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Vegetation ordination at the southern Chihuahuan Desert (San Luis Potosi, Mexico)

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Abstract

Cover data for 93 perennial plant species from fifty 1 ha sites, were used to ordinate desert vegetation in relation to 50 environmental variables at El Huizache Corridor. Cumulative variance recovered in the Bray and Curtis variance-regression ordination was substantial (80%). Community structure of desert plant communities at El Huizache Corridor may be influenced primarily by a combination of landscape and edaphic variables, which in turn may determine the distribution and abundance of moisture and nutrients, and perhaps promote habitat specialization and or competitive exclusion. Secondly, to a lesser extent, climate variables could be influencing community organization at small scale gradients, the longer the gradient the more relevant climatic factors become. First axis represented a landscape gradient; it was positively correlated to exposure, geology, slope angle, rocks, stoniness, iron, January mean temperature, and organic matter content; it was negatively correlated with latitude, longitude, soil depth, and potassium content. The second axis represented mainly a climatic gradient; it was positively correlated with mean precipitation of January, February, July, August, September, November, December, annual mean precipitation, Lang's Index, organic matter content, and stoniness. The third axis represented an edaphic gradient; it was positively correlated with electrical conductivity, Mn, Zn and elevation, and negatively correlated with pH, nitrates, Ca, and disturbance. These findings should guide conservation efforts to maintain species diversity and endemism at this area.

Introduction

A central goal of plant ecology is to understand the factors controlling local distribution of plant species and thus composition of plant communities (Barton 1993). Plant communities change gradually along environmental gradients (Gleason 1926; Curtis 1959; Whittaker 1956; Whittaker 1960; ter Braak and Prentice 1988; Vazquez and Givnish 1988; Givnish 1999), so, the individual response of species to environment and other species presence and/or abundance, lead to assembly rules (Wilson and Gitay 1995; Díaz et al. 1999) . The species distribution reflects the effects of several factors at different scales. Climate, topography, soil chemistry, and soil texture exert progressively finer influences on the geographical distribution of plant species (Ricklefs 1990). Community structure is determined by some environmental factors, for example, species diversity varies within sites (alfa diversity), between sites in a region (beta diversity), and among regions (gamma diversity) (Menge and Olson 1990). Alfa diversity results from niche differentiation within species and beta diversity from the species responses to a range of habitats (Whittaker 1960; Whittaker 1972). Many authors have found that landscape or physiographic factors play an important role in community organization (Rzedowski 1956; Whittaker and Niering 1965; Ricklefs 1973; Phillips and McMahon 1978; Yeaton and Cody 1979; Warren and Anderson 1985; Brown 1988; Rohde 1992; O'Brien 1993; McAuliffe 1994; Valverde et al. 1996 and Hahs et al. 1999; Abd El-Ghani 2000). Others have described climatic variables as major determinants of community organization (Daubenmire 1979; Klaus and Frankenberg 1979; Miles 1981; Bowman et al. 1985; Cramer and Hytteborn 1987; Gentry 1988; Nobel 1994; González-Medrano 1996; Aguado-Santacruz and García-Moya 1998). Some authors have concluded that soil characteristics are the most important factors in community organization (Rzedowski 1965; Sharaf El Din and Shaltout 1985; Abd El-Ghani 1998;. Huerta-Martínez et al. 1999; Abd El-Ghani 2000 and Yoder and Nowak 2000).

Chihuahuan Desert vegetation, particularly in the northern Chihuahuan Desert, has been studied by many authors (Shreve 1942; MacMahon and Wagner 1985; Henrickson and Johnston 1986; Dick-Peddie 1993; Brown 1994; Johnson et al. 2000). However, few studies have been done in the southern Chihuahuan Desert, and few have attempted to establish vegetation-environment relationships (Meyer and García-Moya 1989; Meyer et al. 1992; Valverde et al. 1996). The present study was done at El Huizache, which is one of 155 priority regions for conservation in Mexico identified by the Mexican National Commission for the Knowledge and Use of Biodiversity (CONABIO 1994). The region is considered as a biological corridor because it links several sectors of the Chihuahuan Desert. In addition, it is rich in endemic species and is a center of origin and diversification for cacti. Despite the importance of the region, a management strategy is lacking.

In this paper we aim to describe vegetation-environment relationships, and to generate hypotheses about species distributions such as: vegetation patterns at El Huizache Corridor are determined by a combination of different kind of factors.

