NUMERICAL ANALYSES OF VEGETATION BASED ON ENVIRONMENTAL RELATIONSHIPS IN THE SOUTHERN CHIHUAHUAN DESERT

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ABSTRACT—Relationships between environmental factors and vegetation types in a southern part of the Chihuahuan Desert were explored. Species presence-absence data and cover data from 44 samples were analyzed. Eight categorical and seven continuous environmental variables were recorded at each sampling site. Classification analysis identified four vegetation types: crassicaulous scrub, rosetophyllous scrub, microphyllous scrub, and mesquital. A regression of ordination scores from a principal components analysis on environmental variates indicated that vegetation variation was strongly correlated with geomorphological variables. Discriminant analysis based on environmental variables showed a clear segregation of the four vegetation types.

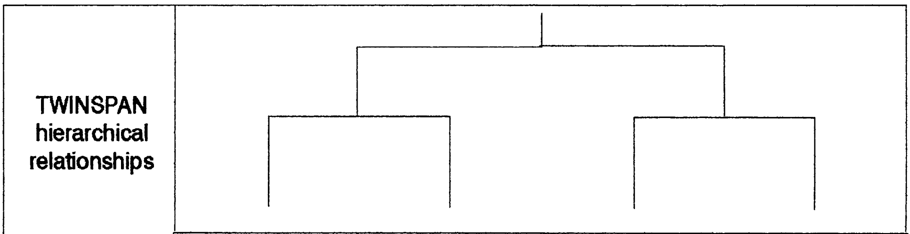
RESUMEN—Se exploraron las relaciones entre el ambiente físico y los tipos de vegetación en la zona sur del Desierto Chihuahuense. Se analizaron datos de presencia-ausencia y cobertura de las especies en 44 muestras, en cada una de las cuales se registraron ocho variables ambientales categóricas y siete contínuas. Un análisis de clasificación reveló la presencia de cuatro tipos de vegetación en el área de estudio: matorral crasicaule, matorral rosetófilo, matorral micrófilo y mezquital. Una regresión entre los puntajes por sitio obtenidos mediante un análisis de componentes principales y las variables ambientales sugirió que la variación de la vegetación está fuertemente correlacionada con la variación de características geomorfológicas. Un análisis discriminante aplicado sobre las variables ambientales mostró una clara segregación de los cuatro tipos de vegetación.

Semiarid ecosystems in North American deserts, such as the Chihuahuan Desert, have relatively high diversity compared with other North American ecosystems (Rzedowski, 1981). This diversity may be a result of high environmental heterogeneity that affects the establishment of species with a variety of functional and structural adaptive strategies (Cornelius et al., 1991).

Many studies of vegetation-environment relationships have been conducted in different desert ecosystems (e.g., Bowers and Lowe, 1986; Dargie and El Demerdash, 1991; Ezcurra et al., 1987; Vetaas, 1992; Zavala-Hurtado et al., in press). However, few have focused on the Chihuahuan Desert, the largest arid biome in Mexico (Montaña, 1988). Three biogeographic subdivisions have been proposed for the Chihuahuan Desert: Trans-Pecos, Mapimian, and Saladan (Morafka, 1977). All studies of vegetation-environment relationships have concentrated on the Trans-Pecos subdivision (Montaña, 1990).

In this paper, we study the spatial distribution of vegetation types in the southern portion of the Chihuahuan Desert (Saladan subdivision) in relation to environmental factors. Montaña (1988, 1990) and Montaña and Greig-Smith (1990) have suggested that floristic variation in the adjacent subdivision of Mapimi is closely related to environmental gradients associated to geomorphology. Thus, we focused our research on geomorphological environmental factors with multivariate analyses.

STUDY AREA—This study was conducted in an area of about 5000 km^2 in the northern Mexican state of Du-



	GROUP 1	GROUP 2	GROUP 3	GROUP 4
Physiognomy	crassicaulous scrub	rosetophyllous scrub	microphyllous scrub	mesquital
Main indicator species	Opuntia rastrera O. leucotricha O. streptocanta	Agave lechuguilla	Larrea tridentata Acacia vernicosa Flourensia cernua	Prosopis glandulosa

FIG. 1—TWINSPAN classification of 44 samples defined by presence-absence and cover abundance of 130 species. A gradient of floristic composition was detected from group 1 to 4 (see text for details).

rango at 24°20′ and 25°12′N and 102°30′, and 103°30′W (INEGI, 1981). Elevation ranges from 1300 m to 2500 m. Average annual rainfall is 300 mm, most of which occurs in summer (June through September). Annual mean temperature is 20.9°C, with a maximum in June (data from San Juan de Guadalupe Meteorological Station, 24°47′N, 102°44′W, 1,570 masl; García, 1973).

