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Assessing the Relative Importance of Climate and Soil for Vegetation Patterns in a Semiarid Land of Central Mexico

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SPECIES distribution along environmental gradients reflects the effects of several factors at different scales. The research was carried out at El Huizache Corridor, in the state of San Luis Potosi, Mexico, which is an important center of origin and diversification of cacti. The aim of the study was to assess the relative importance of climatic and edaphic factors on vegetation distribution. Using partial ordination, we analyzed in 47 sampling sites the relationships between cover values of 93 perennial plant species with 29 climatic and 19 edaphic factors. Variation partition showed that climatic variables were responsible for 14.4%, edaphic variables explained 33.6%, the interaction of both set of variables explained 11.1%; and unexplained or stochastic variation was around 41%. In addition, one vegetation type (submontane shrubland) was related to climatic factors, two (xerophytic shrublands and gypsum grassland) were related to edaphic factors, while succulent scrub was related to both set of factors.

Keywords: Climate, Edaphic, Semiarid vegetation, Variation partition.

Introduction

Understanding the processes controlling the spatial distribution of organisms in natural communities is a long-standing challenge in ecology (Bauman et al., 2019). Species distribution along environmental gradients reflects the effects of several factors at different scales (Givnish, 1999). At present, ecologists have abandoned the notion that community organization is driven by a single monolithic factor, and most reviews on this topic concluded that multiple processes must be invoked in order to explain community organization (Dunson & Travis, 1991); moreover, some authors emphasize the role played by management or environmental variables (Giallonardo et al., 2019) or the spatial factor (spatial distribution of samples) in combination with environmental variables to explain changes in the composition of communities (Bauman et al., 2019; Truchy et al., 2019). At a global perspective about arid environments, vegetation types coincide with the pattern of the water resources of the habitat, not only the water resources of a particular habitat that are controlled by the local topography, also the physical and chemical attributes of the soil are important for it (Abd El-Ghani et al., 2017).

The Huizache Corridor is a semiarid area in Central Mexico with great edaphic variation, as well as climatic variants which makes it interesting for research. In several papers (Meyer, 1986; Meyer & García-Moya, 1989; Meyer et al., 1992) is emphasized the importance of edaphic factors for plant community structure in this area, whereas in others (Hernández & Barcenas, 1996; Hernandez et al., 2001; Flores & Yeaton, 2003) consider climate as the driver factor of communities structure, nevertheless, Huerta-Martínez et al. (2004), included both climatic and edaphic variables in addition to landscape features in the same analysis, they concluded that the most important factors in determining the organization of plant communities in this study area are the landscape features. Therefore, the aim of this work was to assess the relative importance of climate and soil on the organization of shrub communities in the study area.

Methods

Study Area--The study was performed at El

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Huizache Corridor, in the state of San Luis Potosi, Mexico, an area considered of high priority for conservation purposes due to its large number of endemic species, especially cacti (Hernández et al., 2001). This area is located between 22°36' 17" and 23°14'11" N and between 100°01'21", 100°37'30" W, and an elevation from 1200 to 2000 m a.s.l. (Fig. 1).

The region has both residual and sedimentary (alluvial) substrate and gypsum outcrops, a semiarid climate (BS_1), with a mean annual rainfall from 336 to 722mm, and a mean annual temperature from 18 to 22°C (García, 1978) (Fig. 2). The vegetation is composed mainly of calcic desert scrub, piedmont scrub, alluvial desertic shrubland and gypsum grassland (Abd El-Ghani et al., 2017).