Methods

Study area

El Huizache Corridor covers about 1920 km^2, and is located between 22°36'17″ N and 23°14'11″ N and 100°01'21″ W and 100°30'18″ W (Figure 1). The region reaches elevations of up to 2000 m and has sedimentary soils. The climate is semiarid, with mean annual precipitation of 400-600 mm and mean annual temperature ranging from 18 to 22 °C (García 1990). The vegetation comprises mainly xerophytic shrubland dominated by *Yucca filifera* Chab. and *Larrea tridentata* (DC) Coville. At some sites, the vegetation comprises gypsophilic grasslands.

Soil and vegetation sampling

In a region of about 1920 km^2, we selected fifty 1-ha sites, based on their physiognomy, structure and dominant species (Peinado et al. 1995). At each site, four 300-m^2 (30 m$\times$10 m) plots were randomly selected to obtain cover values for each of the 93 perennial species. Fifty environmental variables were measured for each site. Climatic data were obtained from García (1987) and Comisión Nacional del Agua (unpublished data). Soil depth was determined *in situ* and a composite soil sample was taken in the centre of the plot. The soil sample was characterized by measuring 12 variables: Nitrogen content (using Kjeldahl's method, modified for including nitrates [Brenmer 1965a; Brenmer 1965b]); pH (using the 1:2 soil:H_2O ratio); organic matter (Wakley and Black 1934); electrical conductivity (Richards 1954); phosphorus content (Olsen et al. 1954); the macronutrients potassium, calcium, and magnesium (Chapman and Kelly 1930), and the micronutrients iron, copper, manganese, and zinc (Lindsay and Norvell 1978). Vouchers were deposited at IBUG, IIZD and CHAPA Herbaria. Species nomenclature follows the International Plant Names Project (1999).

Unstandardized data were analyzed with Bray-Curtis variance regression ordination, using the Sørensen coefficient of similarity as the distance measure, in PC-ORD 4.10 (McCune and Mefford 1999). The Bray-Curtis variance regression ordination was used because it is considered an effective

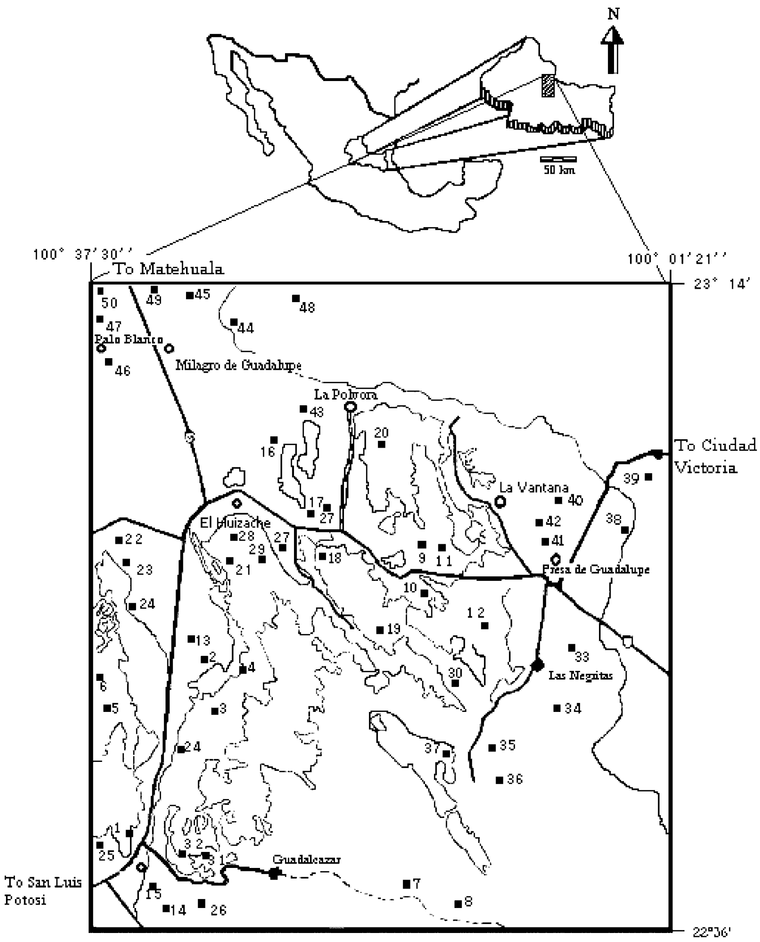

Figure 1. Location of El Huizache Corridor at San Luis Potosi state, Mexico, and sampling sites (•).