Seven different land form types can be recognized in this subdivision of the Chihuahuan Desert: 1) alluvial plains; 2) valleys; 3) rolling hills of calcareous origin; 4) igneous plateaus and low hills; 5) low sierras of calcareous origin; 6) complex sierras of calcareous igneous, and metamorphic origin; and 7) high sierras of calcareous origin (more than 2,000 m) (Programa de Aprovechamiento Integral de Recursos Naturales, in litt.; Valverde, 1994). There are four vegetation types: 1) crassicaulous scrub characterized by large *Opuntia* cacti (mainly *O. leucotricha* and *O. rastrera*); 2) rosettophyllous scrub with rosette-like plants of the genus *Agave* (primarily *A. lechuguilla*); 3) microphyllous scrub with high dominance of small-leaved shrubs as *Larrea tridentata, Acacia* sp., and *Flourensia cernua;* and 4) mesquital characterized by dominance of *Prosopis glandulosa* (Rzedowski, 1981; González-Elizondo et al., 1991).

METHODS—Sampling points were chosen following a stratified and preferential scheme (Matteucci and Colma, 1982) based on cartography and topography of the zone. Our goal was to sample landscape heterogeneity and to select the most common habitat types within a given location (Dargie and El Demerdash, 1991).

The log-series survey method (McAuliffe, 1990) was used to estimate density and cover of plant species present in 44 sampling units of 250 m^2 each. Each sample was subjectively assigned to one of the four vegetation types (see above description) based on its physiognomy and dominant species. Data were collected from July 1990 to June 1991. Two types of environmental data were collected for each sampling unit: 1) eight categorical variables with several levels each, describing geomorphological features, and 2) seven continuous variables describing habitat characteristics (Table 1).

Vegetation analysis used presence-absence data and cover data to compare the quality of both types of information. Cover was estimated as the percentage of sampling area covered by the vertical projection of individuals of each species present. Classification analysis using TWINSPAN (Hill, 1979) and a non-centered principal components analysis using CANOCO (ter Braak, 1987) were applied to each data set.

Relationships between ordination axes and environmental variables (Table 1) were estimated with multiple regression analysis using the GLIM package (Baker and Nelder, 1978). Additionally, stepwise discriminant analysis using SPSS/PC+ (Norusis, 1988) was applied to the significant environmental variables from the regression analysis considering the groups obtained from the TWINSPAN classification. Discriminant analysis was used to enhance the environmental interpretation of the classification groups (Ludwig and Reynolds, 1988).

RESULTS—The TWINSPAN analysis identified four groups (Fig. 1) that coincided with subjectively recognized vegetation types in the field. Group 1 is characterized as crassicaulous scrub, indicated by *Opuntia leucotricha* and *O. rastrera.* These species were associated with *Bouteloua gracilis, Dalea* sp., *Mimosa biuncifera, Acacia constricta, Bursera fagaroides,* and *Phitecelobium* sp. Group 2 represents rosetophyllous scrub, with *Agave lechuguilla* as the indicator species; *Buddleia marrubiifolia, A. striata,* and *Leucophyl-*

TABLE 1—Categorical and continuous environmental variables collected for each sampling unit in Chihuahuan Desert.

