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Functional morphology of a sarcocaulescent desert scrub in the bay of La Paz, Baja California Sur, Mexico [☆]

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Abstract

A functional morphology study of a sarcocaulescent scrub in the Baja California peninsula was performed with the goal of identifying plant functional types. We sampled 11 quadrats in three distinct physiographic units within the sarcocaulescent scrub ecoregion: the open scrub, the clustered scrub, and the closed scrub. We found 41 perennial species, which we characterized using 122 morphology-functional characteristics, corresponding to vegetative parts (stem and leaf), reproductive parts (flower and fruit), and functional phases (phenology, pollination, and dispersal). We used principal components analysis PCA to analyse the relationship between morphological attributes and species, between species and sites, and between morphological attributes and sites. Stem morphology was highly associated with groups of plant species and also with specific communities, forming recognizable stem-morphology syndromes. We also found that flower and fruit attributes are highly correlated with stem morphology. Our analysis allowed the clear identification of four morphological groups in our study area: (a) crassicaulescent plants, or succulent cacti, (b) sarcocaulescent species, (c) woody trees, and (d) woody shrubs. Cacti and sarcocaulescent plants dominate in

the open scrub, woody shrubs dominate in the mounds of the clustered scrub, and woody trees, together with all the previous life-forms, form the more mesic closed scrub. Our results indicate that Forrest Shreve's classification of desert communities based on the external morphology of the plants is statistically robust and reflects a significant underlying pattern.

1. Introduction

Vegetation science has revolved largely around the study of floristic variation. Some authors, however, have also tried to understand plant distribution and abundance not only in floristic terms, but also in terms of plant function (e.g. Box, 1981; Noss, 1990). Plant functional types are sets of characters, or phenotypical syndromes, that tend to co-occur in groups of species and are presumed to possess some adaptive value in specific environments (Sala et al., 1997; Smith et al., 1997). In the last two decades, a number of authors have used functional types for the general description of different plant communities (e.g. Herrera, 1984; Bullock, 1985; Montalvo et al., 1991; Sarmiento, 1992; Paruelo and Lauenroth, 1996; Diaz et al., 1998). Other authors have used the concept of functional types to understand the role of certain plants in the dynamics and function of whole ecosystems (e.g. Paruelo and Tomasel, 1997; Aguiar and Sala, 1998; Lavorel et al., 1999).

The functional approach is not new: In the early 20th Century, Forrest Shreve recognized and mapped the desert ecoregions of the Sonoran Desert and the Peninsula of Baja California based on a complex set of attributes, including dominant landforms, floristics, and, remarkably, the dominant morphology of the plant communities. His usage of plant physiognomy and ecomorphology as a central element in the classification of the greater Sonoran Desert showed an uncanny foresight into discoveries on ecophysiology that were yet to come, and a genius to understand the deep causes of plant distribution and abundance. Shreve recognized three ecoregions in the Sonoran Desert mainland—the Arizona Uplands, the Plains of Sonora, and the Sonoran Foothills—two ecoregions in the Peninsula of Baja California—the Magdalena Plains and the Vizcaíno Desert—and two shared ecoregions —the Lower Colorado Valley that occupies both the western Sonoran mainland and the northern part of the gulf coast in Baja California, and the Central Gulf Coast, a narrow strip along the coasts of the mid-Sea of Cortés.

Based on this approach, he recognized mycrophyllous deserts, where small-leaved shrubs predominate (the Lower Colorado Valley); crassicaulescent deserts, where succulent-stemmed plants, such as giant cacti, dominate (the Arizona Uplands); suffrutescent, or shrub-like, deserts (the Plains of Sonora); arborescent, or tree-like, deserts (the Foothills of Sonora); sarcocaulescent, or fleshy-stemmed, deserts dominated by trees with gigantic trunks with smooth bark (the Central Gulf Coast), and sarcophyllous, or fleshy-leaved, deserts, where plants with succulent leaves often

arranged in basal rosettes, such as agaves, prevail (the Vizcaíno Region; see Shreve and Wiggins, 1964; Ezcurra et al., 2002 for a description of each subdivision).

At the smaller scale of individual plant communities within a larger ecoregion the question remains on how much of the observed floristic variation can be also associated to variation in functional characteristics. For this purpose, we decided to analyse how much change in functional attributes takes place between plant associations that occur within one of Shreve's ecoregions, the sarcocaulescent scrub of the Gulf of California coast in southern Baja California.