technique for revealing ecological gradients (Beals 1973; Beals 1984; Emlen 1972; Emlen 1977; Will-Wolf 1975; Causton 1988; Ludwig and Reynolds 1988; McCune and Beals 1993; McCune and Grace 2002). The Bray-Curtis coefficient, also known as Sørensen's coefficient, was originally applied to presence-absence data, but it works equally well with quantitative data (McCune and Mefford 1999). When Sørensen's coefficient of similarity is used as the distance measure it causes less distortion than Euclidean distance and analyses of presence-absence or quantitative data yield more meaningful results and are less sensitive to outliers (Beals 1984). The Bray-Curtis ordination technique is one of the most useful techniques for community analyses (McCune and Mefford 1999; McCune and Grace 2002). Its use was questioned by Austin and Orloci (1966), but recent authors consider it to be one of the better ordination techniques (McCune and Beals 1993; McCune and Grace 2002). In a comparison of three ordination techniques (Bray-Curtis, Principal Components Analysis, and Discriminant Function Analysis), the Bray-Curtis technique gave, in general, the best ordination results (Kessell and Whittaker 1976). Faith et al. (1987) pointed out that Bray-Curtis distance yields better results with unstandardized data than Chord distance, Kendall's coefficient, Chi squared, Manhattan distance, or Euclidean distance. The Sørensen coefficient of similarity was used originally in Bray-Curtis ordination, and is better than the Euclidean distance because it retains sensitivity in more heterogeneous data sets and gives less weight to outliers (Beals 1984).

The main matrix consisted of 93 perennial species cover data from 50 sites; the secondary matrix (environmental matrix) consisted of 55 environmental variables from 50 sites. Two of the environmental were nominal categorical (slope exposure and geology) and

Table 1. Bray-Curtis ordination for 93 species and 50 sites at El Huizache, San Luis Potosi.

Explained variation	Axis 1	Axis 2	Axis 3
% Extracted	30.05	27.74	11.56
% Cumulative	30.05	57.79	69.35

Table 2. Bray-Curtis ordination results without outliers (93 species and 47 sites).

Explained variation	Axis 1	Axis 2	Axis 3
% Extracted	46.75	20.81	12.05
% Cumulative	46.75	67.56	79.62

the rest were quantitative. After completing Bray-Curtis variance-regression ordination, using all the species cover values from all sites, three outliers were detected. The analysis was then repeated, excluding the three outliers.

Results

Bray-Curtis ordination of the main matrix showed that cumulative variance explained by the first three axes was 30%, 58% and 69% (Table 1). After excluding the three outliers, cumulative variance explained by the first three axes increased substantially to 47%, 68%, and 80% (Table 2). Individual extracted variance increased for axis one, decreased for axis two, and remained statistically similar for axis three (Table 1, Table 2).

A combination of landscape, climatic and edaphic factors influenced the community structure at the study sites. The first axis represented mainly a landscape gradient, but some other variables such as climatic and edaphic were represented too; it was positively correlated with exposure, geology, slope angle, rocks, stoniness, iron, January mean temperature and organic matter content; it was negatively correlated with latitude, longitude, soil depth and potassium content. The second axis represented a mainly climatic gradient but two edaphic variables were represented by this axis too; it was positively correlated with mean precipitation in January, February, July, August, September, November, December; annual mean precipitation; Lang's Index; organic matter content, and stoniness. The third axis represented an edaphic gradient, but factors related to climate were represented too; it was positively correlated with electrical conductivity, Mn, Zn, Longitude and elevation, and was negatively correlated with pH, nitrates, calcium, and disturbance (Table 3).

Table 3. Correlation coefficients between environmental variables and ordination axes without outliers (Bold indicates statistical significance at $p < 0.05$, 45 d.f.).

