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The desert vegetation of El Pinacate, Sonora, Mexico

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Abstract

The Pinacate region is part of the Gran Desierto, one of the driest deserts in North America. The presence-absence of perennial plant species, together with soil and landform characteristics, were registered in 110 sampling sites within this region. A classification and ordination of plant communities showed soil and landform units to be good predictors of plant variation. Plant distribution and species richness were also strongly related to altitude and rockiness. A Generalised Linear Model was used to fit the response curves of individual species.

The environmental factors related with plant distribution are indicators of the water regime within a given site. Plant communities repeat along topographic gradients the large-scale biogeographic variation of the Sonoran Desert. Microphyllous shrubs colonise the drier bajada slopes, while more diverse communities, dominated by cacti and drought-deciduous trees, grow on the wetter pediments and in pockets within rocky soils.

Introduction

The Pinacate region is part of the Gran Desierto in northwestern Sonora, Mexico, one of the driest and most extreme deserts in North America. The area has been subject of scientific attention for its interesting natural features, including its volcanic geology (Gutmann, 1976; Lynch, 1982), vegetation (Felger, 1980), archaeology (Hayden, 1967, 1969, 1976, 1982), and the great diversity of its natural resources (Ives, 1964; May, 1973). In addition to its extreme aridity (average annual rainfall within the area ranges from 120 to less than 50 mm; Ezcurra & Rodrigues, 1986) the area presents two aspects which set it apart from the rest of the Sonoran Desert in Mexico: (a) it has more than 5000 km² of active sand dunes, and (b) it includes the volcanic shield of El Pinacate, which has an extent of over 2000 km². The inland dunes originated from sediments blown eastwards from the delta of the Colorado River (Merriam, 1969; McKee & Breed, 1976), over a period in excess of 10000 years (Felger, 1980). The system is formed mainly by crescentic, barchan and stellar dunes of considerable height (more than 100 m in some parts). In addition, sand of marine origin, composed chiefly by shell fragments, forms a narrow band of longitudinal dunes near the coast (Ives, 1959).

The Pinacate shield was formed during the Quaternary in a series of eruptions dating from the

Pleistocene to the late Holocene. Because of its remarkable landscape, the geology of the Pinacate has been well studied (Arvidson & Mutch, 1974; Bull, 1974; Cortés *et al.*, 1976; Gutmann, 1976; Lynch, 1982). A few pre-Tertiary sierras occur near the shield, formed of intrusive and metamorphic rocks (Merriam, 1972), chiefly Paleozoic gneiss and Cretaceous granite. Tertiary rocks in the area are all of extrusive origin, mostly basalt and tuffs.

In a previous paper (Ezcurra & Rodrigues, 1986) an attempt was made to analyse how large-scale environmental variation (induced by rainfall patterns changing at a geographic scale) may affect the distribution of phytogeographic regions in the whole of the Gran Desierto. The present paper deals with vegetation change at a smaller scale. Its primary purpose is to generate and test statistical hypotheses on the relation between floristic variation and environmental factors.

Methods

Sampling procedure

The study area occupies the central part of the Gran Desierto. It extends from the coast of the Adair Bay in the Gulf of California, to the Mexico-USA border in the north. Its southern limit is the Gulf coast and the 31°30′N parallel. Its western and eastern limits are at 114°00′ and 113°00′W respectively.

One hundred and ten 0.25 ha sites were sampled. Sites along river banks were 20 m wide and 125 m long, while all other sites were square (50 m × 50 m). Sites were located along two main axes of environmental variation following gradient directed transects or "gradsects" (Gillison & Brewer, 1985). The first gradsect ran from the coast of the Adair Bay to the Pinacate volcanic shield, the second from the Pinacate peak to the valley of the Sonoyta River. Additional sites were located in different parts of the area, in some cases to duplicate the gradsect sites and in some other cases to sample sites which looked physiognomically or environmentally different from the ones sampled along the main gradsects.

The presence of every plant species was registered for each site and five environmental variables (altitude, landform, soil unit, surface rockiness and rockiness class) were recorded. Soil samples were taken for laboratory analysis, where electrical conductivity, bulk rockiness (% of particles larger than 2 mm), and percentage sand and clay were determined for each sample. In sites 1 to 50 the abundance of perennials was estimated by line intercept sampling. Within those sites, three 50 m lines were placed randomly in an E-W direction, and three other lines in a N-S direction.

Surface rockiness was estimated visually as the proportion of the soil surface covered by rocks, stones or gravel larger than 1 cm in diameter. Rockiness class complemented this information with four possible categories (0 – no surface rocks; 1 – rocks <2 cm; 2 – rocks >2 and <10 cm; and 3 – rocks >10 cm). Altitude was measured with an altimeter and checked later on the topographic map for possible errors.

Soils were classified following the FAO-UNESCO (1974; see also FitzPatrick, 1980) soil classification system. Six units were recognised: (1) Fluvisols, (2) Lithosols, (3) Regosols, (4) Solonchaks, (5) Vertisols, and (6) Yermosols. The landforms in the area were classified following Bloom (1978), and ten individual landforms within four categories were recognised. Constructional landforms include three units: (1) *Rock outcrops*, (2) *Pavements*, and (3) *Lapilli deposits* (volcanic gravel). Climatic, or arid zone, landforms include four units forming the typical topographic gradient of deserts: (1) *Pediments*, (2) *Bajadas*, (3) *Playas*, and (4) *Sand dunes*. Erosional landforms comprise only one unit, *River beds and banks*, which includes the Sonoyta River and other minor channels, all of them dry most of the time. Coastal landforms include two units: (1) *Saltflats*, of marine and evaporative origin, and (2) *Shell conglomerates* that occur at localised points near the coast.