2. Materials and methods

2.1. The study area

The sarcocaulescent scrub is the typical vegetation of the eastern coast of the southern part of the Peninsula of Baja California (León de la Luz et al., 2000). It lies between the arid Sonoran Desert scrubs to the north, and the dry tropical forests of the Cape Region, to the south, and shares some floristic attributes with both these floristic regions (Shreve, 1937; Shreve and Wiggins, 1964; Rzedowski, 1978; Wiggins, 1980). Climate is arid and hot, frost-free, and with rains concentrated mostly in late summer (September–November) and associated to tropical hurricanes. Mean monthly temperatures vary between 18 °C in January and 30 °C in August. Mean annual rainfall is 180 mm.

Our study was done in El Comitán Experimental Reserve, managed by the *Centro de Investigaciones Biológicas del Noroeste* (CIBNOR) on the edge of the bay of La Paz (24°05′N; 110°21′W; see Fig. 1). The area lies on a wide alluvial plain with gentle (1–5%) slopes that drain towards the bay along shallow erosive troughs running in a predominantly NW–SE direction. The erosive force of the hurricane-fed rains is a major force structuring plant communities. Based on the spatial distribution of dominant plants, and using both aerial photographs (scale 1:75,000) and field recognition, we identified three distinct areas within the larger sarcocaulescent scrub: (a) open scrub, (b) clustered scrub, and (c) closed scrub (Fig. 1).

(a) The open scrub is found on an old alluvial terrace with sandy-clayey soils (haplic yermosols) and rounded boulders. Perennial vegetation is dispersed, with plants 2–5 m apart, and with abundant bare soil exposed between plants (often showing microbiotic crusts). Slopes are the highest of the area (4–5%), and the community is dissected by a network of shallow troughs. (b) The clustered scrub presents similar soils, but devoid of stones. The gentler slopes (2–3%) of this area allow the differential retention of water and debris around the larger perennial shrubs, generating mounds of sand, soil, and litter 1.5–3.0 m wide and 20–70 cm high. The micro-environmental conditions of the mounds promote animal activity and burrowing by kangaroo rats, a fact that enhances soil turnover and infiltration capacity, leading to the formation of fertility islands around the larger plants. (c) The closed scrub is found in the part of the reserve that is nearest to the coast, where slopes are low (<2%) and surface drainage is sluggish and sheet-like. Soils are calcic
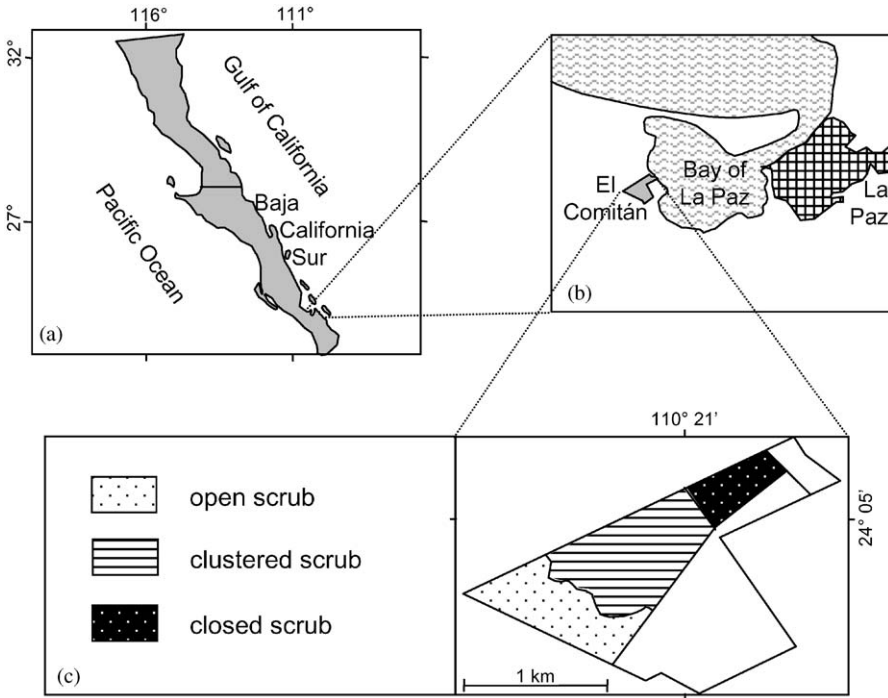
Fig. 1. The study area, showing (a) the peninsula of Baja California, (b) the bay of La Paz, and (c) El Comitán Experimental Reserve, with the different scrub types.