	AXES		
VARIABLES	1	2	3
Latitude	*−0.411*	− 0.260	− 0.216
Longitude	*−0.473*	0.090	*0.434*
Soil depth	*−0.608*	− 0.055	− 0.064
Potassium content	*−0.654*	− 0.267	− 0.236
Exposure	*0.487*	− 0.109	0.199
Geology	*0.611*	0.233	0.243
Slope inclination	*0.674*	0.115	0.156
% Rocks	*0.395*	0.064	− 0.054
Iron content	0.365	0.250	0.135
January mean temperature	*0.435*	− 0.222	− 0.010
Organic matter	*0.614*	0.365	− 0.096
Stoniness	*0.374*	*0.518*	0.106
January mean precipitation	0.032	*0.415*	0.079
February mean precipitation	0.251	0.362	0.195
July mean precipitation	0.165	*0.429*	0.112
August mean precipitation	0.029	*0.422*	0.018
September mean precipitation	− 0.093	*0.406*	0.104
November mean precipitation	0.099	*0.426*	0.111
December mean precipitation	0.196	0.351	0.113
Annual mean precipitation	0.093	*0.425*	0.120
Lang's Index	0.089	*0.432*	0.088
Electrical conductivity	− 0.050	0.127	*0.392*
Manganesse	0.197	0.195	*0.406*
Zinc	0.066	0.086	*0.414*
Elevation	0.004	0.248	*0.497*
pH	− 0.333	− 0.301	*-0.412*
Nitrates	− 0.200	− 0.030	*-0.428*
Calcium	− 0.249	− 0.236	*-0.618*
Disturbance	− 0.269	− 0.222	*-0.430*

The ordination diagram (Figure 2) showed dispersion of sites with respect to the first two axes. On the left of the diagram, sites 45, 46, 47, 48, 49 and 50 (Group IV), correspond to the gypsum grassland and alluvial desert shrubland (Group III). The species correlated to this portion of the axis were *Larrea tridentata*, *Opuntia kleineae* DC, *O. imbricata* DC, *Agave scabra* Salm-Dyck, and *Yucca filifera* (Table 4). On the right, were those sites with shallow soils, steeper slopes and sedimentary substrata (Group I, sites 2, 3, 7, 8, 17, 23, 25, 29, 30, 34, 39, 40 and 42). These sites correspond to submontane shrubland. The species correlated to this portion of the axis were *Neopringlea integrifolia* S. Watson, *Karwinskya*

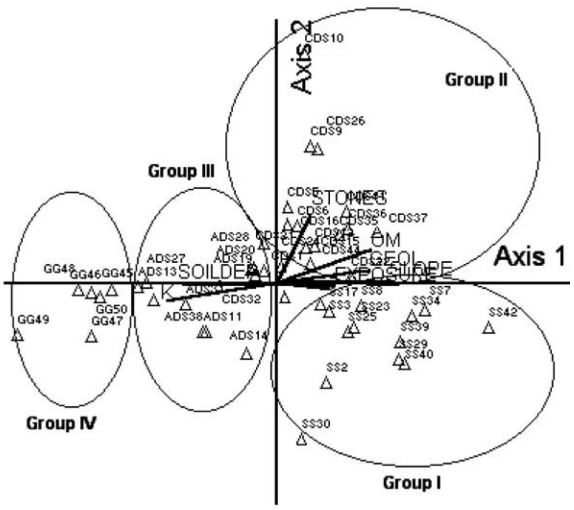

Figure 2. Bray-Curtis ordination of 47 vegetation plots (Δ), derived for cover values of species and overlays of relevant environmental variables (vectors), at El Huizache corridor (ADS= Alluvial desert shrubland, CDS= Calcareous desert shrubland; GG= Gypsum grassland; SS= Submontano shrubland).

Table 4. Correlation coefficients between species and ordination axes in a Bray-Curtis ordination without outliers (Bold indicates statistical significance *p < 0.05; **p < 0.01; 45 d.f.).

SPECIES	AXES 1	2	3
Larrea tridentata	**− 0.830****	− 0.203	− 0.183
Opuntia kleineae	**− 0.470***	− 0.094	− 0.089
Agave striata	**− 0.527***	− 0.061	− 0.206
Opuntia imbricata	**− 0.563***	− 0.156	− 0.225
Yucca filifera	**− 0.443***	− 0.053	− 0.123
Prosopis sp.	**− 0.393***	**− 0.381***	− 0.189
Neopringlea integrifolia	**0.493***	− 0.026	− 0.246
Karwinskya humboldtiana	**0.392***	0.293	0.195
Helietta parvifolia	**0.356***	0.079	**− 0.723****
Hechtia glomerata	**0.526***	**− 0.674****	0.030
Gymnosperma glutinosum	0.013	**− 0.406***	0.094
Maytenus phylantoides	0.008	**− 0.446***	0.085
Krameria cytisoides	0.097	**0.510***	0.216
Dalea bicolor	0.056	**0.399***	0.235
Ageratina sp.	0.065	**0.630****	0.120
Helianthemum glomeratum	0.058	**0.460***	0.134
Penstemon roseus	0.039	**0.502****	0.085
Agave striata	0.133	**0.422***	**0.354***
Gochnatia hypoleuca	0.170	**0.416***	**− 0.463***
Thelocactus hexaedrophorus	0.045	0.098	**− 0.450***
Salvia ballotaeflora	0.221	0.050	**0.415***

