 50 genera and 550 species (Hunt, 1999), and it has been estimated that 73% of the genera and 78% of the species are endemic (Hernández and Godínez, 1994). These plants are mainly distributed in arid and semi-arid regions, which cover about 48% of the Mexican territory and hold 20% of the country's flora.

One of the most important arid environments in North America is the Chihuahuan Desert Region (CDR), which has an overall extension of approximately 507,000 km². Most of the CDR is in Mexico, covering about 20.6% of its terrestrial territory, but it extends into parts of southern Texas, New Mexico and Arizona, in the United States of America (MacMahon and Wagner, 1985). The CDR is considered among the ten most important North American ecoregions, one of the three most outstanding deserts in the world, because of its high biodiversity (Dinerstein et al., 1999), and one of the 37 wilderness areas on the planet (Mittermeier et al., 2002).

According to a recently published checklist (Hernández et al., 2004), there are 329 cactus species in the CDR, representing 22% of the total diversity of this family. This high diversity, as well as the high incidence of endemics (70% of the total number of species are regional endemics) make the CDR the main center of cactus species richness in the world (Hernández et al., 2001, 2004).

During the last decade, several investigations have revealed the general distribution patterns of Cactaceae in the CDR (Hernández and Godínez, 1994; Hernández and Bárcenas, 1995, 1996; Gómez-Hinostrosa, 1998; Bárcenas, 1999; Gómez-Hinostrosa and Hernández, 2000; Hernández et al., 2001). These have shown that the main concentrations of members of this plant family are located in the southeastern segment of this desert area, in parts of the states of San Luis Potosí, and southern Coahuila, Nuevo León and Tamaulipas. Unfortunately, however, our knowledge on the spatial patterns of Chihuahuan Desert Cactaceae remains incomplete.

The component of diversity that measures the differences among communities in terms of species composition is β diversity (Whittaker, 1972; Magurran, 1988). Several factors influencing species turnover have been recognized. On the one hand, there are those related to the environment and its heterogeneity. On the other hand, there are those inherent to the species, like its dispersal ability and tolerance ranges to different environmental factors.

To our knowledge, there are very few examples of studies on β diversity patterns in New World desert communities (Kelt et al., 1996; Osorio et al., 1996; Garcillán and Ezcurra, 2003; Huerta and García, 2004). Moreover, we know only one investigation analyzing β diversity in cactus species assemblages in particular (Mourelle and Ezcurra, 1997). These authors measured the turnover of the main cactus growth forms (columnar, opuntoid and globose) along latitudinal and longitudinal gradients, and among $1^\circ \times 1^\circ$ quadrats in Argentina. Furthermore, they analysed the environmental variables, which in part explained the species turnover.

The aim of the present study was to assess the levels of species turnover among 23 cactus species assemblages along a 250 km longitudinal transect in the southeastern part of the CDR. The study area is located in part of the most cactus-species-rich portions of the CDR, such as Doctor Arroyo, Matehuala, Miquihuana, Aramberri, Ciudad Victoria and Jaumave (Hernández and Bárcenas, 1995). There is a wide range of β diversity formulae. In this study we have chosen the formula proposed by Wilson and Shmida (1984), which is

among those measuring the continuity of species between communities (Koleff et al., 2003). In addition, there are also different indices that allow us to evaluate the biotic similarity among different communities or regions, like Jaccard's similarity index (Magurran, 1988). Thus, to complement the beta diversity analysis, floristic similarity among the different assemblages was calculated using Jaccard's similarity index.

This study departs from the general assumption that the high biodiversity in the desert regions of northern Mexico could be explained, at least in part, by a high species turnover (Rodríguez et al., 2003). We hypothesize that the high degree of narrow endemism in the Cactaceae, the specialized habitat preferences of the species, and the high environmental heterogeneity in the CDR, all contribute to increase species turnover.

2. Study area and methods

2.1. Study area

We sampled the cactus species in 23 localities along an east–west transect in the southeastern part of the CDR, across parts of the Mexican states of Zacatecas, San Luis Potosí, Nuevo León, and Tamaulipas (Fig. 1). The transect had an approximate linear distance of 250 km. The average distance between each of the sampling sites was about

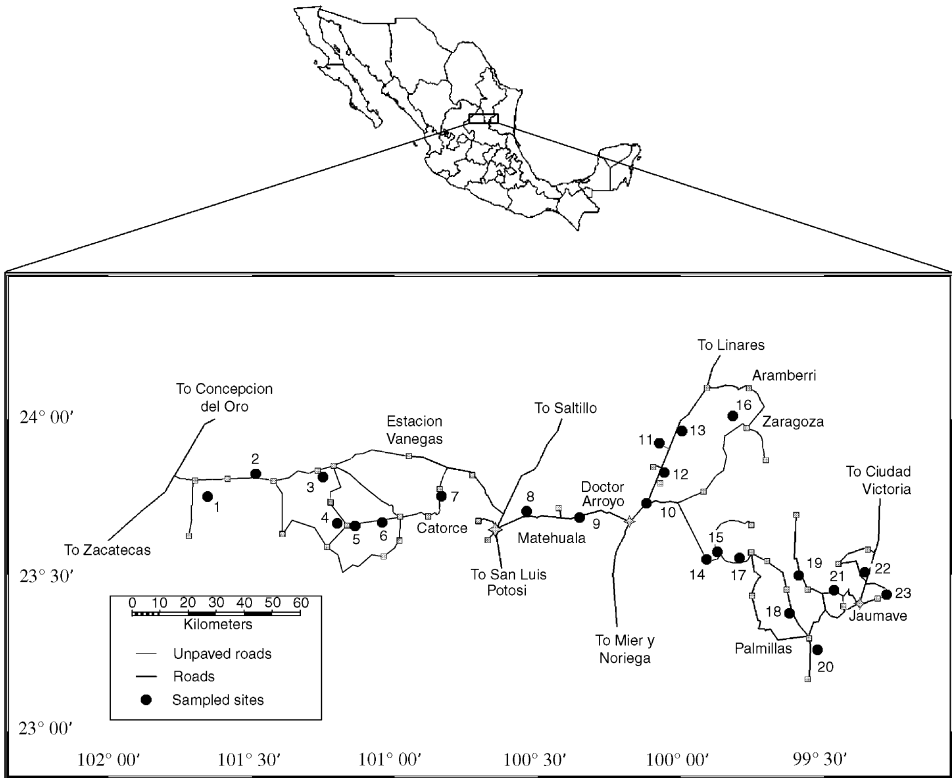


Fig. 1. Study area. The solid dots and the figures indicate the sampled sites (see Table 1).