Variable type	Level	
Categorical		
LF land form	LF1 alluvial plains	
	LF2 valleys	
	LF3 rolling hills of calcareous origin	
	LF4 igneous plateaus and low hills	
	LF5 low sierras of calcareous origin	
	LF6 complex sierras of calcareous, igneous, and metamorphic origin	
	LF7 high sierras of calcareous origin	
MR microrelief	MR1 level	
	MR2 nearly level	
	MR3 slightly wavy	
	MR4 wavy	
	MR5 highly wavy	
	MR6 irregular	
RO rocky outcrops	RO1 non	
	RO2 scarce	
	RO3 moderate	
	RO4 abundant	
	RO5 very abundant	
ST stoniness	ST1 no or very few stones	
	ST2 slightly stony	
	ST3 stony	
	ST4 very stony	
	ST5 excessively stony	
SO soil origin	SO1 residual	
	SO2 alluvial	
	SO3 colluvial	
	SO4 alluvial-colluvial	
ED external drainage	ED1 very scarcely drained	
	ED2 scarcely drained	
	ED3 drained	
	ED4 highly drained	
	ED5 excessively drained	
EG erosion grade	EG1 none	
	EG2 slight	
	EG3 moderate	
	EG4 high	
ET erosion type	ET1 eolian	
	ET2 laminar hydric	
	ET3 furrow hydric	
	ET4 ravine hydric	
Continuous		
SN slope		
PV percent of soil surface covered by vegetation		0–100%
DL percent of soil surface covered by dead leaves		0–100%
FM percent of soil surface covered by fine material		0–100%
GS percent of soil surface covered by gravel and stones		0–100%
PR percent of soil surface covered by rocks		0–100%
SN species number/plot		9–39 species

TABLE 2—Partial correlation coefficients (r) from a multiple regression analysis of environmental variables explaining significantly ($P < 0.05$) the first four axes of PCA.

	Presence-absence data				Cover data			
	Axis1	Axis2	Axis3	Axis4	Axis1	Axis2	Axis3	Axis4
LF land form	0.43	0.60	0.54	N.S.	0.44	0.54	0.65	0.50
MR microrelief	N.S.	0.33	N.S.	N.S.	N.S.	N.S.	0.34	0.41
RO rocky outcrops	N.S.	N.S.	N.S.	N.S.	0.41	N.S.	N.S.	N.S.
ST stoniness	N.S.	N.S.	N.S.	N.S.	0.37	0.36	N.S.	N.S.
SO soil origin	0.41	N.S.	N.S.	N.S.	0.30	0.33	N.S.	0.40
GS gravel and stones %	N.S.	N.S.	N.S.	N.S.	N.S.	0.22	0.20	N.S.
PR rocks %	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	0.22	N.S.
SN species number	0.64	N.S.	N.S.	N.S.	0.28	N.S.	N.S.	N.S.

lum minus were associated species. Group 3 corresponds to microphyllous scrub, characterized by *Larrea tridentata, Acacia vernicosa, Fouquieria splendens, Zinnia acerosa, Parthenium incanum, Flourensia cernua,* and *Cordia gregii,* as well as *Opuntia fulgida* and *O. imbricata.* The fourth group is mesquital, dominated by *Prosopis glandulosa* in association with *Larrea tridentata, Condalia mexicana, Opuntia leptocaulis, Atriplex canescens, Lycium berlandieri,* and *Alliona incarnata.* A gradient of floristic composition can be recognized in these results: there is a gradual turn-over of dominant species from crassi-rosetophyllous shrubs to total dominance of microphyllous shrubs and mesquite.

Figure 2 shows the ordination of vegetation types for presence-absence (Fig. 2a) and cover (Fig. 2b) data along axes 2 and 3. Because ordinations were noncentered, the first principal component (PCA1) was clearly assymetric or unipolar in relation to the remaining components: samples had a positive projection on PCA1 which is related to species frequency (Noy Meir, 1973). Dagnelie (1960, in Noy Meir, 1973) interpreted the first non-centered axis as a general factor that only accounts for the relative abundance of species. The four groups resulting from TWINSPAN were better displayed along axes 2 and 3 (explained variance = 38% and 8%, respectively) in the presence-absence ordination (Fig. 2a) than the corresponding axes (explained variance = 39% and 8%, respectively) in the cover ordination (Fig. 2b).

The first four components of the cover data, and the first three components of the presence-absence data, showed significant F values ($P < 0.05$) and relatively high r values with at least one environmental variable (Table 2). Seven variables (ED, EG, ET, SL, PV, DL, and FM; Table 1) without significant F values for any of these components were discarded after regression analysis.

Segregation of crassicaulous scrub and rosettophyllous scrub from microphyllous scrub and mesquital along axis 2 from both data sets (Fig. 2) is related to land form (Table 2). This variable also was important to the third component (Table 2) in segregating all vegetation types (Fig. 2).