Because of the patchiness of rainstorms in both time and space, ephemerals showed a pronounced variation in their presence within the area, and were omitted from the floristic analysis (ephemerals were absent from many sites solely because of lack of local rains).

Classification

A first evaluation of the distribution of plant communities in relation to environmental factors was obtained from a divisive classificatory procedure (information analysis, Lance & Williams, 1968), using the information statistic of order 2 (Ezcurra & Equihua, 1984; see also Rényi, 1961 and Hill, 1973).

$$I_2 = 2\, s\, n \log n - n \sum_i^S \log (a_i^2 + (n - a_i^2))(1)$$

where *s* is the number of species in the data matrix, *n* is the number of sites, and a_i is the number of sites in which species *i* was present.

The classification procedure consists of searching for the species which divides the original data matrix (**T**) into two submatrices (**H**, where the species is always present, and **G**, where the species is always absent), such that the information change

$\Delta I = I_2(\text{T}) - I_2(\text{G}) - I_2(\text{H})$ is maximum in relation to all other species. Once the original data matrix is divided into two groups, the more heterogeneous of the two is divided according to the presence and the absence of a new indicator species, forming three groups. The procedure is continued, dividing the most heterogeneous group at each stage, until the desired number of groups is reached.

Ordination

A floristic ordination of the data was achieved by a form of non-centred, non-standardised Principal Components Analysis (NPCA, Noy-Meir, 1973; Noy-Meir *et al.*, 1975). In our program species scores are presented and plotted in the same scale as site scores (mathematical details of the procedure can be found in Ezcurra, 1984, 1987). The greatest virtue of this method is that it produces a corresponding and simultaneous ordination of both sites and species, as the analysis makes no difference between loadings for attributes and positions for individuals, the scores for both rows and columns being defined in the same scale.

The scores for the first axis in this ordination method will be all positive (or zero in some cases), as this component extracts the dispersion of the data cluster with respect to the origin. Noy-Meir (1973) has shown that, if there are disjunctions or near-disjunctions in the data set (i.e. if there are two or more distinct and separate submatrices), more than one asymmetric axis will appear. Thus, the ordination can serve to detect disjunct clusters in the data, which form independent floristic sets. For this purpose, the asymmetry (α) of each axis was calculated using the formula proposed by Noy-Meir (1973).

The relationship between the ordination axes and environmental variables was analysed both by direct visual examination of the data plots and through an additive stepwise linear regression procedure. Quadratic terms (allowing for non-linearity) were also tried in the regression function and were incorporated to the model if the fit was improved. Discrete variables or factors (i.e. landforms, soil units and rockiness class) were included, by decomposing them into binary dummy variables. The stepwise procedure was continued while the addition of new variables to the polynomial model decreased the probability (P) of the variance ratio (F) test.

Direct gradient analysis

Once the environmental variables responsible for most of the vegetation variation are identified, it is adequate to describe the distribution of the main plant species as a function of these variables. Generalised Linear Models (GLM) have been shown to be useful for this purpose (Austin & Cunningham, 1981; Austin *et al.*, 1983, 1984). Described originally by Nelder & Wedderburn (1972, see also McCullagh & Nelder, 1983), GLM's are a general class of linear models which can be fitted by maximum likelihood procedures, and explain the variation of an observed dependent variable as a combination of a systematic component (the linear model) and a random component (the error function).

Independent variables can be quantitative, or qualitative (i.e. statistical factors). Both components (linear and random) are linked together by a link function, which has to be defined from a set of possible links. The deviance of a fitted model measures the discrepancy between the data and the fitted values. The change in deviance when a new term is fitted is a measure of the adequacy of that term. For binomial and Poisson data it will be approximately distributed as Chi-square and can be used to test the validity of the new term. For our particular case (species presence-absence data), the error functional was declared to be binomial, and the link function used was a logit transformation.

Results

Classification

The classification was continued until nine groups were obtained. Below this level, subsequent divisions hardly decreased the total heterogeneity in the data matrix, i.e. the information change was small. The corresponding dendrogram is presented in Fig. 1, where the discriminant species are shown. A contingency-table analysis (G-test, Sokal & Rohlf, 1969) showed that the floristic groups are significantly associated ($P < 0.001$) with both landforms and soil units. The discriminant species chosen by the algorithm are all reliable indicators of specific habitats (the floristic list and the original data are given in Ezcurra, 1984). The first division, marked by the presence of *Fouquieria splendens,* clearly separates rocky environments, where *Fouquieria* is
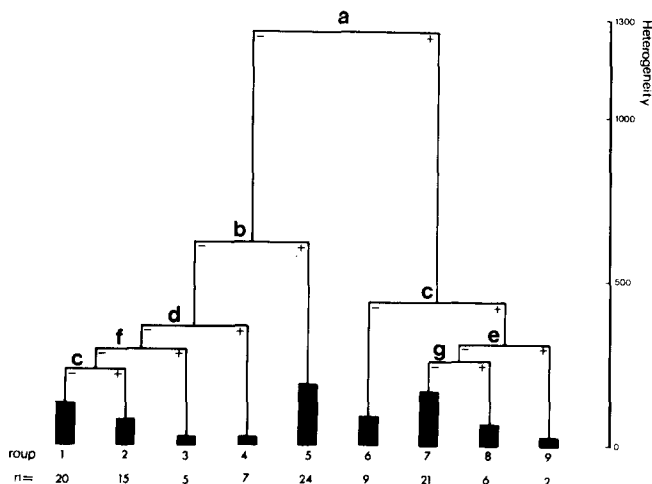
Fig. 1. Dendrogram corresponding to the Information Analysis divisive classification procedure. The presence (+) or absence (−) of the indicator species are shown in each branch. The bars indicate the residual heterogeneity for each group. a. *Fouquieria splendens,* b. *Ambrosia dumosa,* c. *Larrea tridentata,* d. *Salicornia pacifica,* e. *Hyptis emoryi,* f. *Baccharis sarothroides.* g. *Mammilaria microcarpa.*