10 km, and in all cases the vegetation at the sampling sites was in a reasonably good state of conservation. Table 1 shows the exact location of the sites. The study area is located in the Mexican Plateau and the Sierra Madre Oriental physiographic provinces. In all sampling localities, dry or semi-dry climatic types occur (BS₀ and BS₁, García, 1981). The vegetation along the transect is essentially dominated by xerophytic CDR associations,

Table 1
Number, localization, altitude, and ecological characteristics of the sampled sites

Site	State, Municipality	Coordinates	Altitude (m)	Plant association/soil characteristics
1	Zac., El Rucio	23° 45' 05" N 101° 39' 18" W	2240	<i>Larrea</i> scrub/alluvial plain. <i>Agave-Fouquieria</i> scrub/limestone hill
2	Zac., Mazapil	23° 49' 26" N 101° 29' 13" W	2145	<i>Yucca</i> -grassland/alluvial plain with sparse volcanic outcrops
3	SLP, Catorce	23° 48' 53" N 101° 15' 04" W	1925	<i>Larrea-Yucca</i> scrub/alluvial plain
4	SLP, Catorce	23° 39' 56" N 101° 12' 04" W	2015	<i>Larrea-Yucca</i> /alluvial plain. <i>Agave lechuguilla-Yucca</i> scrub/limestone hill
5	SLP, Catorce	23° 39' 27" N 101° 08' 22" W	1915	<i>Larrea</i> scrub/alluvial plain. <i>Opuntia leucotricha-Fouquieria</i> scrub/ volcanic rocky hill
6	SLP, Catorce	23° 40' 09" N 101° 02' 40" W	1815	<i>Larrea</i> scrub/alluvial plain
7	SLP, Catorce	23° 45' 09" N 100° 50' 13" W	2295	<i>Larrea</i> scrub/alluvial plain. <i>Agave lechuguilla</i> scrub/limestone hill
8	SLP, Matehuala	23° 42' 14" N 100° 32' 09" W	1600	<i>Agave lechuguilla-Hechtia</i> scrub/limestone hill
9	NL, Doctor Arroyo	23° 41' 06" N 100° 21' 12" W	1710	<i>Larrea-Prosopis-Yucca</i> scrub/alluvial plain. <i>Agave lechuguilla-Nolina</i> scrub/limestone hill
10	NL, Doctor Arroyo	23° 43' 50" N 100° 07' 14" W	1890	<i>Nolina-Dasyliirion-Yucca</i> scrub/ limestone hill
11	NL, Doctor Arroyo	23° 55' 20" N 100° 04' 30" W	1695	<i>Larrea-Prosopis</i> scrub/alluvial plain. <i>Agave lechuguilla-Hechtia-Dasyliirion</i> scrub/limestone hill
12	NL, Doctor Arroyo	23° 49' 42" N 100° 03' 27" W	1760	<i>Agave spp.-Hechtia-Dasyliirion-Yucca</i> /limestone hill
13	NL, Aramberri	23° 57" N 99° 59" W	1700	<i>Larrea</i> scrub/alluvial plain. <i>Dasyliirion-Yucca-Agave lechuguilla</i> scrub/limestone hill with gypsum outcrops
14	Tamps., Miquihuana	23° 33' 03" N 99° 54' 37" W	1675	<i>Dasyliirion-Agave lechuguilla-Hechtia</i> scrub/limestone hill
15	Tamps., Miquihuana	23° 34' 31" N 99° 52' 22" W	1590	<i>Larrea-Yucca-Prosopis</i> scrub/alluvial plain. <i>Dasyliirion-Agave lechuguilla-Hechtia</i> scrub/limestone hill
16	NL, Aramberri	24° 00' 33" N 99° 49' 07" W	1650	<i>Prosopis-Yucca</i> scrub/alluvial plain. <i>Agave lechuguilla-Hechtia</i> scrub/ limestone hill
17	Tamps., Miquihuana	23° 33' 15" N 99° 47' 40" W	2145	<i>Nolina-Dasyliirion</i> scrub/limestone hill
18	Tamps., Palmillas	23° 22' 40" N 99° 37' 13" W	1705	<i>Hechtia-Agave lechuguilla-Nolina</i> scrub with Leguminosae/limestone hill
19	Tamps., Jaumave	23° 29' 59" N 99° 35' 15" W	1605	<i>Agave lechuguilla-Nolina-Dasyliirion</i> scrub with Leguminosae/limestone hill
20	Tamps., Palmillas	23° 15' 38" N 99° 31' 18" W	1405	Sub-montane scrub with Leguminosae/limestone hill
21	Tamps., Jaumave	23° 27' 5" N 99° 27' 54" W	1135	<i>Hechtia-Agave lechuguilla</i> scrub with Leguminosae/limestone hill
22	Tamps., Jaumave	23° 30' 31" N 99° 21' 28" W	765	<i>Prosopis-Acacia</i> scrub/alluvial plain. <i>Agave lechuguilla</i> scrub/limestone hill.
23	Tamps., Jaumave	23° 26' 14" N 99° 16' 49" W	710	<i>Hechtia</i> scrub mixed with tropical deciduous forest/limestone hill

State abbreviations: Zac. = Zacatecas, SLP = San Luis Potosi, NL = Nuevo León, and Tamps. = Tamaulipas.

such as *Larrea tridentata* (creosote) bush, and rosetophyllous scrub of *Agave lechuguilla*, *A. striata*, and *Hechtia glomerata*. For a detailed description of these vegetation types see Rzedowski (1978).

2.2. Fieldwork

Four expeditions were carried out between December 1998 and June 1999. At each sampling site we recorded all cactus species within eyesight along a three km long line transect, which we searched afoot. These line transects were measured with a digital pedometer (Safety Step Pedometer by Precise) and with the aid of a Global Positioning System. As a result of fieldwork, 406 cactus herbarium vouchers were deposited at the National Herbarium of Mexico (MEXU); a list of these is available upon request. We used the taxonomic framework of Hunt (1999), with some modifications. Table 2 is a list of all cactus species registered along the transect. Cultivated or introduced cactus species were ignored in this study.

2.3. Data analysis

In order to evaluate the rate of occurrence of each species in the transect we calculated its relative frequency (f), according to the following formula: $f = ss/ts$, where ss is the number of sites in which the species occurs and ts the number of total sites.

We considered alpha (α) diversity as a synonym of cactus species richness (number of species in a given sampling site). Beta diversity (β) is a measure of species turnover between site pairs, and is a reflection of the heterogeneity of the different communities regarding their species composition (Magurran, 1988). It was not until recently that a study comparing 24 β diversity formulae and what they really measure was published (Koleff et al., 2003). With the aim of calculating the β diversity values, we used Wilson and Shmida's (1984) formula: $\beta = (b + c)/2 a + b + c$, where β is the beta diversity, a the total number of cactus species that occur in both communities, b the total number of cactus species that occur in the neighboring community but not in the focal one, and c the total number of cactus species that occur in the focal community but not in the neighboring one.

In order to complement the β diversity analysis we calculated Jaccard's index of floristic similarity (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 is the index of similarity, the rest of the components (a , b and c) are the same as above.