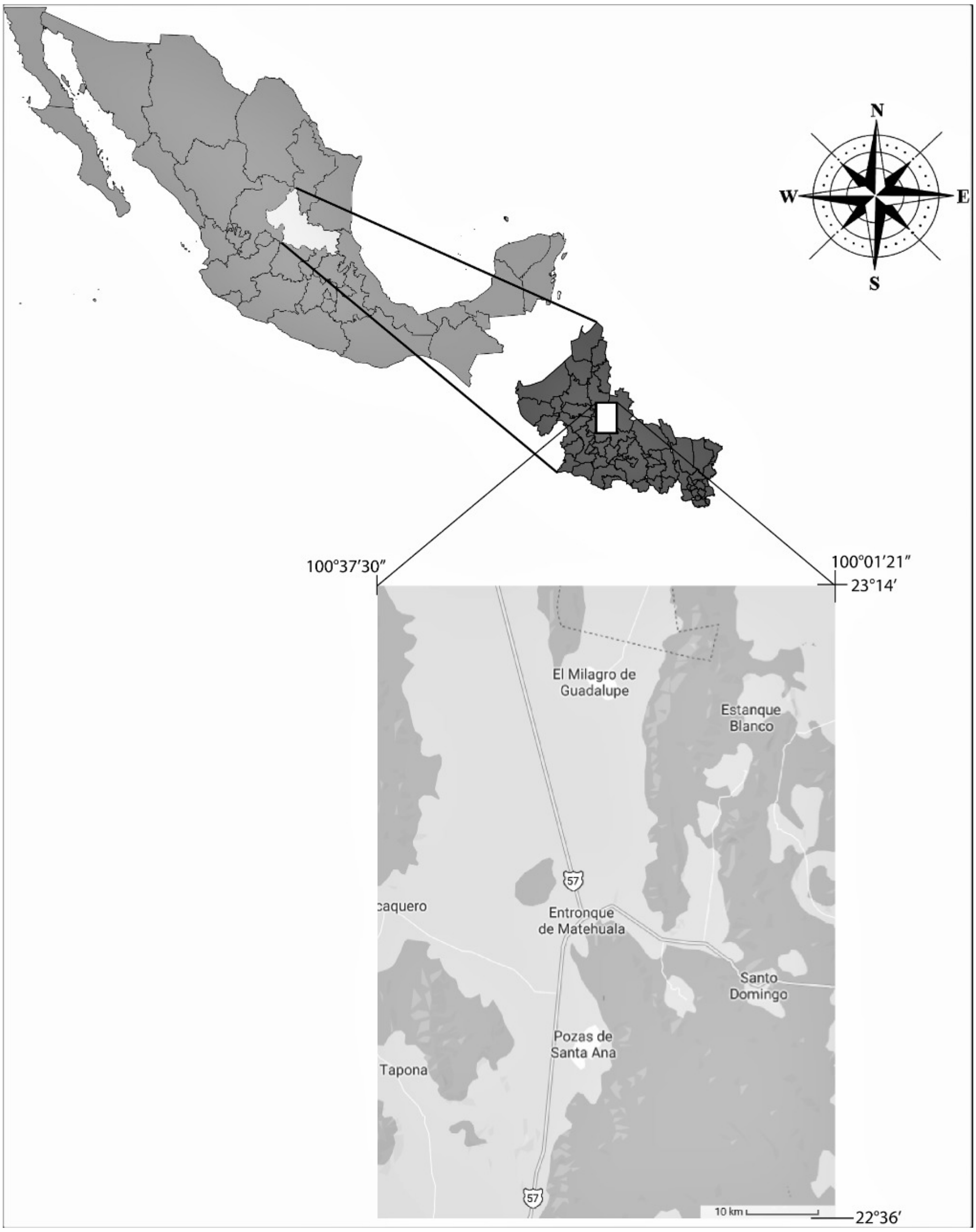

Fig. 1. Geographical location of El Huizache Corridor in San Luis Potosi, Mexico.

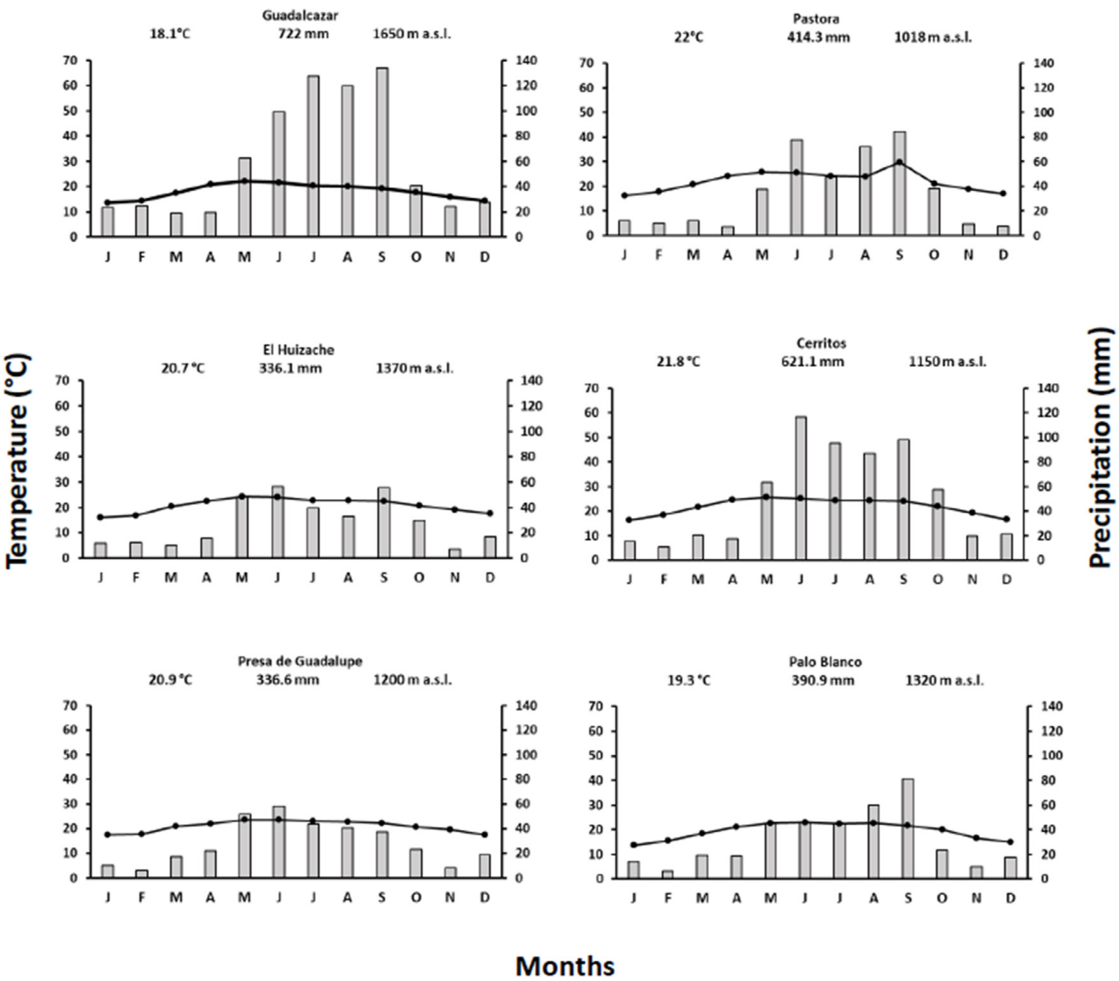

Fig. 2. Climatic diagrams from six weather stations in the study area: a) Guadalcazar, b) Pastora, c) El Huizache, d) Cerritos, e) Presa de Guadalupe and f) Palo Blanco. (Data from 1998-2018).