Discriminant analysis (DA) supported the correspondence between environmental factors and vegetation types. Discriminant functions 1 and 2 explain 87.99% of total variance (50.17% and 37.82%, respectively) of presence-absence groups, and 80.92% (60.62% and 20.30%, respectively) for the cover classification.

Because the algorithm used to extract discriminant functions included a stepwise selection of variables, environmental factors incorporated into functions were only those whose variation was significant for between-group discrimination. All variables selected in the regression analysis (except soil origin, SO, for the cover classification) entered discriminant functions 1 and 2 for both classifications. For the specific case of categorical variables, not all levels entered the model (Table 3). Discriminant function coefficients indicated that variables related to geomorphological characteristics possessed the largest weights (Table 3). Discriminant analysis correctly assigned 97.73% and 93.18% of cases to groups with presence-absence and cover data, respectively. Territories (i.e., portions of the discriminant space "belonging" to each proposed group) of vegetation types were estimated by Thiessen polygons, drawing perpendicular lines to the

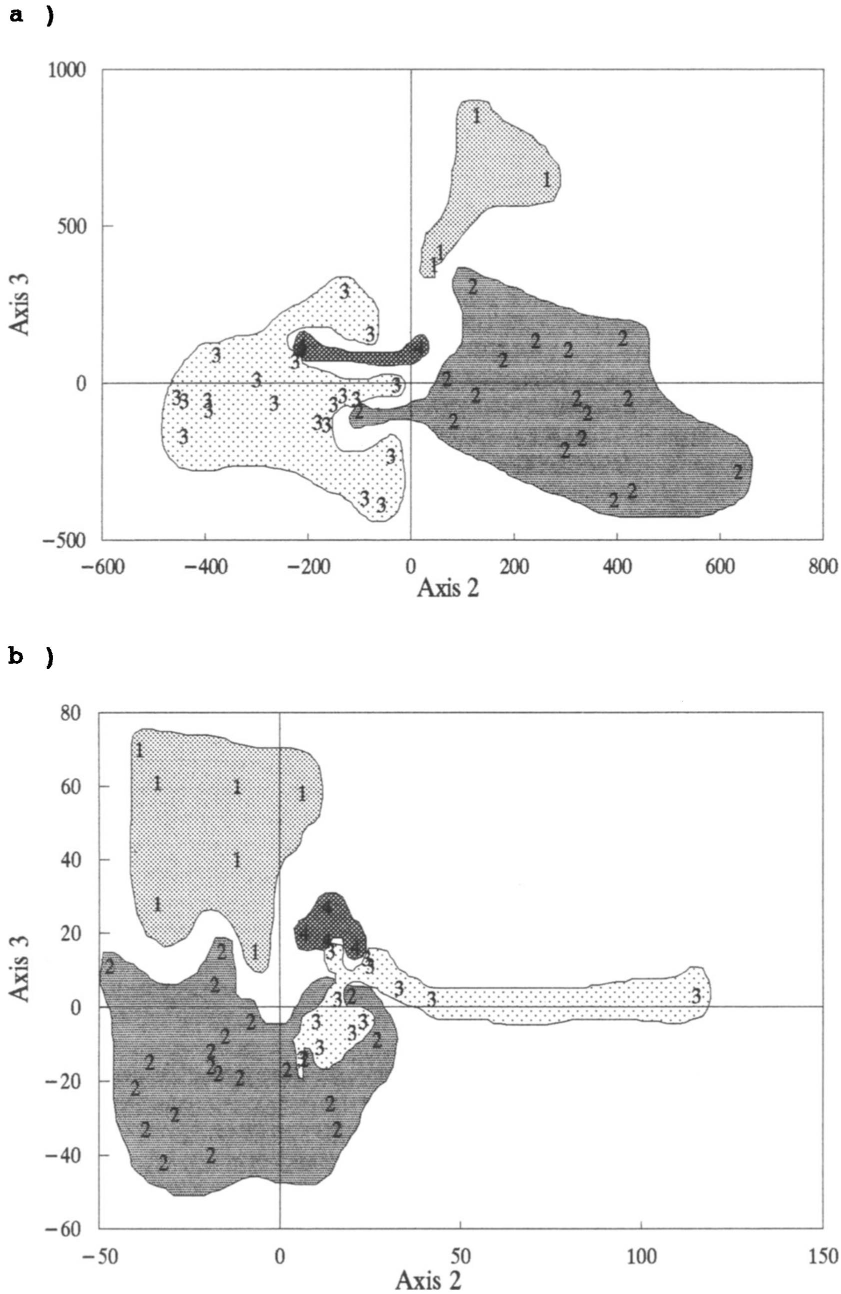


FIG. 2—Principal components ordination of 44 vegetation samples using (a) presence-absence data, and (b) cover data. Labels outlined by shaded and smoothed polygons indicate sample membership to groups defined by TWINSPAN classification: (1) crassicaulous scrub, (2) rosetophyllous scrub, (3) microphyllous scrub, and (4) mesquital.

TABLE 3—Discriminant functions coefficients for significant environmental variables used to classify Chihuahuan Desert vegetation into crassicaulous, rosetophyllous, microphyllous or mesquital types. See Table 1 for variables names.

Data type	Discriminant function		
	1	2	3
Presence-absence			
LF1	0.86282810	3.03152100	−0.28721670
LF5	3.03551700	−0.32772260	1.42530100
LF6	8.69628800	0.74092430	2.51350100
LF7	−2.01892900	−0.82931240	0.80386190
MR1	1.31511000	−1.46369100	−3.07312700