3. Results and discussion

3.1. Species richness

A total of 61 cactus species were found along the transect. With 17 (28% of total) and 11 species (18%) respectively, *Opuntia* (sensu lato) and *Mammillaria* are the best represented genera, as they contain 46% of the species in the sample. In contrast, ten genera are represented by only one species each. As expected, the taxonomic composition reported here resembles that of other studies carried out in nearby localities to our study

Table 2

Cactus species registered along the transect, their frequency, and voucher specimens deposited at the National Herbarium of Mexico (MEXU)

Taxon	Frequency (%)	Voucher*
<i>Ariocarpus kotschoubeyanus</i> (Lem.) K. Schum.	4.4	99
<i>A. retusus</i> Scheidw.	56.5	1
<i>Astrophytum myriostigma</i> Lem.	4.4	350
<i>Coryphantha bergeriana</i> Boed.	47.8	242
<i>C. villarensis</i> Backeb.	4.4	390
<i>C. macromeris</i> (Engelm.) Britton & Rose	4.4	169
<i>C. palmeri</i> Britton & Rose	69.6	386
<i>Echinocactus horizontalis</i> Lem.	26.1	246
<i>E. platyacanthus</i> Link & Otto	73.9	181
<i>Echinocereus cinerascens</i> (DC.) Lem.	8.7	111
<i>E. enneacanthus</i> Engelm.	30.4	356
<i>E. parkeri</i> N. P. Taylor	8.7	82
<i>E. pectinatus</i> (Scheidw.) Engelm.	39.1	17
<i>E. pentalophus</i> (DC.) Lem.	60.9	79
<i>Ferocactus echidne</i> (DC.) Britton & Rose	34.8	85
<i>F. hamatacanthus</i> (Muehlenpf.) Britton & Rose	43.5	177
<i>F. pilosus</i> (Galeotti ex Salm-Dyck) Werderm.	43.5	342
<i>Leuchtenbergia principis</i> Hooker	8.7	101
<i>Lophophora williamsii</i> (Lem. ex Salm-Dyck) J. M. Coulter	13.0	100
<i>Mammillaria albicoma</i> Boed.	8.7	351
<i>M. baumii</i> Boed.	4.4	292
<i>M. candida</i> Scheidw.	47.8	352
<i>M. formosa</i> Galeotti ex Scheidw.	69.6	183
<i>M. heyderi</i> Muehlenpf.	39.1	182
<i>M. klissingiana</i> Boed.	4.4	265
<i>M. magnimamma</i> Haw.	4.4	180
<i>M. melaleuca</i> Karw. ex Salm-Dyck	4.4	377
<i>M. picta</i> Meinsh.	34.8	73
<i>M. prolifera</i> (Mill.) Haw.	4.4	376
<i>M. roseoalba</i> Boed.	8.7	267
<i>Myrtillocactus geometrizans</i> (Mart.) Console	4.4	282
<i>Neolloydia conoidea</i> (DC.) Britton & Rose	65.2	357
<i>Opuntia engelmannii</i> Salm-Dyck ex Engelm.	95.7	263
<i>O. imbricata</i> (Haw.) DC.	78.3	266
<i>O. kleiniae</i> DC.	39.1	74
<i>O. lasiacantha</i> Pfeiff.	4.4	298
<i>O. leptocaulis</i> DC.	78.3	274
<i>O. leucotricha</i> DC.	26.1	270
<i>O. megarrhiza</i> Rose	4.4	379
<i>O. microdasys</i> (Lehm.) Pfeiff.	47.8	260
<i>O. pubescens</i> H. L. Wendl. ex Pfeiff.	4.4	284
<i>O. rastrera</i> Weber	56.5	175
<i>O. robusta</i> H. L. Wendl. ex Pfeiff.	4.4	148
<i>O. sp.</i>	4.4	189
<i>O. stenopetala</i> Engelm.	82.6	394
<i>O. streptacantha</i> Lem.	13.0	144
<i>O. tomentosa</i> Salm-Dyck	13.0	297
<i>O. tunicata</i> (Lehm.) Link & Otto ex Pfeiff.	69.6	359
<i>O. vilis</i> Rose	4.4	168
<i>Pilosocereus leucocephalus</i> (Poselg.) Byles & Rowley	8.7	289

Table 2 (continued)

Taxon	Frequency (%)	Voucher*
<i>Sclerocactus uncinatus</i> (Galeotti) N. P. Taylor	47.8	250
<i>Selenicereus boeckmanii</i> (Otto ex Salm-Dyck) Britton & Rose	4.4	375
<i>Stenocactus</i> sp.	34.8	323
<i>Stenocereus griseus</i> (Haw.) Buxb.	8.7	403
<i>Thelocactus bicolor</i> (Galeotti ex Pfeiff.) Britton & Rose	13.0	223
<i>T. conothelos</i> (Regel & Klein) F. Knuth	39.1	301
<i>T. hexaedrophorus</i> (Lem.) Britton & Rose	30.4	176
<i>T. tulensis</i> (Poselg.) Britton & Rose	13.0	363
<i>Turbincarpus pseudopectinatus</i> (Backeb.) Glass & Foster	8.7	42
<i>T. schmidickeanus</i> (Boed.) Buxb. & Backeb.	4.4	340
<i>T. subterraneus</i> (Backeb.) A. D. Zimmerman	4.4	40

All collection numbers (*) are by B. Goettsch.

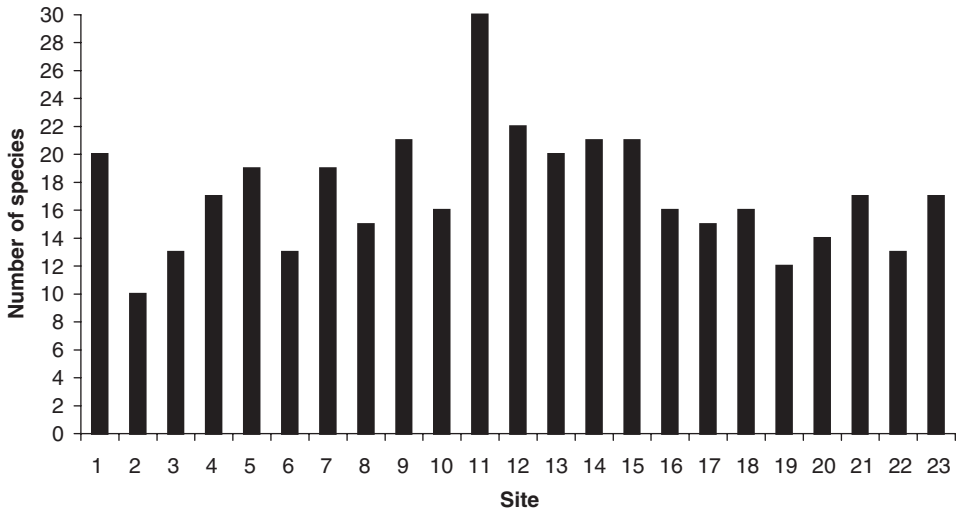


Fig. 2. Variation of cactus species richness along the transect. The values of species richness are also shown in Fig. 3.

area (Gómez-Hinostrosa and Hernández, 2000; Hernández et al., 2001) and in the whole region (Hernández et al., 2004). On the other hand, species richness was somewhat variable among the different localities (Fig. 2). The highest values were registered in the central portion of the transect, most significantly in site 11 (30 spp.).