humboldtiana S. Watson, *Helietta parvifolia* (A. Gray) Benth., and *Hechtia glomerata* Zucc. (Table 4).

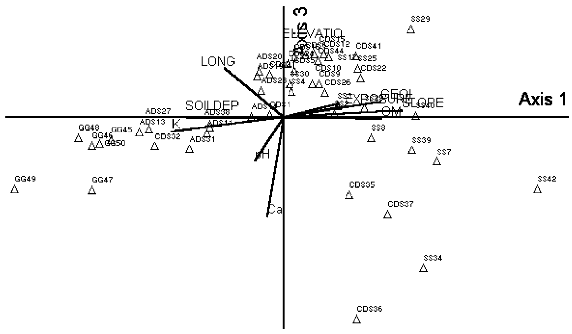

Figure 3. Bray-Curtis ordination of 47 vegetation plots (Δ), derived for cover values of species and relevant environmental variables (vectors), with respect to second and third axes at El Huizache corridor. (ADS= alluvial desert shrubland, CDS= Calcareous desert shrubland; GG= Gypsum grassland; SS= Submontano shrubland).

The second axis represented mainly a climatic gradient. The sites located at vthe upper right portion of diagram (Group II), correspond to calcareous desert shrubland, where the annual mean precipitation, and July and November mean precipitation, were higher. Also, the substrate at these sites was stonier than at other sites. The species correlated to this portion of the axis were *Krameria cytisoides* Cav., *Dalea bicolor* Humb. and Bonpl., *Ageratina* sp., *Helianthemum glomeratum* Lag., *Penstemon roseus* G. Don, *Agave striata* Zucc., and *Gochnatia hypoleuca* A. Gray (Table 4).

The third axis was correlated to some edaphic characteristics. The ordination diagram (Figure 3) showed sites 36, 34, 37, 35, and eventually 49 and, 47) where calcium content, and pH, were higher than at other sites. In such condition grow edaphically restricted species, such as *Helietta parvifolia*, *Gochnatia hypoleuca* and *Thelocactus hexaedrophorus* (Lem.) Britton and Rose (Table 4). Note that *H. parvifolia* was the dominant species in submontano shrubland (Figure 4).

Discussion

Landscape characteristics and soil properties are important determinants of the distribution of vegetation within our study site. These findings support the hypothesis that geology has a major influence on plant community composition in San Luis Potosi state (Rzedowski 1956), and that the processes that limit the distribution and abundance of plants at short elevational gradients are directly related to landscape

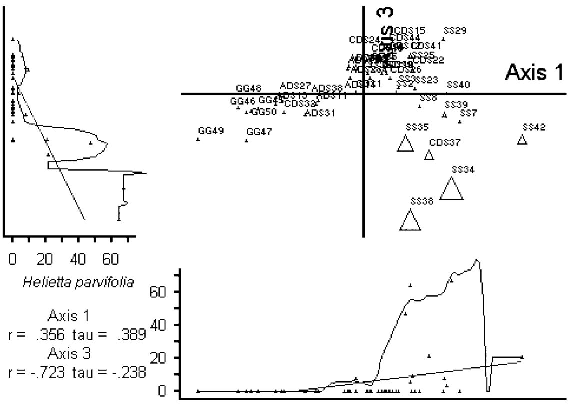

Figure 4. Overlay diagram showing the distribution of *Helietta parvifolia* with respect to the second and third axes, bigger triangles indicate higher cover values of the cited species.

characteristics (McAuliffe, 1994; Vazquez and Givnish 2000). For example, age and stability of substrata, and soil depth, strongly influence the spatial distribution, availability, and vertical movement of water in the substrata (MacAuliffe 1994).