Vegetation Survey--Based on physiognomy, structure and dominant species (Peinado et al., 1995), we selected 50 sites of 1ha. At each site, four stands each of $300m^2$ (30m x 10m) were randomly laid out to obtain cover quantitative values for each of the 93 perennial species encountered, based on the Crown-Diameter Method (Mueller-Dombois & Ellenberg 1974), as follows:

$$\text{cover} = \left(\frac{D1 + D2}{4}\right)^2 \pi$$

where D1 equals the first measured crown diameter and D2, equals the second measurement (perpendicular to the first); the result is expressed in square meters of crown cover.

Plant species were collected and vouchers deposited at Botany Institute of University of Guadalajara Herbaria (IBUG) and Hortorio Herbarium of Colegio de Postgraduados (CHAPA), species were determined according to the nomenclature of The Plant Names Project (1999).

Climate Data--Data from six official weather stations located in the study area were used to derive historical records (from 1998 to 2018) of annual mean temperature, annual mean rainfall, mean temperature oscillation, percentage of winter rainfall, monthly mean precipitation and monthly mean temperatures, as well as Lang's Index.

Soil Sampling and Analysis--Soil depth, and the percentages of rocks, stones, and gravel were determined *in situ*. Three soil samples from the first 30 cm in depth was taken at each of the selected study sites, after a composed sample was made for the fertility analysis that included the following parameters: pH (1:2 soil:H_2O); electrical conductivity, organic matter, nitrogen, phosphorus, potassium, calcium, magnesium, iron, copper, manganese, sodium, and zinc content (Haluschak, 2006; Jones, 2018).

Ordination—A Detrended Correspondence Analysis was performed in order to know the length of gradient, after it, two canonical correspondence analyses (CCA) were run using both climatic and edaphic variables as explanatory variables, along with species cover values, using CANOCO 4.0 (ter Braak & Šmilauer, 1999). Three sites were excluded from analysis because they were marked as outliers. Soil chemical variables were log-transformed to make the analyses more biologically meaningful (Palmer, 1993; Pan et al., 1998). Two additional partial ordinations were performed using the two sets of variables (Borcard et al., 1992; Økland & Eilertsen, 1994, Borcard et al., 2018) to obtain the variation partition. The main matrix included 47 sites and quantitative values of the cover provided by 93 species (as was described above); Secondary matrices (environmental) included 47 sites and quantitative determination of 29 climatic (historical records as described above) (Table 1), and 19 edaphic variables (Table 2).

The following variances were differentiated:

• V(A) is the variance explained by the climatic variables A (Table 1);

• V(B) is the variance explained by the edaphic variables B (Table 2);

• V(A|B) is the variance explained by A only, i.e. the variance explained by A when B is removed (declared as covariables); V(B|A) is the variance explained by B only, i.e. the variance explained by B when A is removed (declared as covariables);

• The shared variance is V(A)-V(A|B) or V(B)-V(B|A);

• V(A+B) is the variance explained by A+B:

V(A|B) + V(B) or V(B|A) +V(A).

TABLE 1. Mean and standard error values of climatic variables used in the environmental ordination at El Huizache Corridor, San Luis Potosi, Mexico.

Month	Temperture (°C)				Precipitation (mm)			
	Suc	Sub	Gyp	Xer	Suc	Sub	Gyp	Xer
Jan	15.2±0.3	16.1±0.3	14.6±0.7	15.4±0.5	17.0±1.0	13.3±0.9	13.1±0.7	14.1±1.2
Feb	16.5±0.4	16.9±0.3	16.0±0.4	17.0±0.5	16.6±1.5	10.1±1.4	7.0±1.0	10.7±2.0
Mar	19.7±0.4	20.0±0.3	19.1±0.5	20.0±0.5	16.4±1.0	16.4±0.9	17.1±1.5	16.4±1.3
Apr	22.6±0.4	22.0±0.2	21.6±0.2	22.9±0.5	17.2±0.6	19.1±1.3	18.6±0.8	15.9±1.7
May	24.0±0.3	23.5±0.3	23.0±0.3	24.3±0.5	57.4±1.8	51.5±1.8	46.7±1.1	50.5±3.4
Jun	23.5±0.4	23.4±0.3	23.2±0.2	24.0±0.5	90.7±5.4	66.0±3.7	50.0±2.3	77.1±9.3
Jul	22.0±0.4	22.6±0.2	22.6±0.1	23.1±0.5	89.4±8.3	59.0±6.4	43.8±0.9	65.1±10.7
Aug	22.3±0.4	22.3±0.2	22.8±0.0	23.1±0.4	83.2±7.9	58.9±6.0	52.1±5.0	70.0±8.7
Sep	22.0±0.6	22.5±0.7	22.0±0.1	23.9±1.1	98.9±7.1	64.8±7.0	69.7±7.7	83.8±9.0
Oct	20.0±0.4	20.1±0.2	20.2±0.2	20.6±0.4	42.3±2.4	28.3±1.6	24.5±1.0	36.9±4.5
Nov	18.0±0.4	18.5±0.3	17.5±0.6	18.2±0.5	17.3±1.6	11.1±1.1	9.2±0.5	13.00±2.1
Dec	16.0±0.3	16.6±0.3	15.8±0.5	16.3±0.4	21.8±1.2	19.0±1.3	17.4±0.2	17.3±2.1
Annual	20.1±0.4	20.3±0.3	19.8±0.3	20.7±0.5	568.3±36.3	418.6±27.5	372.7±11.5	472.0±47.6