Fig. 3 shows the individual pattern of distribution of each species along the transect. A first pattern can be illustrated by four species (*Opuntia engelmannii*, *O. stenopetala*, *O. imbricata* and *O. leptocaulis*) that are widespread and have an almost continuous distribution along the transect. On the other hand, some species, such as *Echinocactus horizontalionius* and *Sclerocactus uncinatus*, tend to be localized towards the western portion of the transect, whereas *Stenocereus griseus* and *Pilosocereus leucocephalus* are found in the east. Some other species (e.g. *Thelocactus bicolor* and *T. tulensis*) are found

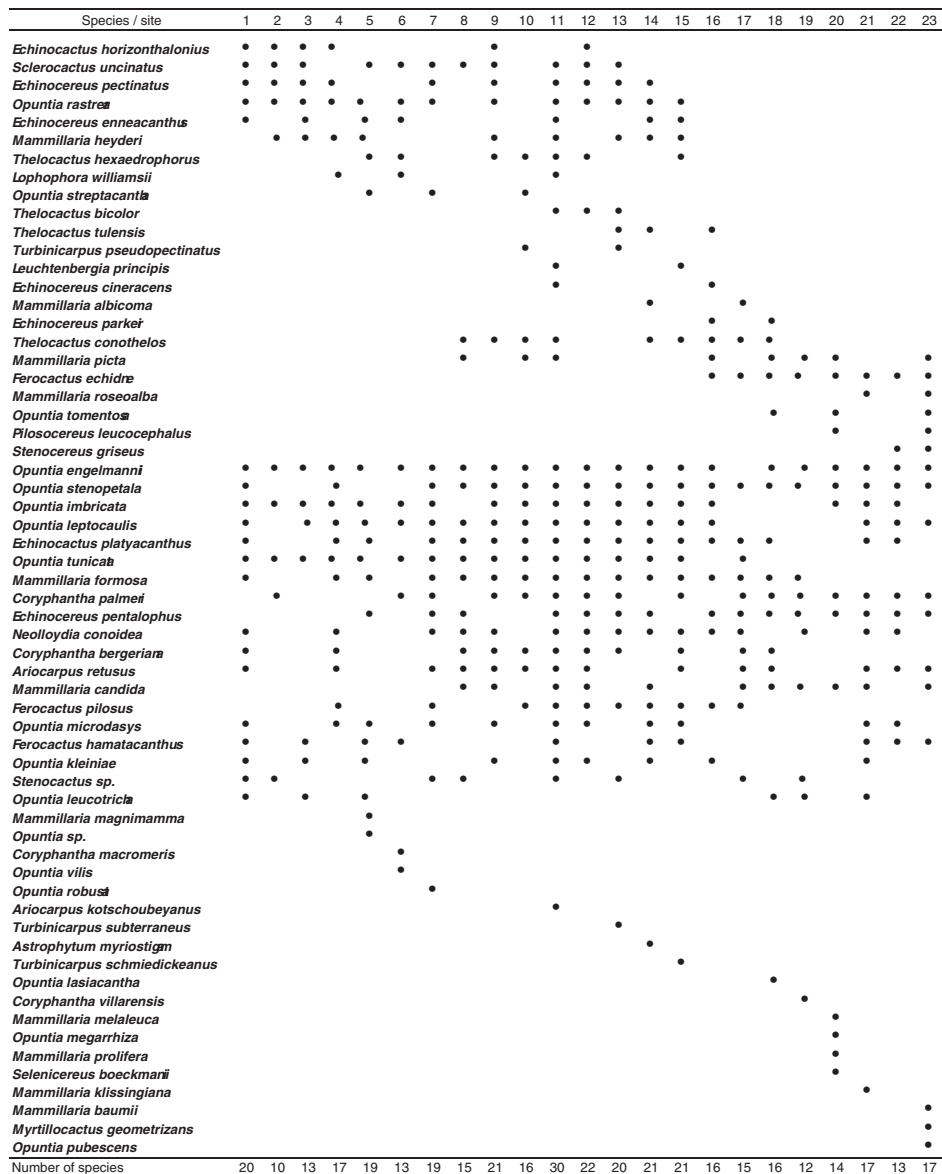


Fig. 3. Presence (●) of cactus species and total number of species per sampling site.

only in the central part of the transect. An additional pattern is displayed by several of the species whose distribution range is extremely restricted (e.g. *Ariocarpus kotschoubeyanus*, *Mammillaria baumii*, *Selenicereus boeckmanii*, *Turbinicarpus schmidickeanus*, *T. subterraneus*).

The four different distribution patterns described in the previous paragraph favor a higher α diversity in the sites located at the central part of the transect. This is due to the overlapping effect of the species distributed at the eastern, central, and western portions of

the transect. Interestingly, the geographic localization of the most α diverse sites (sites 9–15) coincide longitudinally with the Huizache region (22°30'–23°00' lat. N, 100°00'–100°30' long. W). With an outstanding diversity of Cactaceae (75 spp.), this 2855 km² area is considered the most diverse in terms of cactus species richness and endemism at the global scale (Hernández et al., 2001).

3.2. Relative frequency

Fig. 4 shows the number of species grouped according to the different values of relative frequency (see also Table 2). In total, there are 17 different values of relative frequency for the 61 species. It is observed that 27 species (44.3%) have frequencies above the mean value ($f = 28.3\%$). In contrast, it is outstanding that 52.5% of the species are recorded only in three or less of the sampling sites ($f = <13\%$). This pattern is a clear reflection of the markedly restricted and/or highly discontinuous distribution of the Chihuahuan Desert Cactaceae (see Fig. 3).