MR3	1.40907800	0.02239525	−1.24332800
MR5	−4.03492900	−5.01674600	2.37337600
RO1	−0.55903630	3.21294500	0.03698585
RO3	1.59959700	3.52727500	−1.84908900
RO4	−2.18601900	−1.26211000	1.16017100
ST1	0.65612240	0.58756810	2.96516400
ST3	0.95785050	1.02342900	−0.76896510
ST5	2.41820900	−0.62739470	−0.31824460
SO1	0.38779830	1.60043300	0.34379120
SO2	−0.66535760	0.99862320	2.39759300
GS	−0.06560739	−0.00076015	0.02107014
PR	0.03743031	0.02750683	−0.01132112
SN	0.15064850	−0.08325622	0.05096553
Constant	−4.39888600	−0.83765140	−1.10319100
Cover data			
LF1	3.15039500	4.36414700	−1.62072300
LF2	2.87819100	3.67328000	1.23124300
LF3	0.63836490	1.54053300	−0.57494210
MR3	−0.05858938	1.41107000	0.65933070
MR1	−0.23778800	1.43169300	−1.31363600
LF6	0.17361420	4.20343600	4.86664100
LF5	−0.49671870	0.57591410	1.50705100
RO1	2.43002900	−0.09993343	0.77943700
RO4	−1.77488800	−3.04825300	−1.03713700
RO5	−2.01188400	−2.76422600	−0.65198550
ST1	3.58259200	−4.11507100	2.92414500
GS	−0.04371385	−0.05166313	0.02345817
PR	0.03960626	0.11753900	0.11175520
SN	0.00282137	0.13090130	0.03030411
CONSTANT	−0.95173450	−4.33727300	−2.84357400

mean distance between two adjacent centroids in the space defined by the first two discriminant functions (Fig. 3).

DISCUSSION—Subjective field definition of vegetation types was supported by TWINSPAN classification. Similar vegetation types were recognized by MacMahon (1979 in Schmidt, 1989) and Rzedowski (1981). A floristic dominance gradient was identified. This gradient extends from succulent species (mainly cacti of the *Opuntia* genus) through crassi-rosetophyllous species (mainly *Agave*), to microphyllous shrubs and scrub dominated by mesquite, *Prosopis glandulosa*.

Ordination analysis followed by stepwise regression and discriminant analysis suggested that environmental factors related to geomorphology, for presence-absence data, and species richness were the most important factors related to the distribution of vegetation types. Land form type (LF) was an important factor in our results. In regression analysis this variable was significant ($P < 0.05$) for seven out of eight ordination axes