Suc= Succulent scrub, Sub= Submontane shrubland, Gyp= Gypsum grassland, Xer= Xerophytic shrubland.

TABLE 2. Mean and standard error values of edaphic variables used in the environmental ordination at El Huizache Corridor, San Luis Potosi, Mexico.

Variable	Unit	Suc	Sub	Gyp	Xer
Siol depth	cm	8.9±0.7	9.7±0.8	15.0±0.0	15.0±2.6
Stoniness	%	35.3±5.6	21.6±6.1	0.0±0.0	5.0±1.4
Gravel	%	50.9±5.9	47.4±10.0	0.0±0.0	30.6±10.0
Rocks	%	11.5±3.6	16.7±6.5	0.0±0.0	0.6±0.5
pH	-----	7.7±0.0	8.1±0.0	8.3±0.2	8.1±0.1
Electric conductivity	dS/m	1.0±0.0	0.4±0.1	0.9±0.4	0.8±0.3
Organic Matter	%	7.4±0.6	7.4±0.9	3.0±0.2	3.9±0.5
P Olsen	ppm	8.4±1.1	13.3±1.3	12.6±0.7	13.2±2.1
P Bray	ppm	1.1±0.2	1.0±0.4	2.1±2.0	0.9±0.5
N-NH4	ppm	37.9±2.1	41.2±3.1	41.4±5.6	34.9±3.4
N-NO3	ppm	26.3±1.5	32.3±2.2	33.5±1.3	30.7±4.2
K	ppm	493.1±50.7	937.9±141.7	1324.7±81.4	1318.8±147.2
Ca	ppm	3202.7±317.8	8320.7±1011.4	12471.5±148.0	8320.7±1566.0
Mg	ppm	186.9±23.1	240.1±40.6	180.0±39.1	224.7±33.9
Na	ppm	36.2±9.3	109.9±17.0	185.7±24.6	504.8±338.6
Fe	ppm	1.6±0.1	2.0± 0.2	1.2±0.0	1.1±0.1
Cu	ppm	0.24±0.0	0.3±0.0	0.1±0.0	0.3±0.0
Mn	ppm	3.8±0.3	2.4±0.4	2.4±0.4	2.7±0.3
Zn	ppm	3.0±0.6	1.5±0.4	0.3±0.0	0.9±0.4

Suc= Succulent scrub, Sub= Submontane shrubland, Gyp= Gypsum grassland, Xer= Xerophytic shrubland.

Results

Environmental ordination with climate. Climatic variables were responsible for explaining 25.53% of the total plant species variation [(1.745x100)/6.834] (Økland & Eilertsen, 1994). The extracted values of the percentage of the variance of species data were 7.6, 14.2 and 19.3% for the first three axes respectively (V(A)), (Table 3).

Figure 3 and Table 3 show the presence of precipitation and temperature gradients in the study area (axes one and two). There were four groups of sites; group one contained sites with succulent scrub, where the monthly mean precipitation was higher throughout most of the year. Group two was an ecotone of submontane shrubland and succulent scrub plant species. Group three consisted of sites with submontane shrubland, with a higher monthly mean temperature throughout the year but containing the highest amount of xerophytic vegetation. Group four consisted of two subgroups, corresponding to a combination of gypsum grassland (lower part) and xerophytic shrubland (upper part), with both having a higher mean winter precipitation.

Environmental ordination with soil. The second environmental ordination using edaphic variables explained 44.7% of the total variation [(3.055x100)/6.834], (Økland & Eilertsen, 1994). The cumulative percentage of variation in species consisted of 8.8, 15.4 and 21.5% for the first three axes respectively (V(B)), (Table 2). The ordination diagram (Fig. 4) shows four groups of sites corresponding to vegetation types. Group one, corresponding to gypsum grasslands and xerophytic shrublands, were positively significant correlated with K, P, and soil depth (Table 4). Group two represented vegetation growing on the transition zone between the alluvial and residual substrate and it is related to EC. Group three was formed by sites with succulent scrubs, in which OM, stoniness, rocks, Zn, and Mn were correlated. Finally, Group four, representing submontane shrubland, was significant negatively correlated with electrical conductivity and significant positively with OM (Table 4 and Fig. 4).

TABLE 3. Summary of environmental and partial CCA results using species cover data and two sets of explanatory variables (edaphic and climatic) at El Huizache, San Luis Potosi, Mexico.