The lowest frequency value ($f = 4.4\%$; Table 2) in the transect correspond to 19 species found in only one sampling site, which notably constitute 31.2% of the species. It is important to mention that the overall distribution range of some of these taxa (e.g. *Mammillaria melaleuca*, *M. klissingiana*, and *Turbinicarpus subterraneus*) is extremely narrow (H.M. Hernández, unpublished data). It has to be considered, however, that not all of the low frequency species are narrow endemics. Species such as *Coryphantha macromeris*, and *Mammillaria magnimamma* are rather widespread, but in this study they were found at the edge of their distribution range. Also, it is notable that 65% of the species with low frequencies are located in Tamaulipas, most notably at sites 20 and 23, each with four low frequency species. This is congruent with previous findings showing

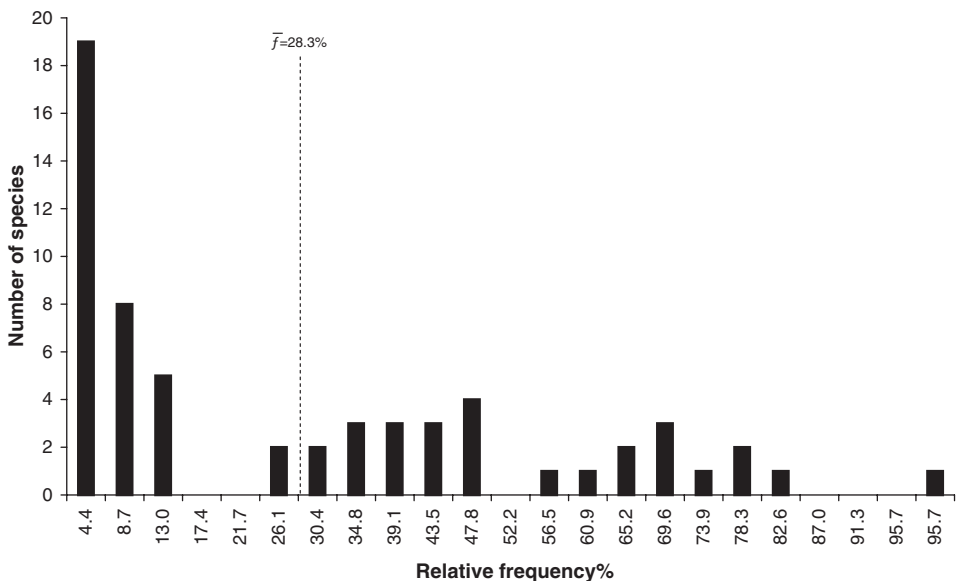


Fig. 4. Frequency distribution of the species in the transect. The dotted line indicates the mean value of the frequencies.

that geographically rare cactus species tend to congregate towards the southeastern portion of the CDR (Hernández and Bárcenas, 1995; Gómez-Hinostrosa and Hernández, 2000; Hernández et al., 2001).

It is likely that the low frequency of some of these species can be associated with their fruit characteristics. For instance, *Ariocarpus kotschoubeyanus*, *Astrophytum myriostigma*, *Turbincarpus schmiedickeanus*, and *T. subterraneus* have small relatively dry fruits which are unattractive to potential medium- or long-distance seed dispersers. In addition, fruits in some of these species are concealed among the tubercles. In contrast, the usually widespread species of *Opuntia* have large, fleshy, and highly attractive fruits to frugivorous vertebrates (Reyes-Agüero et al., in press).

In the other extreme of Fig. 4 there are the species with the highest frequency values, corresponding to *Opuntia engelmannii* ($f = 95.7\%$), *O. stenopetala* ($f = 82.6\%$), *O. imbricata* and *O. leptocaulis* ($f = 78.3\%$). All of these species have a very large distribution range in the CDR. The wide distribution range of most Mexican *Opuntia* species probably is a consequence of their successful reproductive (Palleiro, 2001; Reyes-Agüero et al., in press) and dispersal mechanisms (Johnson, 1918; González and Quintana, 1986; Bregman, 1988).

Echinocactus platyacanthus is also present at a high frequency ($f = 73.9\%$; Table 2). This species is widely distributed in the southern half of the CDR, extending southwards to the Tehuacán Valley (see Fig. 6 in Gómez-Hinostrosa and Hernández, 2000). This species, together with *Ferocactus histrix*, is the most abundant and widespread barrel cactus in Mexico (Del Castillo and Trujillo, 1991). Unfortunately, the seed dispersal mechanism of *E. platyacanthus* is unknown.

3.3. Beta diversity

The β diversity values for all pairs of contiguous and non-contiguous sites were calculated. According to the results in Table 3, in all cases the values were higher than zero, indicating that all the sites are different in terms of their cactus species composition. The lowest value was $\beta = 0.12$, among sites 9 and 12. In the same way, no total species turnover was registered, even among the most distant sites, as none of the values reached $\beta = 1$. The highest recorded value was $\beta = 0.93$ for sites 3 and 17, which only shared one cactus species (*Opuntia tunicata*).

As far as the analysis of contiguous sites is concerned (Table 3, squared values), site pair 6–7 have the highest β diversity value ($\beta = 0.56$). These two sites are separated by the Sierra de Catorce mountain range, and are slightly contrasting ecologically; site 6 was a plain with alluvial, deep soils covered by creosote bush (*L. tridentata*), whereas site 7 was at the interface of a plain similar to that in site 6 and a rocky slope with *Agave*—*Hechtia* rosetophyllous bush. It is well known that a number of cactus species tend to have preferences to grow in specific soil conditions. For instance, *Coryphantha macromeris* and *Lophophora williamsii* are usually found in alluvial plain areas, whereas *Neolloydia conoidea*, *Ariocarpus retusus* and *Opuntia stenopetala* tend to favor limestone, rocky slopes. In this connection, site pairs 4–5 and 13–16 also registered high β diversity values ($\beta = 0.50$), which may be explained by the fact that these pairs of sites have contrasting soil types (Table 1). In addition, the presence of rare (*Turbincarpus subterraneus* and *T. pseudopectinatus*) and infrequent (*Mammillaria magnimamma*, *L. williamsii*, *O. streptacantha*, and *Thelocactus tulensis*) species in some of these sites contributes to increase the β diversity values (see Table 2).

Table 3
Beta diversity (above diagonal) and Jaccard's similarity values (below diagonal) among sample sites