xerosols, and vegetation cover is high, with almost no soil exposed outside plant canopies. Because of the distance to the coast and the intensity of the drainage pattern, there is a noticeable salinity gradient between the three areas: mean surface soil salinity in the open scrub is $0.08 \, \text{mS cm}^{-1}$, similar to the clustered scrub, where it is $0.06 \, \text{mS cm}^{-1}$, but lower than the closed scrub, where it reached $0.56 \, \text{mS cm}^{-1}$.

2.2. Sampling procedure

We sampled 11 sites, each one consisting of $30 \, \text{m} \times 30 \, \text{m}$ ($900 \, \text{m}^2$) quadrats (León de la Luz et al., 1996 estimated a minimal sampling area for perennial plants of 800–$1000 \, \text{m}^2$ in this area). Four quadrats were located in the open scrub area, four in clustered scrub, and three in closed scrub. In each quadrat we registered all perennial species and their respective life-form. Plants were collected for morphological analysis in the laboratory. We sampled a total of 41 species in all quadrats (see Appendix A).

Each species was described according to 122 attributes representing its external morphology (see electronic appendix of this paper); 55 attributes described vegetative morphology (28 leaf and 27 stem attributes), 47 attributes described reproductive morphology (26 flower and 21 fruit attributes), and 20 attributes

described dynamic aspects such as phenological phases or interactions with other species. The morphological descriptions were done for plants observed and collected in August–October 2001, during the rainy season. Apart from direct observations, information on interactions with other species or phenological dynamics were complemented with published work (e.g. Turner et al., 1995; León de la Luz et al., 1996).

2.3. Data analysis

With the data set, we constructed a floristic species × sites presence–absence matrix, describing the occurrence of each species in the 11 quadrats. Additionally, we constructed a second presence–absence matrix, describing the occurrence of the 122 morphological and functional attributes on the 41 species. This matrix was later subdivided into its subset components, separating stem, leaf, flower, fruit, or functional attributes for individual analysis of their occurrence in the 41 species. Finally, by multiplying the attributes × species matrix (A) with the species × sites matrix (B), we obtained an attributes × sites matrix (C), which contains the frequency with which a given attribute is observed in any given site (i.e. the number of species in any given site that possess a certain attribute). All three matrices were analysed by eigenvector ordination methods. We used principal component analysis (PCA, unstandardized data with Gower double centring), and tested the significance of each axis using the broken-stick test to identify axes that explain more variation than can be attributed to chance alone (Jackson, 1993; Legendre and Legendre, 1998).

3. Results

3.1. Species distribution

The PCA of the species × sites matrix yielded two significant axes that were also highly associated with the main physiognomic areas of the reserve (Fig. 2a). Together, axis 1 (explaining 27% of the matrix's variation) and axis 2 (18% of the variation) clearly recovered the main scrub gradient, yielding a typical horseshoe arrangement with closed scrubs in one extreme of the gradient and open scrubs in the other. Using a simple one-way ANOVA test, we found that the axes were significantly associated with scrub type ($p = 0.0003$ and 0.04, respectively, for axes 1 and 2).