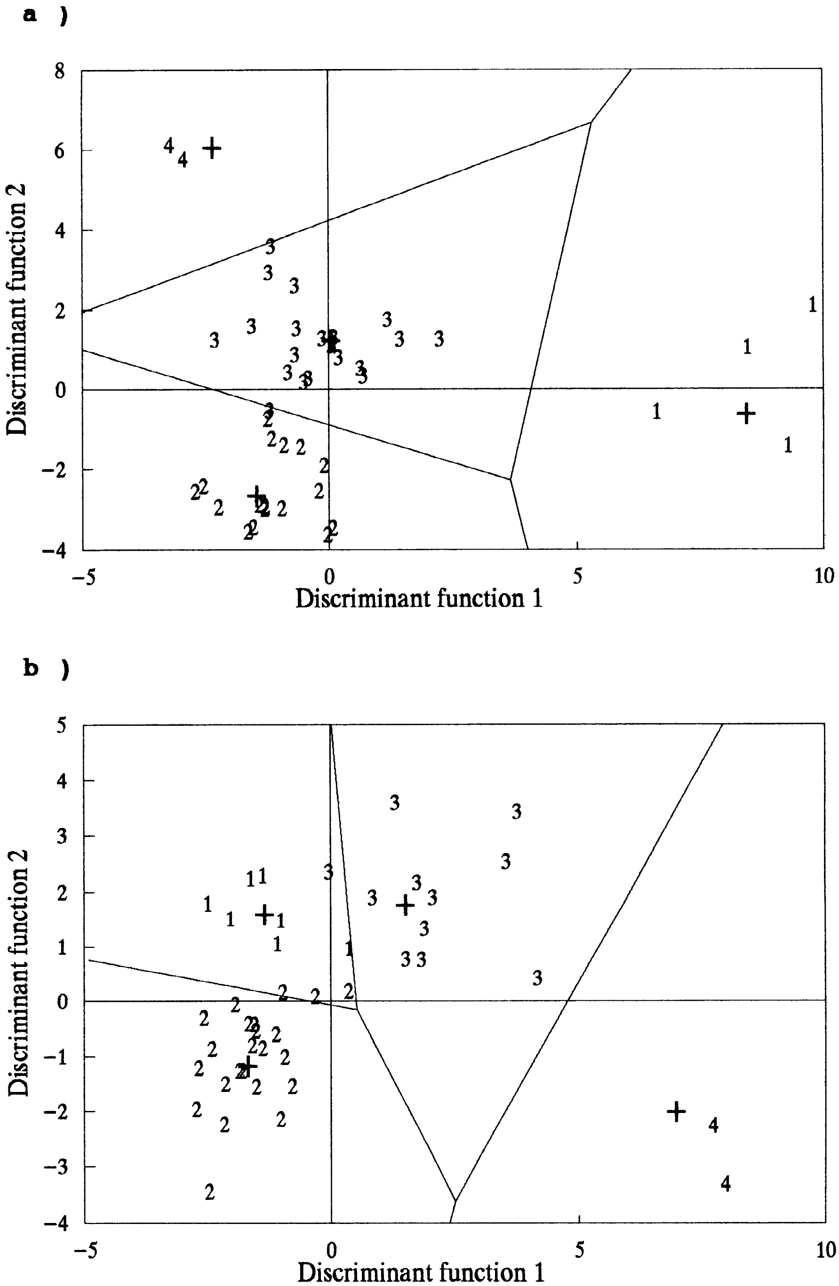


FIG. 3—Bidimensional arrangement and territories of four vegetation types defined by (a) presence-absence data, and (b) cover data in a space defined by the first two functions of a multiple discriminant analysis. Labels indicate sample membership to groups defined by TWINSPAN classification: (1) crassicaulous scrub, (2) rosetophyllous scrub, (3) microphyllous scrub, and (4) mezquital; + indicates the centroid of the corresponding group.

with high r values (from 0.44 to 0.66). Furthermore, species richness increased from $\overline{X} = 16$ species/plot in alluvial plains (LF1) to $\overline{X} = 23$ species/plot in high sierras of calcareous origin (LF 7). Land form type had the greatest number of levels and the highest discriminant coefficients in the discriminant functions. This is because land form type represents an indirect environmental gradient along which temperature, exposure (Noy Meir, 1973; Ward et al., 1993), soil, and geologic substrate change. This is supported by similar results obtained for other desert regions in relation with geologic substrate (Ward et al., 1993) and for the Mapimi region in the Chihuahuan Desert (Montaña, 1988, 1990; Montaña and Greig-Smith, 1990).