The dominance of *L. tridentata* in soils with alluvial substrata has been documented by MacAuliffe (1994), Johnson et al. (2000) and is supported in this study; land form age and stability affect the structure of populations of long-lived *Larrea tridentata*. Individuals of this shrub species can exhibit clone-like growth and increase considerably in diameter over time spans of many centuries or millennia. The growth and persistence of this long-lived clones in some parts of the landscape apparently contribute to the exclusion of other species (McAuliffe 1994). Soil characteristics correlated with the first axis suggest that fertile soils were those where potassium and organic matter are higher. Sites with high values of organic matter content lead to good water retention capacity (Sharaf El Din and Shaltout 1985; Abd El-Ghani 1998). Abd El-Ghani (2000) mentioned that organic matter content plays an important role as a key element for the soil fertility in arid ecosystems in Egypt. Variation in the amount and source of organic matter on the soil creates parallel gradients of acidity, soil moisture, and available nitrogen. Such factors often interact in complex ways to determine the distributions of plants (Ricklefs 1990). Potassium is often a limiting factor in soils, because it has low mobility and is frequently unavailable to plants (Molles 1999). The high levels of Potassium in soils in our study site could be related to strong microbiological activity, e.g., by mycorrhizal fungi, which increase the availability of phosphorus and potassium for plants (Huerta-Martínez et al. 1999).

Yoder and Nowak (2000), reported that live and dead roots of *L. tridentata*, *Ambrosia dumosa* and *Lyucium pallidum*, were colonized by vesiculo-arbuscular mycorrizhal fungi, which play an important role in the acquisition of phosphorus by plants. Cross and Schlesinger (1999), found greater concentrations of available soil nutrients (–NO_3-N, total N, organic C, K, Cl and P) under *L. tridentata* canopy than in open areas. How many species in the study area have mycorrhizal associations? Is Potassium involved in other interactions, such as competition or facilitation? These are questions that need to be answered in future research.

The second axis was related to mean monthly rainfall. This supports the findings of Aguado-Santacruz and García-Moya (1998), who pointed out that summer precipitation showed one of the highest correlations with the first two species axes at the southernmost part of the North American Graminetum ($r = 0.77$ and $r = -0.39$ respectively). The strong influence of precipitation on species distribution has been documented by other authors (Whittaker and Niering 1975; Hadley and Szarek 1981; Ehleringer and Mooney 1983; Nobel 1994). and it is well known as the limitative factor in arid and semiarid ecosystems. However, our results suggest that water (in the rainfall form) was not the major factor involved in community organization at the El Huizache Corridor, and was only second in importance after landscape features because their correlations with second and first axes respectively.

The dominance of *H. parvifolia* in sites covered by submontane shrublands was reported by Rzedowski (1956), and is supported by this study. In many cases, the dominance of one shrub in a plant community may be caused by negative interactions such as competition or allelopathic effects. For example, Graue and Rovalo (1982) pointed out that the dominance of *H. parvifolia* is caused by the liberation of some alkaloids present in leaves, which dissolved in the rain, inhibits germination and growth of other plant species. In this study, we found that high values of pH could be another factor inhibiting the establishment of a great number of plant species. Correlation of Ca and pH with third axe suggest that an edaphic control on species establishment could be happening in the study area and promote habitat specialization for some species. In arid and semiarid regions often the main source of calcium is carbonate ($CaCO_3$)

(Nelson 1982; Haby et al. 1990), but often are gypsum outcrops ($CaSO_4 \cdot 2H_2O$) (Parsons, 1976), which explains the fact that the highest values of calcium were recorded in gypsum grasslands. Calcium is a key element determining floristic composition, because saturates the cation exchange capacity and modifies soil pH (to alkaline) (Etherington 1982). The four vegetation types have alkaline soils (> 7.0), but the extreme value was recorded in gypsum grassland (8.27). High concentrations of calcium and alkaline pH affect directly the availability of N, P, K, Mg, Fe, Mn, Zn and Cu (Maldonado et al. 2001). The species growing in such soils must have specials adaptations for the utilization of calcium, such as the ability of link calcium ions in their vacuoles through the formation of calcium oxalate crystals (Larcher 1975).

Our results demonstrate that three clear gradients influence the structure of plant communities in our study site; a combination of landscape features, climate, and soil properties explain the organization of plant communities. To maintain the diversity and structure of plant communities at El Huizache Corridor, conservation efforts should focus on conserving these landscape features.

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