Some of the most characteristic species for the open scrub sites are *Caesalpinia placida*, the dominant shrub in the open scrubland, *Bursera odorata*, *Ferocactus peninsulae*, and *Stenocereus thurberi* (Fig. 2b). In the clustered scrub, the most typical species are *Adelia virgata*, *Agave datylio*, *Bursera epinnata*, *Castela peninsularis*, *Condalia globosa*, *Krameria parvifolia*, *Larrea tridentata*, and *Melochia tomentosa*. Lastly, the characteristic species of the closed scrub are *Capparis atamisquea*,
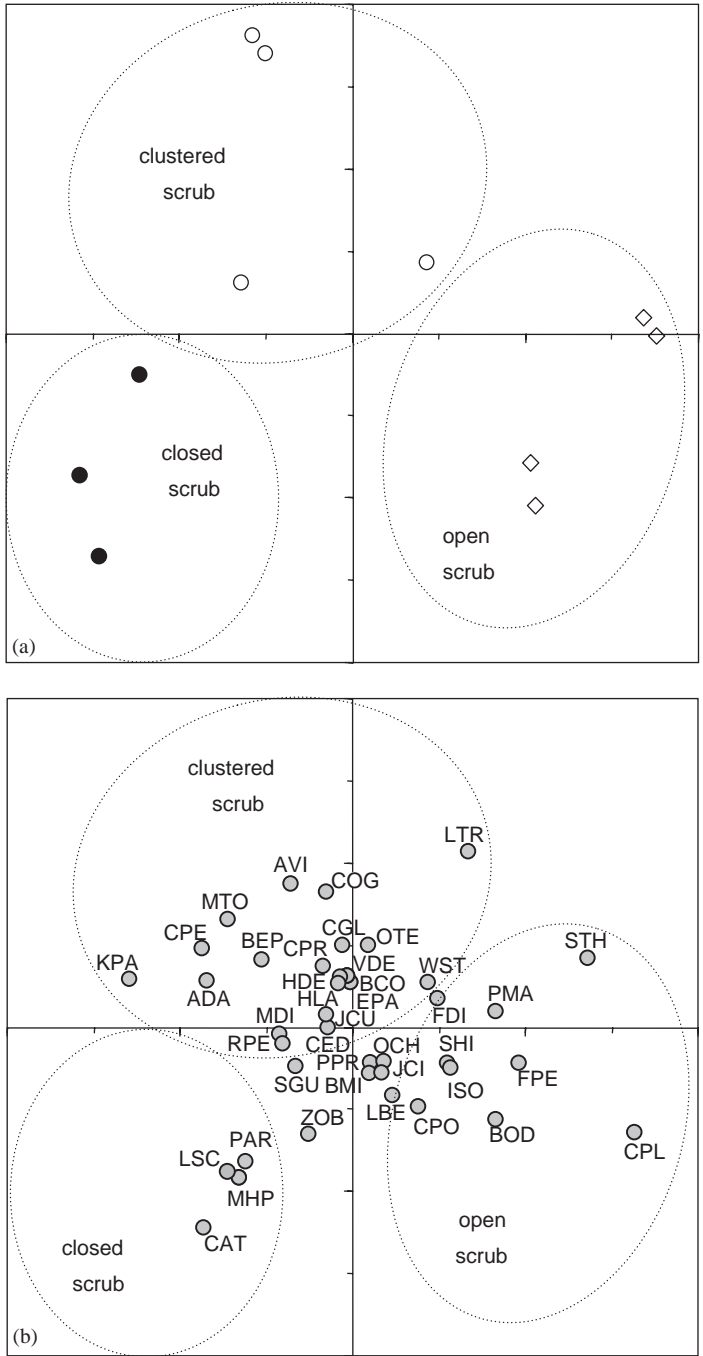
Fig. 2. Principal components biplot showing (a) the distribution of the 11 quadrats in reduced species-space, and (b) the distribution of the 41 species in site-space (see Appendix A for species codes). In both plots, the abscissa corresponds to principal axis 1, and the ordinate to axis 2.

Lophocereus schottii, *Maytenus phyllanthoides*, *Prosopis articulata*, and *Ziziphus obtusifolia*.

3.2. Morphological and functional attributes of the species

The broken-stick test detected significant PCA axes for the stem morphology × species matrix, for the floral morphology matrix, and for the fruit morphology matrix. That is, these three sets of characters are significantly associated with some species, or, to put it in more biological terms, there are clearly identifiable syndromes for stem, flower, and fruit morphology. In contrast, we did not detect significant multivariate axes for leaf morphology or for phenological/functional characteristics, a fact that evidences that there are no distinct groups of species sharing common characteristics for these two sets of attributes. Additionally, there was a very significant correlation between the species PCA axes for stem morphology, and the axes for floral and fruit morphology. The first axes of all three matrices were significantly correlated, and axes 2 for the same three matrices were also highly correlated. That is, species showing a given stem morphology also tend to show a specific floral morphology and a corresponding fruit morphology. This allows us to conclude that there are groups of plants that tend to show correlated traits in stem, flower, and fruit morphology.