the most constant species, from non-rocky substrates, where *Fouquieria* does not grow. This division reduces the heterogeneity of the data matrix by 17%, showing the marked difference between the vegetation of rocky and non-rocky areas. A description of the more significant environmental and vegetational characteristics of the floristic groups can be obtained from this analysis:

Group 1

(No characteristic species) This group is mostly associated with Regosols and dunes. Dune communities are species-poor and extremely heterogeneous, showing little similarity among themselves. Moving barchan dunes are colonised by *Helianthus niveus, Pethalonix thurberi, Croton wigginsii, Psorothamnus emoryi* and *Eriogonum deserticola;* partially fixed dunes are colonised by *Ephedra trifurca, Tiquilia plicata* and *Hilaria rigida* (three species with prostrate or stoloniferous growth), while dunes with a fresh-water aquifer near the surface show abundant growth of *Cercidium floridum* and of a multi-stemmed phreatophytic form of *Prosopis glandulosa.* Coastal dunes exposed to salt-spray from the sea are usually covered by the halophytic *Frankenia palmeri, Atriplex polycarpa* and *A. canescens,* while further inland other dunes of coastal origin will show *Haplopappus acradenius* and *Wislizenia refracta* as

the dominant species. Dune vegetation is very variable in its cover values, ranging from 0.1% in moving barchan dunes to 12% in fixed inland dunes.

Group 2

This vegetation type is defined by the presence of *Larrea tridentata* and the absence of all other characteristic species. It is mostly associated with Regosols on sandy bajadas and old fixed dunes, and is formed by monospecific *Larrea* stands. It is the most species-poor floristic group in the area, and shows an average cover of 8%.

Group 3

Baccharis sarothroides, a riparian composite is the characteristic species in this group. These sites are found in playas or along the Sonoyta River, at the bottom of the valley, and are subject to seasonal flooding. Typical species in these habitats are *Prosopis glandulosa, Cercidium floridum, Lycium* spp., *Atriplex polycarpa* and *Baccharis salicifolia* on the banks, while *Psorothamnus spinosa, Croton californicus* and *Pethalonix thurberii* dominate on the gravelly river-beds. *Hymenoclea salsola* and the characteristic species, *Baccharis sarothroides,* are common on both habitats. Playas show poorer stands with *Prosopis* and *Baccharis.* On the more saline banks *Prosopis glandulosa* is replaced by the salt tolerant "tornillo" (*Prosopis pubescens*). The vegetational cover of riparian sites was found to be maximal on river banks (50%) dominated by *Prosopis glandulosa.* The gravelly river beds, where *Prosopis* does not grow, showed a lower mean cover (11%) and a more even distribution of abundances. The clayey playas were also dominated by *Prosopis,* but showed relatively low cover values (11%) compared to river-bank sites.

Group 4

The characteristic species of this group is *Salicornia pacifica,* an obligate halophyte growing on the coast of the Adair Bay. The group is associated with Solonchaks in coastal saltflats, and represents the halophytic coastal vegetation. Other typical species in this area include *Batis maritima,* various chenopods (*Nitrophila occidentalis, Sarcobatus vermiculatus, Allenrolfea occidentalis, Atriplex* spp., and *Suaeda* spp.), and four grasses (*Distichlis palmeri, D. stricta, Monantochloe littoralis,* and *Sporobolus airoides*).

Coastal halophytes which are subject to periodic flooding by seawater presented the highest cover values in the whole area (62%). The abundance of halophytes decreases rapidly with distance to the coast. The *Distichlis* and *Monanthocloe* saline grassland communities found further inland showed a cover of 16%. At the highest end of the saltflats there was usually no vegetation except for some isolated patches with *Nitrophila* and *Sarcobatus.*

Group 5

This group is characterised by the presence of *Ambrosia dumosa* and the absence of *Fouquieria*. This association, typical of the Lower Colorado Valley Subdivision of the Sonoran Desert, represents the typical *Larrea-Ambrosia* microphyllous scrub of lower bajadas and sandy plains. It is found mostly on deep sandy or loamy soils (Regosols and Yermosols) and showed an average total cover of 9%.

Group 6

Characterised by the presence of *Fouquieria splendens* and the absence of *Larrea*, this floristic group is associated to deep lapilli deposits, where *Larrea* does not grow. The lapilli associations of the Pinacate peak (ca 1000 m above sea level) are dominated by *Encelia farinosa, Fouquieria splendens,* and *Opuntia bigelovii, Eriogonum fasciculatum* and *Justicia californica* are also common on these sites. The lower altitude lapilli deposits near the Elegante Crater (ca 250 m above sea level) are colonised by a more diverse community, with *Fouquieria splendens, Carnegia gigantea, Olneya tesota, Opuntia bigelovii, Cercidium microphyllum, Cereus schottii* and *Hymenoclea salsola*. The high altitude lapilli sites had a relatively high total cover (22%), possibly due to a more favourable water balance, and were dominated by the abundant growth of *Encelia farinosa*. The low altitude lapilli sites had a relatively low cover (9%), but showed a higher diversity.