Beta/ S _j	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1		0.47	0.27	0.24	0.33	0.52	0.28	0.38	0.22	0.50	0.32	0.19	0.35	0.37	0.32	0.56	0.54	0.61	0.63	0.82	0.46	0.52	0.78
2	0.36		0.30	0.41	0.59	0.48	0.45	0.68	0.42	0.69	0.55	0.50	0.40	0.68	0.61	0.85	0.76	0.85	0.73	0.75	0.78	0.74	0.85
3	0.57	0.53		0.47	0.31	0.38	0.56	0.71	0.41	0.72	0.49	0.49	0.52	0.47	0.53	0.72	0.93	0.86	0.84	0.85	0.60	0.69	0.80
4	0.61	0.35	0.36		0.50	0.60	0.28	0.44	0.21	0.39	0.36	0.23	0.30	0.37	0.26	0.52	0.50	0.64	0.72	0.81	0.59	0.53	0.82
5	0.50	0.26	0.52	0.33		0.44	0.42	0.59	0.40	0.54	0.39	0.41	0.54	0.35	0.40	0.60	0.76	0.71	0.74	0.82	0.50	0.56	0.78
6	0.32	0.35	0.44	0.25	0.39		0.56	0.71	0.53	0.59	0.49	0.54	0.58	0.59	0.47	0.79	0.86	0.86	0.84	0.78	0.67	0.62	0.73
7	0.56	0.38	0.28	0.57	0.41	0.28		0.35	0.30	0.37	0.35	0.22	0.28	0.40	0.35	0.49	0.41	0.60	0.55	0.70	0.50	0.44	0.72
8	0.46	0.19	0.17	0.39	0.26	0.17	0.48		0.33	0.35	0.38	0.35	0.43	0.44	0.44	0.42	0.27	0.35	0.41	0.66	0.56	0.57	0.69
9	0.64	0.41	0.42	0.65	0.43	0.31	0.54	0.50		0.35	0.25	0.12	0.32	0.33	0.24	0.51	0.44	0.51	0.64	0.71	0.45	0.53	0.74
10	0.33	0.18	0.16	0.43	0.30	0.26	0.46	0.48	0.48		0.43	0.37	0.39	0.51	0.30	0.44	0.42	0.44	0.64	0.67	0.64	0.59	0.76
11	0.52	0.29	0.34	0.47	0.44	0.34	0.48	0.45	0.59	0.39		0.23	0.32	0.29	0.25	0.43	0.47	0.57	0.57	0.68	0.49	0.53	0.70
12	0.62	0.33	0.35	0.63	0.41	0.30	0.64	0.48	0.79	0.46	0.63		0.29	0.35	0.30	0.47	0.41	0.53	0.59	0.67	0.44	0.49	0.69
13	0.48	0.43	0.32	0.54	0.30	0.27	0.56	0.40	0.52	0.44	0.52	0.56		0.41	0.37	0.50	0.49	0.67	0.63	0.76	0.62	0.58	0.78
14	0.44	0.19	0.36	0.46	0.48	0.26	0.43	0.38	0.50	0.32	0.55	0.48	0.41		0.29	0.35	0.44	0.62	0.64	0.71	0.42	0.47	0.68
15	0.52	0.24	0.31	0.58	0.43	0.36	0.48	0.38	0.62	0.54	0.59	0.54	0.46	0.56		0.51	0.44	0.57	0.70	0.77	0.53	0.47	0.74
16	0.29	0.08	0.16	0.32	0.25	0.12	0.35	0.41	0.32	0.39	0.39	0.36	0.33	0.48	0.32		0.48	0.44	0.50	0.60	0.45	0.45	0.70
17	0.30	0.14	0.04	0.33	0.13	0.08	0.42	0.58	0.38	0.41	0.36	0.42	0.35	0.38	0.38	0.35		0.35	0.41	0.66	0.56	0.57	0.69
18	0.24	0.08	0.07	0.22	0.17	0.07	0.25	0.48	0.32	0.39	0.28	0.31	0.20	0.23	0.28	0.39	0.48		0.36	0.47	0.52	0.59	0.58
19	0.23	0.16	0.09	0.16	0.15	0.09	0.29	0.42	0.22	0.22	0.27	0.26	0.23	0.22	0.18	0.33	0.42	0.47		0.46	0.45	0.52	0.59
20	0.10	0.14	0.08	0.11	0.10	0.13	0.18	0.21	0.17	0.20	0.19	0.20	0.13	0.17	0.13	0.25	0.21	0.36	0.37		0.55	0.56	0.48
21	0.37	0.13	0.25	0.26	0.33	0.20	0.33	0.28	0.36	0.22	0.34	0.39	0.23	0.41	0.31	0.38	0.28	0.32	0.38	0.29		0.20	
22	0.32	0.15	0.18	0.30	0.28	0.24	0.39	0.27	0.31	0.26	0.30	0.35	0.27	0.36	0.36	0.38	0.38	0.27	0.26	0.32	0.29		0.40
23	0.12	0.08	0.11	0.10	0.13	0.15	0.16	0.19	0.15	0.14	0.18	0.18	0.12	0.19	0.15	0.18	0.19	0.27	0.26	0.35	0.42	0.43	

 Contiguous sites
 Highest values
 Lowest values

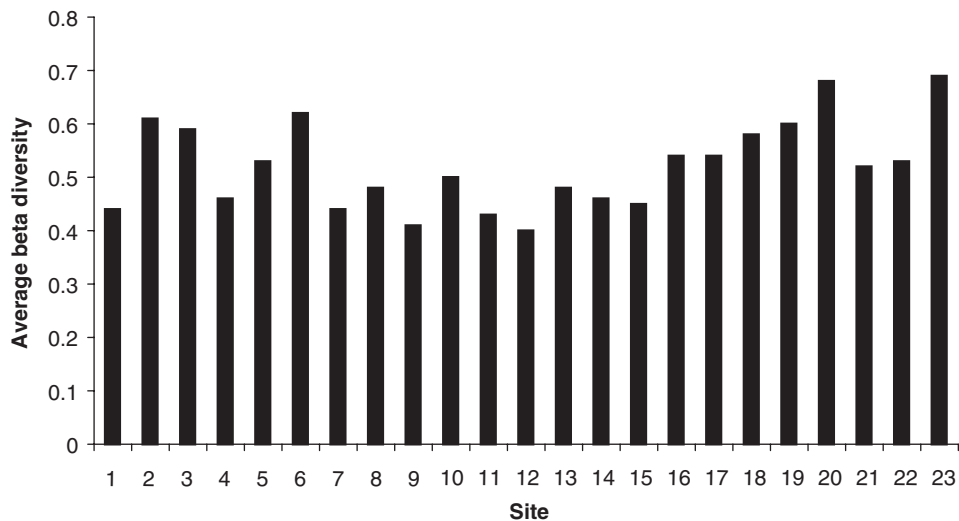


Fig. 5. Average β diversity value of each sampling site.

As expected, the β diversity values were significantly higher among non-contiguous pairs of sites, as compared to the contiguous ones. The highest values corresponded to the site pairs 3–17 ($\beta = 0.93$), and 6–17, 3–18 and 6–18 ($\beta = 0.86$). These four pairs of sites differed in environmental characteristics such as slope, soil type and vegetation type.

An additional way of assessing the differences among the cactus species assemblages is by calculating the average β diversity values of one site in respect to the remaining ones. In Fig. 5 such average figures are shown. Sites 2, 3, 6, 19, 20, and 23 are the ones with the highest values.

Mourelle and Ezcurra (1997), in their study on Argentinean cactus species turnover, grouped the β diversity values in three categories: high for the values ranging from 0.661 to 1.0, medium for $\beta = 0.331$ –0.66, and low for $\beta = 0$ –0.33. If we adopt this criterion, most of the values (76.2%) between contiguous sites correspond to the medium category, and the remaining to the low category. However, if we consider the figures for the non-contiguous sites, 24.1% of them fall in the high category, 64% in the medium category, and the remaining 11.9% in the low category. Moreover, if we use the average values of Fig. 5, 13% of the sites fall in the high category, and the remaining 87% correspond to medium category. Also, the average value of all site combinations ($\beta = 0.52$) fall in the medium category. However, bearing in mind that the scale of the present work is considerably smaller than that used by Mourelle and Ezcurra (1997), the β diversity values reported here may be considered as comparatively higher.