Kind of ordination	Cumulative percentage variance of species data per axis			Sum of all canonical eigenvalues	Total inertia
	Axis 1	Axis 2	Axis 3		
1) Climatic as explanatory variables (no covariables) (V(A))	7.6	14.2	19.3	1.745	6.834
2) Edaphic as explanatory variables (no covariables) (V(B))	8.8	15.4	21.5	3.055	6.834
3) Climatic using edaphic as covariables (V(A|B))	7.8	14.1	18.7	0.985	6.834
4) Edaphic using climatic as covariables (V(B|A))	8.9	16.5	23.5	2.295	6.834

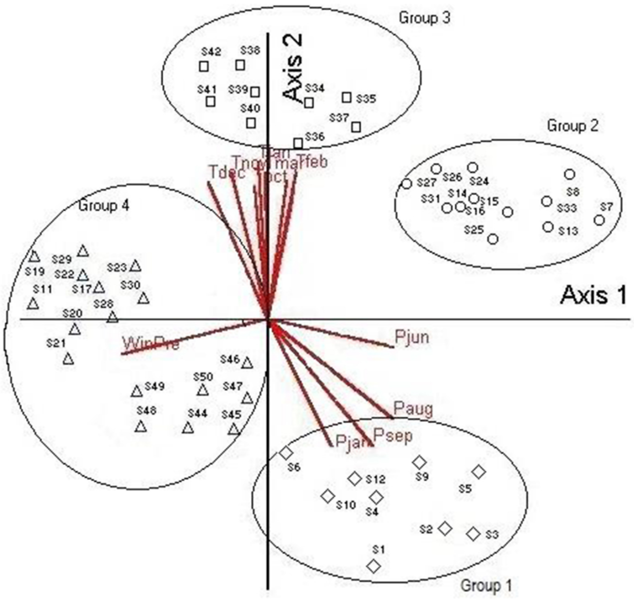

Fig. 3. CCA with climatic variables (vectors) and cover values of 93 perennial species at 47 sites at El Huizache Corridor, San Luis Potosi, Mexico [(◊) succulent scrub, (○) ecotone of submontane shrubland and succulent scrub, (□) submontane shrubland, (∆) a combination of gypsum grassland (lower part) and xerophytic shrubland (upper part)].

TABLE 4. Correlation coefficients of climatic variables and ordination axes of CCA at El Huizache Corridor, San Luis Potosi, Mexico. In bold those with statistical significance (α≤0.05).

Month	Temperature			Precipitation		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Jan	0.010	0.872	-0.140	0.349	-0.757	0.265
Feb	0.214	0.826	-0.518	0.207	-0.684	0.370
Mar	0.061	0.824	-0.498	0.503	-0.204	-0.078
Apr	0.424	0.563	-0.649	-0.222	-0.091	0.249
May	0.343	0.597	-0.593	0.295	-0.243	-0.021
Jun	0.218	0.666	-0.583	0.721	-0.130	-0.260
Jul	0.204	0.735	-0.627	0.540	-0.515	0.105
Aug	0.128	0.648	-0.717	0.689	-0.568	0.131
Sep	0.431	0.522	-0.327	0.573	-0.716	0.051
Oct	-0.002	0.748	-0.663	0.659	-0.053	-0.494
Nov	-0.119	0.832	-0.357	0.565	-0.504	0.016
Dec	-0.254	0.784	-0.255	0.035	-0.485	0.191
Annual	0.177	0.774	-0.533	0.609	-0.512	0.008

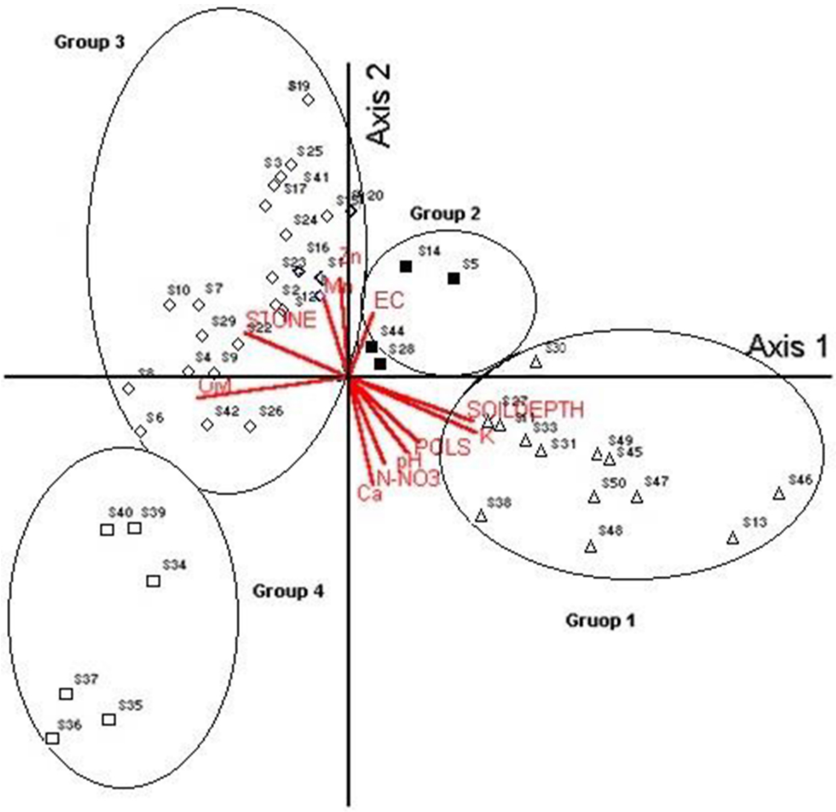

Fig. 4. CCA with edaphic variables (vectors) and cover values of 93 perennial species at 47 sites at El Huizache Corridor, San Luis Potosi, Mexico [(∆) gypsum grasslands and xerophytic shrublands, (■) transition zone between the alluvial and residual substrate, (◊) succulent scrubs, (□) submontane shrubland].