Based on the results above, we merged all three matrices (stem, flower, and fruit) into a single matrix of 74 morphological attributes × 41 species, describing the distribution of morphological attributes within the species set. This matrix was subject again to PCA, and yielded three significant axes, jointly explaining 62% of the variation (Fig. 3). Very clear clusters of species can be seen on each axis. Axis 1 separates succulent cacti from the rest of the species, axis 2 separates trees from woody shrubs (Fig. 3a), and axis 3 separates sarcocaulescent and sarcophyllous plants from the greater cluster (Fig. 3b). In all cases, one-way ANOVA tests showed these clusters to be significantly distinct ($p < 0.000001$).

Using the PCA biplot, we could identify the main attributes that differentiate each morphological type. The main characteristics separating cacti along axis 1 are the succulent, photosynthetic, spiny trunks, the soft woody tissues with abundant non-specialized parenchyma, and the storage capacity of the stem. A number of other characteristics are also associated to these, such as spiny, hemicyclic flowers with predominantly reddish corollas, a thorny or densely hairy indumentum, and the production of abundant nectar. The fruits are large berries, often produced in numerous amounts, with hairy or thorny garments, containing hundreds of small seeds.

Woody desert trees are characterized along axis 2 by a microphanerophyte life-form, and by the angularly branched, open canopies, the presence of short shots (brachyblasts), the tough bark, and the frequent presence of gums, resins, or latex. Associated with these stem attributes, the flowers are predominantly yellow and dialypetalous, arranged in dense inflorescences, and producing abundant nectar, while the fruits are chiefly drupes or legumes produced in large numbers with relatively large seeds.
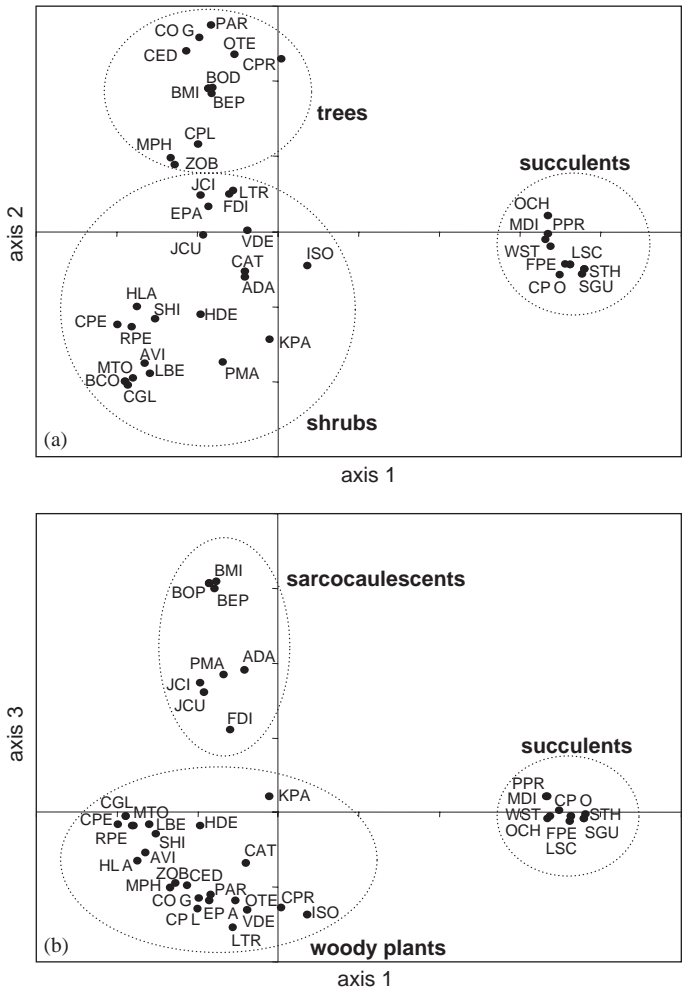
Fig. 3. Principal components plots showing the distribution of the 41 species in the multi-variate space defined by the morphological attributes (stem, flower, and fruit): (a) axis 1 vs. axis 2, and (b) axis 1 vs. axis 3 (see Appendix A for species codes).

In contrast, desert shrubs are nanophanerophytes with open branching, closed, dense canopies, and soft bark. The flowers are predominantly gamopetalous, with mostly solitary flowers and corollas in various colours. Fruits are capsules and achenes, produced in relatively low numbers with intermediate size seeds.