3.4. Floristic similarity

Beta diversity and similarity are opposite concepts. For this reason, their corresponding numerical values are expected to be inversely proportional (Table 3). Thus, the highest similarity value ($IS_J = 0.79$) was between sites 9 and 12, which shared 19 cactus species, and, as expected, the lowest β diversity corresponded to these sites. On the other hand, site

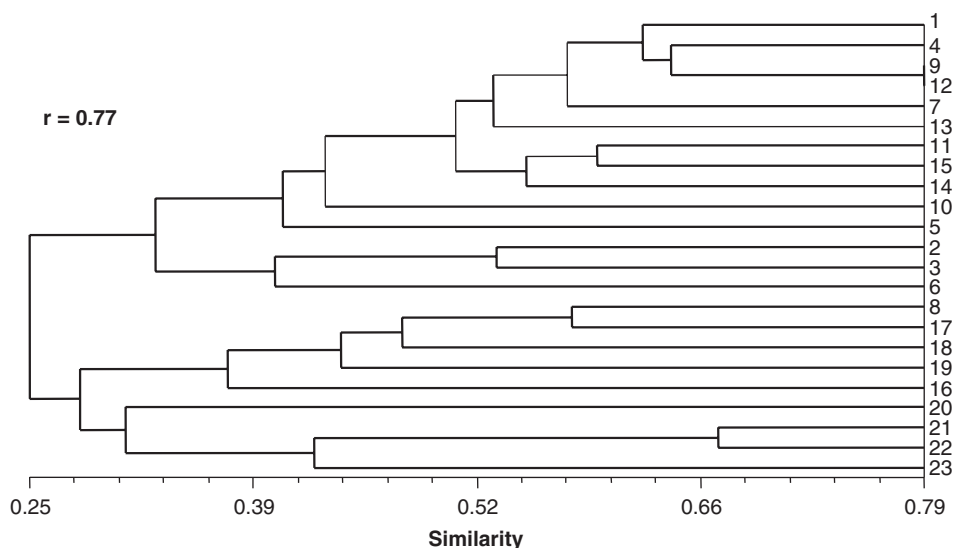


Fig. 6. Phenogram derived from the Jaccard's similarity values among the sampled sites.

pair 3–17, sharing only one species, had the lowest similarity ($IS_J = 0.04$) and the highest β diversity (Table 3). In congruence with the above, no similarity values equal to one were observed, as a reflection of the fact that none of the site pairs were identical in terms of cactus species composition.

The similarity values were used to generate the phenogram of Fig. 6. Taking the index of similarity of $IS_J = 0.39$ as a baseline, the sites are grouped in four clusters. The first one contains 11 of the 23 sites, primarily located at the western and central portions of the transect, in parts of the states of Zacatecas, San Luis Potosí, Nuevo León, and in western Tamaulipas (Fig. 1). The second cluster is formed by sites 2, 3, and 6, all of which are located in the plains, at the western extreme of the transect. The last two clusters are located in the eastern part of the transect, in Tamaulipas. On the other hand, it is interesting to notice that sites 16 and 20 are somewhat isolated from the remaining ones. These are located at the northeastern and southeastern extremes of the transect respectively, and contain a number of infrequent cactus species (e.g. *Echinocereus cinerascens*, *E. parkeri*, *Mammillaria melaleuca*, *M. prolifera*, and *Opuntia megarrhiza*).

4. Final considerations

The most frequent species having an almost continuous distribution along the transect belong to the genus *Opuntia*. The presence of some of these species increases α diversity values in some of the sites. However, β diversity values decrease as a consequence of the homogenization in the composition of the cactus assemblages. As expected, the highest β diversity values were among non-contiguous sites. No identical or totally different cactus assemblages were registered. Moreover, the highest β diversity values were found among sites with contrasting environmental characteristics. Regarding species richness, the sites

where hills and plains interface creating environmental heterogeneity usually had higher α diversity values than the more homogeneous environments.

The observed turnover in the cactus assemblages may be explained by a combination of different factors. Probably the most important one is the great edaphic heterogeneity found in the Chihuahuan Desert. In this desert, as in all of North American deserts, soils vary tremendously in texture and chemical composition. In connection to this, the fidelity of many of the cactus species to specific soil types and textures (Bárceñas, 1999) is probably responsible, at least partially, for the patchy and highly discontinuous distributions observed (Fig. 3). Indeed, local patchiness and geographic discontinuity are the two spatial patterns that increase β diversity values.

An additional factor determining species turnover could relate to differences in the dispersal ability among the species. As it was mentioned before, most of the species of *Opuntia*, which are usually common locally and widely distributed, obviously have an efficient endozoochorous seed dispersal mechanism. The fleshy, highly attractive fruits are consumed by a variety of vertebrates, primarily mammals and birds, which play an important role on the dispersal of the seeds (Bregman, 1988; Mandujano et al., 1997). Moreover, the three chollas found in this study (*O. imbricata*, *O. kleiniae*, and *O. leptocaulis*) are able to reproduce asexually due to their detachable stem segments.

In contrast, the narrow distribution range of some of the species may be explained, at least in part, by their poor dispersal and establishment ability. Fruits of many of the infrequent species (e.g. *Ariocarpus*, *Mammillaria*, *Thelocactus*, *Turbinicarpus*, etc.) are small, relatively dry, and are frequently hidden among the tubercles or spines (cf. Zavala-Hurtado and Valverde, 2003). Seeds of some of these species probably are dispersed by short-ranging animals, such as ants (Bregman, 1988). It has to be recognized that we know very little about the seed dispersal of cacti. Detailed information of these mechanisms would provide insight into the relationship between dispersal ability and distribution size.

Our observations clearly show continuous spatial changes in cactus species composition, with relatively high β diversity values. It must be emphasized however, that species turnover is attributable to the replacement of different species in space, which was not the case in this study. The β diversity values reported here are strongly determined by the intermittent pattern of distribution of many of the cactus species, rather than by a real species substitution. As shown in Fig. 3, a considerable number of species (e.g. *Opuntia microdasys*, *O. kleiniae*, *Mammillaria candida*, *Echinocereus pentaloophus*, *Neolloydia conoidea*, *Ferocactus hamatacanthus*, etc.) appear on and off along or in fragments of the transect, artificially increasing the β diversity values. In this respect, it is evident that the observed intermittency is linked to the scale used in this study. It has to be considered, however, that several restricted micro-endemic species, such as *Turbinicarpus subterraneus*, *M. melaleuca*, and *M. baumii*, contributed to a real turnover.