Partial ordination. The results of partial ordination performed with each set of variables are summarized in Table 3, which shows that the highest cumulative percentage of variation in species up to axis three was obtained when the ordination was constrained by edaphic variables, with climatic covariables. The lowest value for cumulative percentage variance in species up to axis three was obtained when the ordination was constrained by climatic variables with edaphic covariables.

The Total inertia was 6.834, so the percentage of variation obtained was calculated in four steps:

1) CCA of the species matrix constrained by climatic variables (V(A)), was the sum of all canonical eigenvalues [(1.745) (100) / 6.834 = 25.5%]

2) CCA of the species matrix constrained by edaphic variables (V(B)), was the sum of all canonical eigenvalues [(3.055) (100) / 6.834 = 44.7%]

3) Consisted of step 1, after removing the effect of edaphic variables (V(A|B)) (using them as covariables), which was the sum of all canonical eigenvalues [(0.985) (100) / 6.834 = 14.4%]

4) Consisted of step 2, after removing the effect of climatic variables (V(B|A)), (using them as covariables), which was the sum of all canonical eigenvalues [(2.295) (100) / 6.834 = 33.6%]

The overall amount of variation in species matrix is obtained by adding steps (1) and (4) or steps (2) and (3): 25.5 + 33.6 = 59.11% or 44.7 + 14.4 = 59.11%

The complete variation in the species matrix was partitioned as:

Variation due to climate (3) was 14.4%; variation due to the interaction of climatic and edaphic variables was (1) – (3) or (2) – (4) = 11.1%; variation due to edaphic variables (4) was 33.6%; and unexplained variation and stochastic fluctuations was 100-59.11 = 40.89% (Fig. 5).

TABLE 5. Correlation coefficients of soil variables and ordination axes of CCA at El Huizache Corridor, San Luis Potosi, Mexico.

Variable	Axis 1	Axis 2	Axis 3
K	**0.684**	-0.343	-0.173
Soil depth	**0.667**	-0.271	-0.108
P	**0.382**	**-0.400**	-0.245
OM	**-0.793**	-0.132	0.119
Stoniness	**-0.543**	0.261	-0.249
Rocks	**-0.430**	-0.074	-0.129
Fe	**-0.402**	0.121	-0.131
pH	0.315	**-0.465**	-0.292
N-NH4	-0.055	**-0.444**	0.103
N-NO3	0.192	**-0.531**	0.086
Ca	0.130	**-0.661**	-0.217
Cu	-0.047	**-0.421**	0.047
EC	0.129	**0.378**	**0.389**
Mn	-0.129	**0.474**	**0.482**
Zn	-0.040	**0.593**	**-0.462**

In bold those with statistical significance.

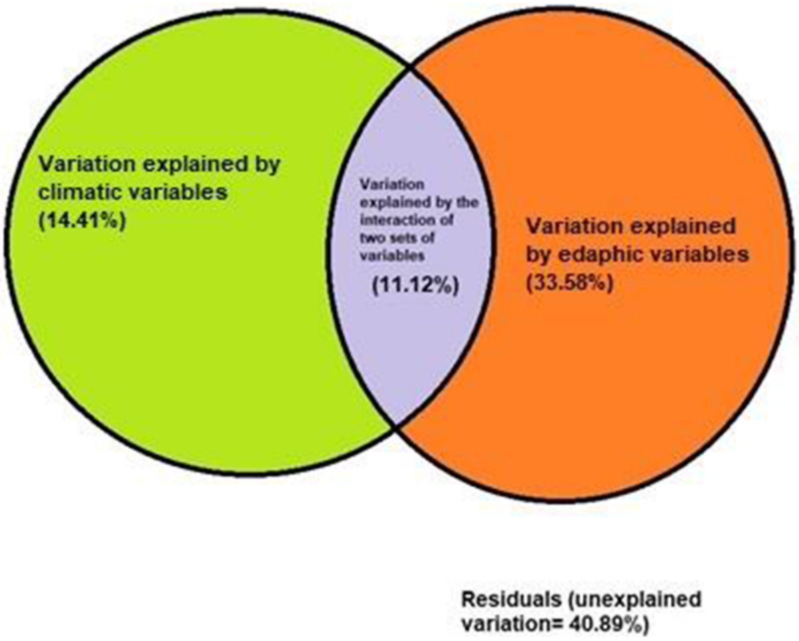

Fig. 5. Variation partition between edaphic and climatic variables in vegetation data at El Huizache, San Luis Potosi, Mexico.