Groups 7 and 8

Both these groups are characterised by the presence of *Fouquieria splendens* and *Larrea tridentata*, and by the absence of *Hyptis emoryi*. Group 7 lacks *Mammilaria microcarpa*, and is associated to dry rocky pavements and rock outcrops. In addition to the characteristic species, *Jatropha cuneata, Encelia farinosa, Bursera microphylla, Carnegia gigantea, Cercidium microphyllum* and *Ferocactus acanthodes* are common in this vegetation type. Group 8, characterised by *Mammilaria,* corresponds well with protected rocky areas and rocky pediments. These communities are floristically richer than those of group 7 and present a denser cover. In addition to the species in group 7, *Olneya tesota, Krameria grayi, Opuntia fulgida* and *Ambrosia deltoidea* are common in these more humid environments. The fern *Notholaena parryi* is frequently found on the higher sites within this group, growing in the shade of large rocks. Mean cover on dry rocky sites and shallow pavements (group 7) was 10%; while rocky pediments and protected rocky sites (group 8) showed mean cover values of 17% and 27%, respectively.

Group 9

This group, associated with arroyos, contains most of the species present in groups 7 and 8 plus some other species found exclusively along these wetter habitats. *Solanum hindsianum, Hibiscus denudatus, Calliandra eriophylla, Lycium* spp., and the characteristic species *Hyptis emoryi,* are all frequent along these seasonal rocky waterways. Arroyos showed a relatively high cover (22%).

Ordination

Complete data matrix

The whole data matrix (110 sites × 100 species) was subjected to NPCA. The first ten axes were extracted. The ordination showed some sites with zero scores on the first axis, indicating disjunctions in the data set. Two other asymmetric components (axes 3 and 6, $\alpha > 0.75$) were also obtained. All other axes showed symmetric ($\alpha < 0.50$) scores.

Axis 1 ($\alpha = 1.0$) was highly associated with soil units ($p < 0.001$), excluding Solonchaks from coastal saltflats and Vertisols from playas. This axis showed high scores for typical inland desert sites and species. Axis 2 ($\alpha = 0.42$) was associated with landform and % clay ($p < 0.001$) separating rock outcrops with fine soil in one extreme, and bajadas and fixed dunes with loamy and sandy substrates on the other. Axis 3 ($\alpha = 0.78$) was chiefly associated with river beds and banks ($p < 0.001$) and separated the riparian sites along the Sonoyta River which are characterised by the presence of *Prosopis glandulosa, Baccharis sarothroides, B. salicifolia, Hymenoclea salsola, Atriplex polycarpa* and *A. canescens*. These sites correspond well with group 3 of the floristic classification. Axis 4 ($\alpha = 0.18$) was associated with landform ($p < 0.001$), and axis 5 ($\alpha = 0.14$) with soil units ($p < 0.01$). Axis 6 ($\alpha = 0.95$), the third asymmetric component, was associated with saltflats ($p < 0.001$). This axis identifies coastal halophytic vegetation and is similar to group 4 of the floristic classification. Typical species along this axis are *Salicornia pacifica, Distichlis palmeri, Allenrolfea occidentalis, Batis maritima, Frankenia palmeri, Atriplex barclayana, A. pacifica,* and *Suaeda californica*.

The complete data matrix can be divided into three distinct floristic sets: inland desert, riverbank, and coastal halophytic vegetation, identified by axes 1, 3 and 6, respectively. However, because the disjunction between inland desert and riparian sites is only partial, axes 4 and 5 showed a combined gradient with sites belonging to both environments. For this reason, it was decided to perform a second analysis taking only into consideration the 89 typical inland desert sites and species.

Masked data matrix

For this analysis all sites and species that had zero or near-zero scores along axis 1 of the first ordination were eliminated. As expected, only one asymmetric component (axis 1) was extracted. Because this first axis goes from the origin of the coordinates to the centre of the cluster, sites having higher total abundances project further away from the origin than sites with low abundances. In the case of presence absence data, axis 1 will reflect the species-richness of each site, the more diverse sites having higher scores. Axis 2, analysing the residual floristic variation, showed a significant correlation ($r = 0.35$, $p < 0.001$) with axis 1. This indicates that floristic variation (axis 2) and species-richness (axis 1) are associated, and suggests that diversity may vary along similar environmental gradients as plant community composition. The regression analysis singled soil class as the variable most associated to species richness ($r^2 = 0.25$, $p < 0.001$). Plant communities on Lithosols and Fluvisols are significantly more diverse than those on Yermosols, which in turn are richer than Regsol sites. If only continuous environmental variables are considered, diversity is best predicted by surface rockiness ($r^2 = 0.21$, $p < 0.001$). The fitted model (*div.* = $4.4 + 0.042 \cdot$ *% surface rockiness*) predicts, on average, a doubling in species richness when going from non-rocky to rocky habitats (Fig. 2).

Axis 2 (explaining 14.4% of the residual dispersion) was highly associated with landform and elevation ($r^2 = 0.55$, $p < 0.001$). Sites with high scores along axis 2 correspond to dunes and lower bajadas, while sites with low scores along axis 2 are found on rocky landforms at higher elevations. This component extracts the main floristic variation in the area, from rocky communities at higher elevations to sandy, deep-soil communities at lower altitudes. If discrete variables (soil units, landforms, and rockiness class) are excluded from the regression analysis, then surface rockiness becomes the best variable to describe axis 2 ($r^2 = 0.41$, $p < 0.001$). Axis 3 (explaining 8.0% of the dispersion), also showed a significant relation with landform ($r^2 = 0.38$, $p < 0.001$). This relation is mostly due to the high scores of lapilli gravelly sites, which

separate along this axis.