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References

- Bárceñas, R.T., 1999. Patrones de distribución de cactáceas del estado de Guanajuato. Tesis de Licenciatura. Facultad de Ciencias. Universidad Nacional Autónoma de México, Mexico.
- Bregman, R., 1988. Forms of seed dispersal in Cactaceae. *Acta Botanica Neerlandica* 37, 395–402.
- Del Castillo, R.F., Trujillo, S., 1991. Ethnobotany of *Ferocactus histrix* and *Echinocactus platyacanthus* (Cactaceae) in the semiarid central Mexico: past, present and future. *Economic Botany* 45, 495–502.
- Dinerstein, E., Olson, D., Atchley, J., Loucks, C., Contreras-Balderas, S., Abell, R., Iñigo, E., Enkerlin, E., Williams, C.E., Castilleja, G. (Eds.), 1999. *Ecoregion-Based Conservation In The Chihuahuan Desert: A Biological Assessment And Biodiversity Vision*. WWF, CONABIO, PRONATURA and ITESM, Washington, DC.
- García, E., 1981. Modificaciones al sistema de clasificación climática de Köpen para adaptarlo a las condiciones de la República Mexicana. Offset Larios, Mexico.
- Garcillán, P.P., Ezcurra, E., 2003. Biogeographic regions and β -diversity of woody dryland legumes in the Baja California peninsula. *Journal of Vegetation Science* 14, 859–868.
- Gómez-Hinostrosa, C., 1998. Diversidad, distribución y abundancia de cactáceas en la región de Mier y Noriega, México. Tesis de Licenciatura. Facultad de Ciencias. Universidad Nacional Autónoma de México, Mexico.
- Gómez-Hinostrosa, C., Hernández, H.M., 2000. Diversity, geographical distribution, and conservation of Cactaceae in the Mier y Noriega region, Mexico. *Biodiversity and Conservation* 9, 403–418.
- González, M., Quintana, P.F., 1986. Seed predation and dispersal in a dominant desert plant: *Opuntia*, ants, birds, and mammals. In: Estrada, A., Fleming, T.H. (Eds.), *Frugivores and seed dispersal*. Dr. W. Junk Publishers, Dordrecht, pp. 273–284.
- Hernández, H.M., Bárceñas, R.T., 1995. Endangered cacti in the Chihuahuan Desert. I. Distribution patterns. *Conservation Biology* 9, 1176–1190.
- Hernández, H.M., Bárceñas, R.T., 1996. Endangered cacti in the Chihuahuan Desert. II. Biogeography and Conservation. *Conservation Biology* 10, 1200–1209.
- Hernández, H.M., Godínez, H., 1994. Contribución al conocimiento de las cactáceas mexicanas amenazadas. *Acta Botanica Mexica* 26, 33–52.
- Hernández, H.M., Gómez-Hinostrosa, C., Bárceñas, R.T., 2001. Diversity, spatial arrangement, and endemism of Cactaceae in the Huizache area, a hot-spot in the Chihuahuan Desert. *Biodiversity and Conservation* 10, 1097–1112.
- Hernández, H.M., Gómez-Hinostrosa, C., Goetsch, B., 2004. Checklist of Chihuahuan Desert Cactaceae. *Harvard Papers in Botany* 9, 51–68.
- Huerta, F., García, E., 2004. Diversidad de especies perennes y su relación con el ambiente en un área semiárida del centro de México: implicaciones para la conservación. *Interciencia* 29, 435–441.
- Hunt, D., 1999. *CITES Cactaceae Checklist*, second ed. Royal Botanic Gardens Kew—International Organization for Succulent Plant Study, Milborne Port.
- Johnson, D.S., 1918. The fruit of *Opuntia fulgida*. A study of perennation and proliferation in the fruits of certain Cactaceae. Carnegie Institute, Washington.
- Kelt, D.A., Brown, J.H., Heske, E.J., Marquet, P.A., Morton, S.R., Reid, J.R.W., Rogovin, K.A., Shenbrot, G., 1996. Community structure of desert small mammals: comparisons across four continents. *Ecology* 77, 746–761.
- Koleff, P., Gaston, K.J., Lennon, J.J., 2003. Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* 72, 367–382.
- MacMahon, J., Wagner, F., 1985. The Mojave, Sonoran and Chihuahuan Deserts of North America. In: Evenari, M., Noy-Meier, I., Goodall, D. (Eds.), *Hot Deserts and Arid Shrublands, Ecosystems of the World*, vol. 12A. Elsevier, Amsterdam, pp. 105–202.
- Mandujano, M.C., Golubov, J., Montaña, C., 1997. Dormancy and endozoochorous dispersal of *Opuntia rastrera* seeds in the southern Chihuahuan Desert. *Journal of Arid Environments* 36, 259–266.
- Magurran, A., 1988. *Ecological diversity and its measurement*. Princeton University Press, New Jersey.
- Mittermeier, R.A., Goetsch, C., Robles-Gil, P., Pilgrim, J., Fonseca, G., Konstant, W.R., Brooks, T. (Eds.), 2002. *Wilderness: Earth's Last Wild Places*. CEMEX, Mexico.
- Mourelle, C., Ezcurra, E., 1997. Differentiation diversity of Argentine cacti and its relationship to environmental factors. *Journal of Vegetation Science* 8, 547–558.
- Mueller-Dombois, D., Ellenberg, H., 1974. *Aims and Methods of Vegetation Ecology*. Wiley, New York.

- Osorio, O., Valiente, A., Dávila, P., Medina, R., 1996. Tipos de vegetación y diversidad β en el Valle de Zapotitlán de las Salinas, Puebla, México. Boletín de la Sociedad Botánica de México 59, 35–58.
- Palleiro, N., 2001. Propagación vegetativa a través de frutos abortados de *Opuntia microdasys* (Lehman) Pfeiffer, en el Desierto Chihuahuense. Tesis de Licenciatura. Facultad de Ciencias. Universidad Nacional Autónoma de México, Mexico.
- Reyes-Agüero, J.A., Aguirre, J.R., Valiente-Banuet, A., in press. Reproductive biology of *Opuntia*: a review. Journal of Arid Environments.
- Rodríguez, P., Soberón, J., Arita, H.T., 2003. El componente Beta de la diversidad de mamíferos de México. Acta Zoológica Mexicana (n. s.) 89, 241–259.
- Rzedowski, J., 1978. Vegetación de México. Ed. Limusa, Mexico.
- Whittaker, R.H., 1972. Evolution and measurement of species diversity. Taxon 21, 213–251.
- Wilson, M.V., Shmida, A., 1984. Measuring beta diversity with presence-absence data. Journal of Ecology 12, 1055–1064.
- Zavala-Hurtado, J.A., Valverde, P.L., 2003. Habitat restriction in *Mammillaria pectinifera*, a threatened endemic Mexican cactus. Journal of Vegetation Science 14, 891–898.