Discussion

Variation partitioning is an approach to the analysis of a response variable or data table, using two or more explanatory variables or data tables. For simple response variables, the analysis is carried out using partial linear regression. Partial canonical analysis, is available in CANOCO and also in vegan, it allows ecologists to partition the variation of a response data table among two explanatory tables, using RDA or CCA. The variation-partitioning approach was first advocated by Borcard et al. (1992), in the context of spatial analysis in which a species composition response table Y is partitioned between a matrix of environmental variables and one describing the spatial relationships among the sampling sites. The variation in Y is partitioned into four fractions, three of which can be interpreted separately or in combinations: a) the non-spatially-structured component of the variation of Y explained by the environmental variables, b) the spatially-structured component explained by the environmental variables, c) the amount of spatially-structured variation of Y not explained by the environmental variables used in the analysis, and d) the unexplained (residual) variation (Legendre & Birks, 2012).

In our work, the first CCA demonstrated that climatic variables were important for submontane scrublands and succulent scrub. Submontane scrublands contain a type of vegetation determined by a thermal gradient (Rzedowski, 1956), whereas succulent scrub areas contain a type of vegetation driven by both edaphic and climatic (precipitation) variables. The small effect of only the climatic variables on species variation in this study suggests the presence of complex gradients arising from the effects of different mixed factors (climatic, edaphic and/or landscape features), thus accounting for a greater percentage of cumulative variance such as in Huerta-Martínez et al. (2004).

In addition, the mean temperature in December, January, February and March may determine flowering season and mean precipitation of June, August, and September may determine the fruiting season of most plant species at El Huizache (Rzedowski, 1956). September average temperature is a key factor for seed germination and seedling establishment, whereas January average precipitation when it occurs increases the amount of residual soil humidity, which promotes reproductive success. Axis two represents a thermal gradient, the lower portion of which is correlated with the coldest portion of the study area, and this factor has been found to influence plant reproduction. For instance, during 1999 and 2000, there was a frost event in late February-early March, which affected the flowering of *Echinocactus platyacanthus* and *Ferocactus pilosus* (personal observations). Extreme freezing temperatures are known to be a mechanism limiting the distribution of some species in the study area, especially arborescent cacti (Flores & Yeaton, 2003).

Although there is great heterogeneity in soil from one type of vegetation to another, soil factors seemed to be important in explaining the distribution patterns of only two types of vegetation in this area: succulent scrub and xerophytic shrubland. Both were correlated to particular soil characteristics, thus confirming the findings of Rzedowski (1965). It is important to highlight that Ca soil concentration, as shown in the CCA, was lower in areas of succulent scrub than in areas of gypsum grasslands. In the first case, the soils were calcareous, thus containing higher concentrations of calcium carbonate. The apparently contradictory observation of a lower Ca soil concentration in succulent scrub areas, despite their higher concentrations of calcium carbonate, may result from the method used to measure calcium content in the soil (Chapman & Kelly, 1930), which uses ammonia to determine the extractable fraction of calcium (Piper, 1944). The ammonia solution dissolves carbonates because of that it is not possible to detect Ca in soil samples; in contrast, this method can detect Ca in sulfates ($CaSO_4 \cdot 2H_2O$), which are present in gypsum soils.

Interactions between climatic and edaphic variables were demonstrated using partial CCA. The common fraction arises because explanatory variables in different sets are correlated (Borcard et al., 2018). However, the shared variation between the soil and climate matrices was as high as 11.12% in our study. This suggests that there is no interaction between these two types of variables and that they mediate the community composition separately rather than in combination.

Climate constrains the distribution of many species, and some soil properties (pH, Ca concentration), may lead to habitat specialization by increasing environmental stress. Although slightly more than half the total variation (59%), could be explained by edaphic and climatic variables, the remainder corresponded to stochastic variations or to other types of variables such as landscape features or biotic interactions. It is clear that types of vegetation are not randomly distributed throughout the Huizache Corridor.

Conclusion

The study represents systematic quantification of relationships between two particular sets of environmental factors (climate and soil), across large contiguous sampling sites in an arid region of Central Mexico. Our results suggested that vegetation distribution was determined by climatic factors (submontane shrubland), soil factors (xerophytic shrublands and gypsum grassland), and by a combination of both climatic and soil factors (succulent scrub).

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Authors contribution: Francisco Martin Huerta Martinez conceived the idea of the work, carried out the field work and part of the analyzes. Cecilia Neri Luna did field work, laboratory work, and assisted in the writing of the manuscript. Alejandro Muñoz Urias collaborated in the field work, the statistical analyzes and in the writing of the manuscript. Jose Pedro Castruita Dominguez collaborated in the field and laboratory work and in the writing of the manuscript. Francisco Javier Sahagun Sanchez collaborated in the field work and development of some of the figures and in the writing of the manuscript.

Ethical approval: Not applicable.

References

Abd El-Ghani, M.M., Huerta-Martínez, F.M., Hongyan, L., Qureshi, R. (2017) "*Plant Responses to Hyperarid Desert Environments*". Springer. 598p.

Bauman, D., Vleminckx, J., Hardy, O.J., Drouet, T. (2019) Testing and interpreting the shared space-environment fraction in variation partitioning analyses of ecological data. *OIKOS,* **128**, 274-285

Borcard, D., Legendre, P., Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology,* **73**, 1045-1055.

Borcard, D., Gillet, F., Legendre, P. (2018) "*Numerical Ecology with R, Use R!*", 2nd ed. Springer. Switzerland. 244p.