The main topographic sequence in the area (valley bottom and dunes → bajadas → pediments and lower rocky slopes → exposed rocky slopes → high altitude lapilli sites) is recovered by axes 2 and 3, forming a typical arch cluster (Fig. 2). *Prosopis glandulosa*, a typical playa and river bank species, and also a frequent dune phreatophyte, together with *Atriplex canescens*, which grows in similar environments but is more salt-tolerant, occupy one extreme of the floristic gradient. These species are followed by the strict psammophytes *Ephedra trifurca* and *Hilaria rigida*, which are in turn replaced by the microphyllous xerophytes *Larrea tridentata* and *Ambrosia dumosa*, growing in lower bajadas and other typically dry environments. *Ambrosia deltoidea* and *Krameria grayi*, two typical species of pediments and upper bajadas, follow along the gradient, and are subsequently replaced by the typical species of rocky habitats: *Jatropha cuneata*, *Fouquieria splendens*, *Carnegia gigantea*, *Cercidium microphyllum* and *Opuntia bigelovii*. *Encelia farinosa*, the dominant species in the high altitude gravelly soils, occupies the extreme of the gradient.

Direct gradient analysis

The twenty-two most common species in the area (all present in more than five sites) were fitted as a function of the environmental variables by means of a GLM stepwise regression procedure. The predicted values of the model are to be interpreted as the expected probability of finding the species within a site presenting a particular combination of the independent variables. As with floristic ordination axes, soil and landform were generally the best predictors of individual species distribution (Table 1). If only the quantitative variables were taken into account, surface rockiness and altitude emerged as the variables which most frequently gave the best fit to the distribution of individual species.

Based on these results, the final model chosen for direct ordination was based on surface rockiness and altitude, taken as the two main independent variables responsible for vegetation variation
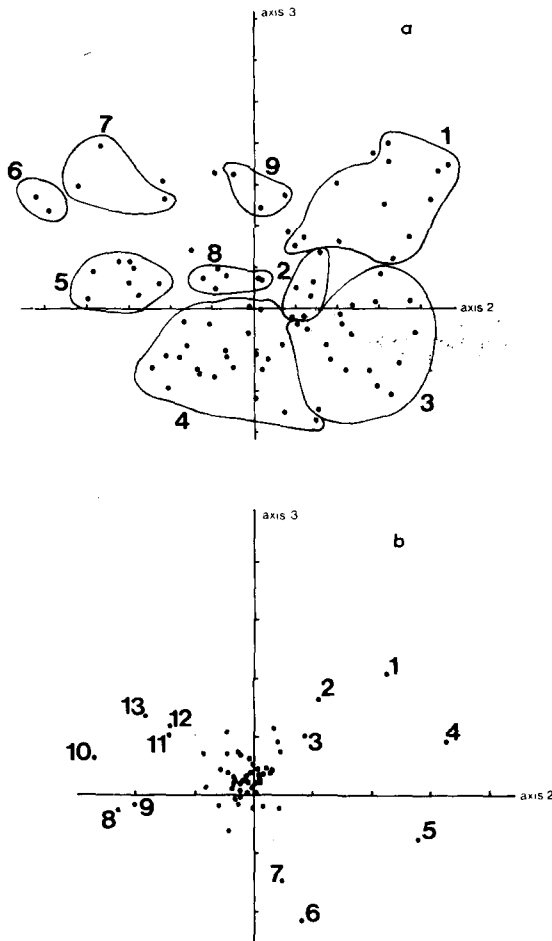
Fig. 2. (a), Principal component analysis for the 89 inland desert sites, axes 2 and 3. The numbers indicate groups of sites belonging to a same landform: 1. dunes, 2. sandy bajadas, 3. bajadas, 4. pediments and protected rocky soils, 5. dry rocky soils, 6. high altitude lapilli sites, 7. low altitude lapilli sites, 8. sandy pediments, 9. riparian sites. (b), Species ordination, axes 2 and 3. The numbers indicate the species with high scores: 1. *Hilaria rigida*, 2. *Atriplex canescens*, 3. *Ephedra trifurca*, 4. *Ambrosia dumosa*, 5. *Larrea tridentata*, 6. *Ambrosia deltoidea*, 7. *Krameria grayi*, 8. *Fouquieria splendens*, 9. *Jatropha cuneata*, 10. *Encelia farinosa*, 11. *Carnegia gigantea*, 12. *Cercidium microphyllum*, 13. *Opuntia bigelovii*.

(linear and quadratic terms were used for both variables, an interaction term rockiness × altitude was also tried but the addition of this term did not improve significantly the fit for any species). The response surface fitted significantly ($p < 0.05$) the distribution of twenty species. The fit was not sig-

Table. 1. Best predictors of species presence, according to the fitted generalised linear model. The degrees of freedom (d.f.) and the fit (r^2 = (total deviance − residual deviance)/total deviance) are indicated for each model. The fit was highly significant ($P < 0.001$) for all species. Numbers in column 2 refer to environmental variables; 1 = altitude; 2 = landform; 3 = soil unit; 4 = surface rockiness; 5 = rockiness class; 6 = clay, or sand*; 7 = conductivity; 8 = bulk rockiness.