Despite the importance of land form, other variables were also relevant. Variation in soil microrelief (MR), rocky outcrops (RO), stoniness (ST), percent soil surface covered by gravel and stones (GS), and percent of soil surface covered by rocks (PR) may influence the establishment pattern of species favoring heterogeneity of soil moisture distribution (Ayyad, 1981; Noy Meir, 1973; Olsvig-Whittaker et al., 1983; Wondzell et al., 1990; Ward et al., 1993) and solar radiation incidence. Establishment of plant communities is also affected by parent material from which soil is originated (SO). Mesquitales are found in low-stony alluvial soils in plains. Rosetophyllous scrub is found in high-stony sedimentary calcareous soils with many rocky outcrops on low sierras and hills. Crassicaulous scrub occupies igneous plateaus, low sierras, and complex sierras with stony soils. Microphyllous scrub is common on low slopes and plains with few stones and deep alluvial soils.

Vegetation types were clearly segregated by three discriminant functions using both presence-absence data as well as cover data. Nevertheless, floristic and environmental interpretations differed. The first function using cover data discriminated vegetation types more efficiently than the first discriminant function using presence-absence data. This is because there were some common species between mesquital, rosetophyllous, and microphyllous scrub that differed markedly in their cover and abundance values. In contrast, because crassicaulous scrub was composed of a small group of characteristic species, information about their presence was more important than their quantity because abundance of most of the noncharacteristic species would make crassicaulous scrub very similar to both rosetophyllous and microphyllous scrub. In the case of second discriminant function the situation was reversed: the second function based on presence-absence data discriminated between groups more efficiently than the second cover-based function.

Additionally, the relative importance of environmental factors was different in discriminant analyses based on presence-absence data and cover data. The first discriminant function of presence-absence data discriminated crassicaulous scrub because factors with highest weight were complex sierras (LF6), low sierras (LF5), excessively stony (ST5), and stony (ST3). The second discriminant function separated efficiently rosetophyllous and microphyllous scrub and mesquital. In this function high weights of no rocky outcrops (RO1) and plains (LF1), characteristics of mesquital and microphyllous scrub, and moderate rocky out-crops (RO3) and residual soils (SO1), characteristics of rosetophyllous scrub, were important.

Segregation of mesquital from the other vegetation types in the first cover discriminant function was caused mainly by the higher weight of no or very few stony (ST1), plains (LF1), valleys (LF2), and no rocky out-crops (RO1). The other three vegetation types were more similar because the coefficients for higher levels of categorical variables for land form type (LF3 to LF7), microrelief (MR2 to MR6), rocky out-crops (RO2 to RO5), stoniness (ST2 to ST5) and the continuous variables percentage of soil surface covered with gravel and stones (GS) and with rocks (PR) were rather low. The second cover function discriminated better between rosetophyllous, crassicaulous, and microphyllous scrub because of the relatively high importance of LF6, LF3, and MR3.

CONCLUSIONS—The multivariate approaches used in this paper produced a fairly interpretable scheme of a complex data base from Saladan subdivision vegetation in the Chihuahuan Desert.

As expected in this subdivision of Chihuahuan Desert, floristic variation was significantly correlated to geomorphologic features, particularly land form type (LF). These results agree with other studies in arid ecosystems (Ayyad, 1981; Ezcurra et al., 1987; Montaña, 1988; Cornelius et al., 1991; McAuliffe, 1994). As a matter of fact, increase in species richness from alluvial plains to high sierras of calcareous origin is probably due to a proportional increase in landscape heterogeneity. As a consequence, crassicaulous, rosetophyllous, and microphyllous scrubs are richer than mesquital (Valverde, 1994).

Both presence-absence and cover data proved to be efficient in discriminating the four vegetation types. They provided complementary information about vegetation-environment relationships (Green, 1979 in Zavala-Hurtado, 1986).

Presence-absence data are more efficient to describe vegetation in sites with high beta-diversity (Montaña and Ezcurra, 1982). On the other hand, in sites with relatively low interplot floristic heterogenity (low beta-diversity), cover data would be more efficient (Montaña and Ezcurra, 1982, 1991).

Territory maps illustrate limits and domain of vegetation types in space defined by relevant environmental variables. This has practical applications in identifying vegetation types from cartographical information of the environmental variables identified here.

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