Bremner, J.M. (1965 a) Inorganic forms of nitrogen. In: "*Methods of soil analysis Part 2, Agronomy Monographs*", C.L. Black (Ed.), 9, pp. 1179-1206. ASA and SSSA, Wisconsin, USA.

Bremner, J.M. (1965 b) Total nitrogen. In: *Methods of soil analysis Part 2, Agronomy Monographs*", C.L. Black (Ed.), 9, pp. 1149-1178. ASA and SSSA, Wisconsin, USA.

Chapman, H.D., Kelly, W.P. (1930) The determination of the replaceable bases and bases exchange capacity of soils. *Soil Science,* **30**, 391-406.

Dunson, W.A., Travis, J. (1991) The role of abiotic factors in community organization. *American Naturalist,* **138**, 1067-1091.

Flores, F.J.L., Yeaton, R.I. (2003) The replacement of arborescent cactus species along a climatic gradient in the southern Chihuahuan Desert: Competitive hierarchies and response to freezing temperatures. *Journal of Arid Environments,* **55**, 583-594.

García, E. (1978) Sistema de clasificación climática de Köppen (Modificado para adaptarlo a las condiciones de la República Mexicana). México, D.F.

Giallonardo, T., Angiolini, C., Ciaschetti, G., Landi, M., Pirone, G., Frattaroli, A.R. (2019) Environment or management? Relative importance for floristic composition of sub-Mediterranean hay meadows in Central Italy. *Applied Vegetation Science*, **22**, 336-347.

Givnish, T.J. (1999) On the causes of gradients in tropical tree diversity. *Journal of Ecology,* **87**, 193-210.

Haluschak, P. (2006) Laboratory methods of soil analysis. Canada-Manitoba Soil Survey, 3-133.

Hernández, H.M., Bárcenas, R.T. (1996) Endangered cacti in the Chihuahuan Desert: II. Biogeography and conservation. *Conservation Biology,* **10**, 1200-1209.

Hernández, H.M., Gómez-Hinostrosa, C., Bárcenas, 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.

Huerta-Martínez, F.M., Vázquez-García, J.A., García-Moya, E., López-Mata, L., Vaquera-Huerta, H. (2004) Vegetation ordination at the southern Chihuahuan Desert (San Luis Potosi, Mexico). *Plant Ecology,* **174**, 79-87.

Jones, J. (Ed.) (2018) "*Soil Analysis Handbook of Reference Methods*". CRC Press. 264p

Legendre, P., Birks, H.J.B. (2012) From Classical to Canonical Ordination. In: "*Tracking Environmental Change Using Lake Sediments, Developments in Paleoenvironmental Research*", Birks, H.J.B., Lotter, A.F., Juggins, S., Smol, J.P. (Eds.), 5, pp. 201-248. Springer ScienceCBusiness Media B.V. Dordrecht Heidelberg, New York, London DOI 10.1007/978-94-007-2745-8 8.

Meyer, S.E. (1986) The ecology of gypsophile endemism in the eastern Mojave Desert. *Ecology,* **67**, 1303-1313.

Meyer, S.E., García-Moya, E. (1989) Plant patterns and soil moisture regime in gypsum grasslands of north central Mexico. *Journal Arid Environment,* **16**, 147-155.

Meyer, S.E., García-Moya, E., Lagunes-Espinoza, L.C. (1992) Topographic and soil surface effects on gypsophile plant community patterns in central Mexico. *Journal of Vegetation Science,* **3**, 429-438.

Mueller-Dombois, D., Ellenberg, H. (1974) "*Aims and Methods of Vegetation Ecology*". John Wiley & Sons, New York, USA.

Økland, R.H., Eilertsen, O. (1994) Canonical correspondence analysis with variation partitioning: some comments and an application. *Journal of Vegetation Science,* **5**, 117-126.

Palmer, M.W. (1993) Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology,* **74**, 2215-2230.

Pan, D., Bouchard, A., Legendre, P., Domon, G. (1998) Influence of edaphic factors on the spatial structure of inland halophytic communities; A case study in China. *Journal of Vegetation Science,* **9**, 797-804.

Peinado, M., Alcaráz, F., Aguirre, J.L., Delgadillo, J. (1995) Major plant communities of warm North American deserts. *Journal of Vegetation Science*, **6**, 78-94.

Piper, C.S. (1944) "*Soil and Plant Analysis*". Interscience Publishers, Inc., New York, USA.

Rzedowski, J. (1956) Notas sobre la flora y la vegetación del estado de San Luis Potosí. III. Vegetación de la región de Guadalcazar. *Anales del Instituto de Biología,* **27**, 169-228.

Rzedowski, J. (1965) Vegetación del estado de San Luis Potosí. *Acta Científica Potosina,* **5**, 5-291.

The Plant Names Project (1999) International plant names index. [accesed June 5th, 2019] URL: http://www.ipni.org/ipni/query ipni.html/

Ter Braak, C.J.F., Šmilauer, P. (1999) Canoco for Windows. Software for Canonical Community Ordination (V. 4.0) Microcomputer Power. Ithaca, New York, USA.

Truchy, A., Göthe, E., Angeler, D.G., Ecke, F., Sponseller, R.A., Bundschuh, M., Johnson, R.K., McKie, B.G. (2019) Partitioning spatial, environmental, and community drivers of ecosystem functioning. *Landscape Ecology,* **34,** 2371-2384.