species	best model	d.f.	r^2
Ambrosia deltoidea	3 + 2	10	0.42
A. dumosa	3 + 5	7	0.19
	+ 6*		
Encelia farinosa	4	1	0.32
Bursera microphylla	8 + 2	8	0.50
Carnegia gigantea	1 + 3	4	0.29
Ferocactus acanthodes	2 + 3	10	0.54
Opuntia bigelovii	2 + 6	8	0.46
O. fulgida	2 + 1	8	0.58
Atriplex canescens	1 + 2	8	0.54
A. polycarpa	4 + 7	2	0.48
Ephedra trifurca	2 + 3	10	0.49
Jatropha cuneata	4 + 2	8	0.47
Cercidium floridum	2 + 1	12	0.71
	+ 3		
C. microphyllum	3 + 2	10	0.41
Olneya tesota	2 + 3	10	0.43
Prosopis glandulosa	2 + 3	11	0.60
	+ 6		
Fouquieria splendens	4 + 5	4	0.44
Frankenia palmeri	1	1	0.73
Krameria grayi	2 + 3	10	0.50
Hyptis emoryi	5	3	0.33
Hilaria rigida	2 + 4	10	0.47
Larrea tridentata	2 + 7	12	0.61
	+ 1 + 5		

nificant for *Ambrosia dumosa*, *Hymenoclea salsola* and *Olneya tesota*, three species that, on the other hand, do show a significant association with soil and landform. *A. dumosa* has a significant rejection for shallow soils (Lithosols) and a weak but significant preference for deeper soils. *Hymenoclea salsola* has a strong association with deep, gravelly Fluvisols (river beds and banks, and the lower lapilli deposits). *O. tesota* has a significant preference for deep soils with loose rocky substrates (lapilli deposits, pavements, pediments, arroyos and river banks), and does not grow on dunes, lower bajadas or exposed rock outcrops (Lithosols).
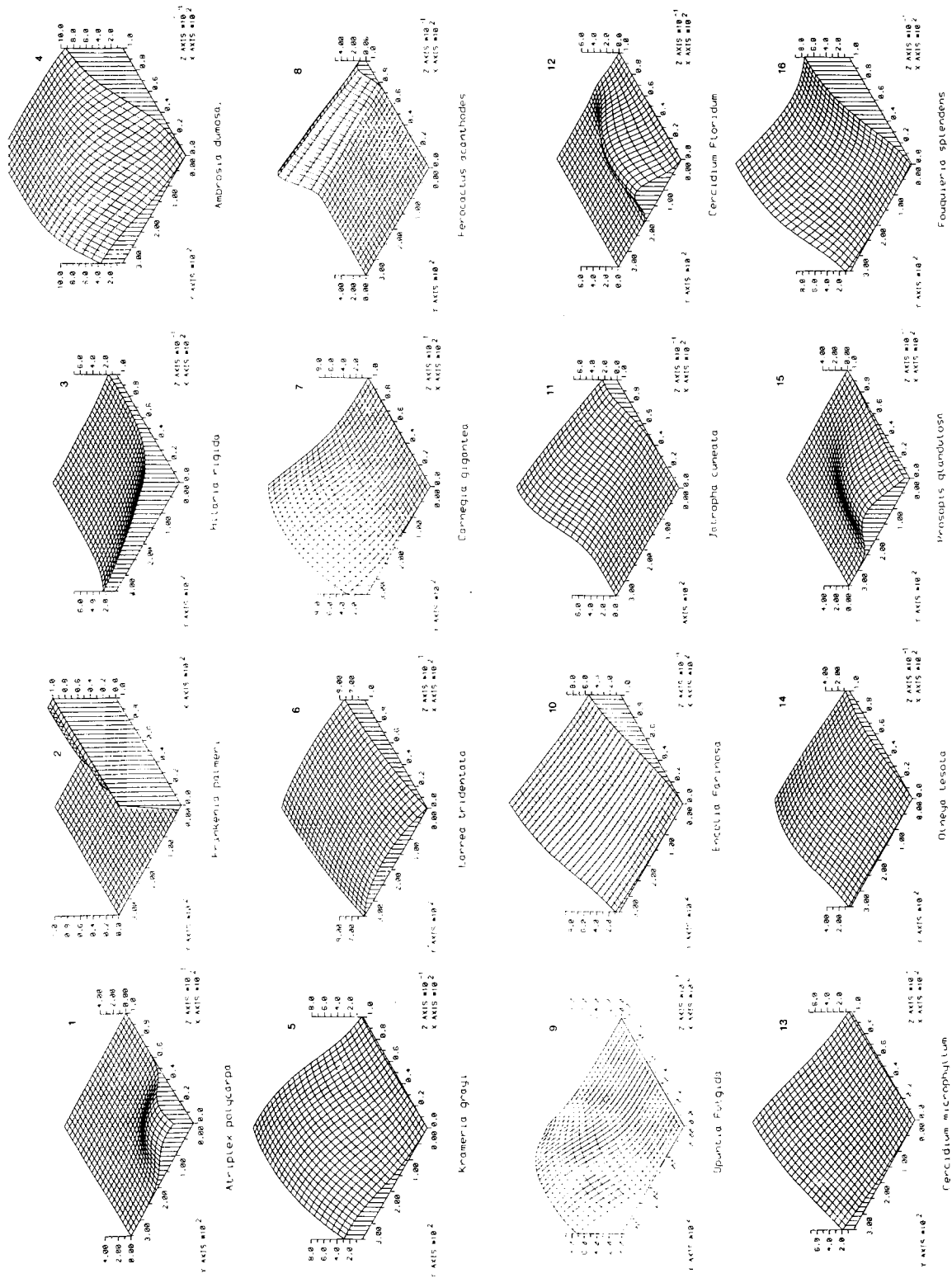
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Fig. 3. Direct gradient analysis showing the response surface (z axis) for 16 desert perennials, as a function of surface rockiness (x axis) and altitude (y axis). Rockiness ranges from 0 to 100% and altitude from 0 to 350 m above sea level. The response values estimate the probability of finding a given species in a site with given altitude and rockiness. The species are ordered according to their life-form and water physiology: 1–2, halophytes; 3, psammophyte; 4–6, microphyllous shrubs (true xerophytes); 7–9, cacti; 10–16, drought-deciduous perennials.

The fitted surfaces can be plotted as a function of the two independent variables (altitude and rockiness), giving a probability response surface for each species. But the data points are not evenly distributed on this two-dimensional space, as the two independent variables are themselves associated. From sea-level to ca 350 m the data points are well dispersed, and there is only a weak positive correlation between rockiness and altitude. But above 350 m surface rockiness always presents high values, and becomes asymptotic with the 100% maximum. Hence, two-dimensional (altitude-rockiness) response surfaces are only valid for elevations below 350 m. Above this height, the GLM prediction is valid only for rocky environments. Fig. 3 shows the response surfaces for 16 species. Within the plotted range, some species respond mainly to altitude (*Frankenia palmeri, Cercidium floridum, Carnegia gigantea, Opuntia fulgida*), while others respond more to rockiness (*Ferocactus acanthodes, Encelia farinosa, Jatropha cuneata*). In general, every response surface is quite unique and shows little resemblance to those of other species. *Cercidium floridum* shows high abundances at around 100 m altitude, where the valley of the Sonoyta River and other areas with shallow water tables are found. A similar distribution is observed for *Prosopis glandulosa* and *Atriplex polycarpa,* two riparian species. *Cercidium microphyllum*, on the other hand, grows more abundantly on rocky foothills.

The main environmental variation for the whole rockiness-altitude space can be summarised along a non-linear, one-dimensional gradient. Rockiness at sea level is generally low, and tends to increase with altitude up to approximately 350 m, where it reaches its maximum (100%). To simulate empirically this main trend, a non-linear equation of the type

$$rockiness = 100 \, (1 - \exp \, (-b \cdot altitude))^a \quad (2)$$

was fitted to the data. The fit was highly significant ($r^2 = 0.57$, $p < 0.001$) with values $a = 1.69$ and $b = 0.007$ for the parameters. Thus, the two variables were reduced to one non-linear combination, and the direct ordination was performed along the composite altitude-rockiness gradient going from

non-rocky sites at sea level to rocky sites at higher elevations.

These direct ordinations, for the twenty-two species analysed, are shown in Fig. 4 where a similar gradient to the one described by the indirect ordination procedure can be seen. The extreme of the gradient is occupied by *Frankenia palmeri* and *Atriplex polycarpa,* two halophytes which grow on coastal dunes. These species are followed by *Ephedra trifurca* and *Hilaria rigida* on the non-saline inland dunes. The dune species are followed along the gradient by the typical valley-bottom species *Atriplex canescens, Prosopis glandulosa* and *Cercidium floridum,* all three occurring along the Sonoyta River, and the last two species also occurring on dunes with a fresh-water aquifer near the surface. From 100 m upwards, the typical inland. desert gradient occurs. The microphyllous species *Larrea tridentata* and *Ambrosia dumosa* are the only species with high probability of occurrence in the lower bajada sites. As the sites get higher and rockier, the upper bajada species *Ambrosia deltoidea, Krameria grayi* and *Olneya tesota* become more frequent. This community is gradually replaced by the rocky site association with *Fouquieria splendens, Encelia farinosa, Jatropha cuneata, Carnegia gigantea, Cercidium microphyllum, Bursera microphylla, Ferocactus acanthodes* and *Opuntia fulgida*. At higher altitudes the species composition becomes poorer, and the typical volcanic ash (lapilli) community appears.

Discussion

Plant variation within the Pinacate inland desert is strongly related to variations in the physical substrate. Some vegetation types occur in distinct sites with no intermediate or transitional samples represented in the data set. These sites are associated with distinct environments of discrete occurrence, and there is no gradual replacement of species leading to them. Disjunct associations are found in coastal saltflats, moving dunes, and in valley-bottom communities (river beds, banks and playas). The rest of the sites (inland desert samples) vary in a continuous way and show no disjunctions
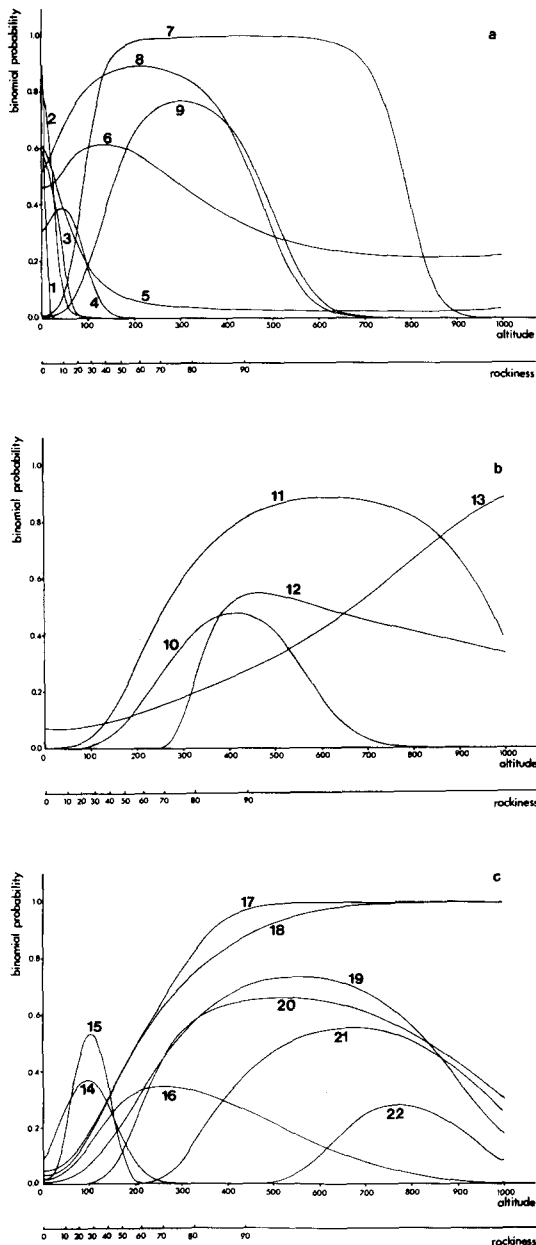
Fig. 4. Direct gradient analysis showing the response function of 22 desert perennials along a composite altitude-rockiness gradient: (a) halophytes, psammophytes and microphyllous shrubs, (b) cacti, (c) drought-deciduous perennials. The species are indicated by numbers: 1. *Frankenia palmeri,* 2. *Atriplex canescens,* 3. *Ephedra trifurca,* 4. *Atriplex polycarpa,* 5. *Hilaria rigida,* 6. *Ambrosia dumosa,* 7. *Ambrosia deltoidea,* 8. *Larrea tridentata,* 9. *Krameria grayi,* 10. *Opuntia fulgida,* 11. *Carnegia gigantea,* 12. *Ferocactus acanthodes,* 13. *Opuntia bigelovii,* 14. *Prosopis glandulosa,* 15. *Cercidium floridum,* 16. *Olneya tesota,* 17. *Fouquieria splendens,* 18. *Encelia farinosa,* 19. *Cercidium microphyllum,* 20. *Jatropha cuneata,* 21. *Bursera microphylla,* 22. *Hyptis emoryi.*

within the data set.

Within the inland sites, two discrete variables (soil and landform) proved to be the best predictors of plant distribution. If the analysis was restricted to continuous variables, then soil rockiness and altitude emerged as the best predictors of plant variation. In a desert, all these variables are associated with the water regime of a site. This points to differences in available soil moisture as the main cause of plant distribution. In general, rocky substrates are more heterogeneous and patchy than non-rocky ones. Rocky areas produce runoff that partially concentrates in soil pockets within a given site, while the excess flows towards rocky pediments. Thus, both micro and macrotopography contribute towards higher water availability in rocky soils and determine more favourable water conditions on higher rocky soils than lower loamy bajadas, which receive very little runoff. More favourable water conditions on higher, rocky soils than on lower, loamy bajadas have also been demonstrated by Yang & Lowe (1956) for a topographic gradient in the Sonoran Desert. Likewise, Olsvig-Whittaker *et al.* (1983) have shown that in the Negev Desert rockiness is related to available water.

The rockiness-altitude gradient repeats at a smaller scale the east-west climatic and phytogeographic gradient of the Sonoran Desert (Ezcurra & Rodrigues, 1986). This gradient becomes obvious when going from sandy non-rocky alluvial sites at sea level to rocky sites at higher elevations. The drier bajadas are dominated by xeromorphic microphyllous shrubs, while pediments and rocky soils support a richer flora with abundance of succulents and drought-deciduous species. Rocky-soil communities are floristically and structurally related to the Arizona Uplands Subdivision of the Sonoran Desert (Shreve & Wiggins 1964). Bajada communities, on the other hand, are dominated by xerophytic microphyllous shrubs (mostly *Larrea tridentata* and *Ambrosia dumosa*), and are floristically and structurally related to the Lower Colorado Valley Subdivision, the driest part of the Sonoran Desert.

The relation between rockiness and species richness has been previously reported for both the Sonoran Desert and the Monte region in Argentina

(Barbour & Diaz, 1973). Higher rocky soils, although frequently presenting low total covers, will allow a more diverse flora to grow, including more mesic species such as *Hyptis emoryi*. Drought-deciduous and succulent plant species are more frequent in rocky habitats, while the true xerophytes *Larrea tridentata* and *Ambrosia dumosa* dominate in bajadas and other extremely dry environments. These two species showed a poor response to direct gradient analysis, as they will also occur in many rocky habitats. Their presence in dry bajadas does not indicate a "preference" for these habitats, but rather a capacity to survive drought better than other desert species.

Rockiness can have an additional effect on community structure, by providing protection and refuge for seeds, and increasing the change of establishment of some species. Very little is known on the impact of seed predation on the structure of perennial desert communities, as most of the existing work has concentrated on annuals (Brown *et al.*, 1979; Davidson *et al.*, 1980). There is, though, much evidence that granivory can have a strong effect on the structure of these communities (Yeaton, 1978; Inouye *et al.*, 1980; Fonteyn & Mahall, 1981).

Although there is little information on the subject, some studies indicate that vegetation change in deserts can be relatively quick. Hastings & Turner (1972) and Martin & Turner (1977) have shown that substantial physiognomical changes in this part of the Sonoran Desert can be observed in a decade, and suggest that rainfall cycles might be partly responsible for this variation. A similar pattern has been reported by Ives (1955), specifically for the Pinacate region. Therefore, the direct gradient analyses presented in Figs. 6 and 7 are to be interpreted as instantaneous pictures of the species oscillating responses, which can vary considerably over long periods of time.

Acknowledgements

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