Finally, the main morphologic characteristics of sarcocaulescent perennials are the soft-wooded, fleshy stems, with smooth, decorticating, often photosynthetic bark. Their flowers have mostly gamopetalous, frequently reddish, smooth perianths, often dioecious or sexually imperfect. Seeds are frequently arilated.
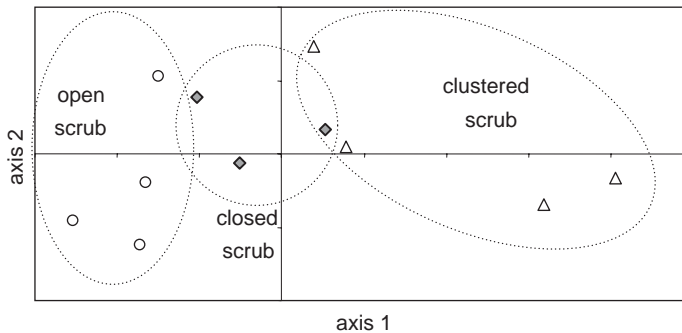
Fig. 4. Principal components plot showing the distribution of the 11 quadrats in the multi-variate space defined by the morphological attributes (stem, flower, and fruit).

3.3. The distribution of morphological attributes among sites

The attributes × sites matrix (C) contained the frequency of appearance of 74 morphological attributes on 11 sites. When analysed through a PCA, only one significant axis was found, concentrating 71% of the variation in the data set (Fig. 4). This axis clearly separated the three scrub types: the open scrub in one extreme, the clustered scrub on the other, and the closed scrub occupying an intermediate position ($p = 0.02$ for the one-way ANOVA test). It is interesting to note that, while the closed scrub and the open scrub occupied extremes of the floristic gradient, in the morphological gradient it is the open scrub and the clustered scrub that occupy the extremes, with the closed scrub occupying an intermediate position.

The open scrub is dominated by small shrubs or chamaephytes, with succulent or sarcocaulescent stems often with smooth or decorticating bark, and also by some plants with climbing habit. The flowers are large, hemicyclic or frequently zygomorphic, with thorny or glandular indumentums. Fruits are often berries, or have glandular or thorny pericarps. Seeds are small and often arilated. These attributes coincide well with the external morphology of the dominant plants of this community, i.e. cacti, *B. odorata*, and *C. placida*. In the clustered scrub, plants with hard, woody, erect stems dominate. Flowers are small, cyclic, actinomorphic, with smooth double perianth, monoecious, and sexually perfect. Dominant seed characteristics are medium size and few in numbers. These attributes coincide well with the principal plants in this environment, e.g. *A. virgata*, *L. tridentata*, *C. globosa*, or *C. peninsularis*. In the closed scrub, fleshy and succulent plants co-dominate with woody perennial trees; hence the intermediate position of this community along the morphology gradient.

4. Discussion and conclusions

Other studies on the functional morphology of plants in drylands of the American Continent mention plant life-form as one of the leading elements to characterize

vegetation function (e.g. Morello, 1958; Solbrig and Orians, 1977; Sarmiento, 1992; Sala et al., 1997; Aguiar and Sala, 1998). In our study, we found that stem morphology is highly associated with groups of plant species, forming recognizable stem-morphology syndromes, and also with specific communities. We also found that flower and fruit attributes are highly correlated with stem morphology. Our analysis allowed the clear identification of four morphological groups in our study area: (a) crassicaulescent plants, or succulent cacti, (b) sarcocaulescent species, (c) woody trees, and (d) woody shrubs. We also found that these life-forms dominate differentially in the different environments of our study region; while cacti and sarcocaulescent plants dominate in the open scrub, woody shrubs dominate in the clustered scrub, and all these life-forms, together with woody trees, congregate in the more mesic closed scrub.

Many other reproductive traits—flower and fruit morphology—are correlated with the distribution of these stem morphs. It is not clear for us at this stage how much of this correlation is the result of an adaptive process, and how much of it is simply the result of taxonomical restrictions in phenotype. For example, all stem-succulents (crassicaulescent plants) in our study area belong to the family Cactaceae; most sarcocaulescent species belong to the families Burseraceae, Fouquieraceae, and Anacardiaceae; a large proportion of the woody trees are legumes, and woody shrubs are dominated by the families Asteraceae, Rhamnaceae, Solanaceae, Capparaceae, and Zygophyllaceae.

The occurrence of a great richness of sarcocaulescent species in this region is still a matter of further investigation. Although present in other Mexican deserts, plants with fleshy, gigantic stems seem to be the identifying mark of the peninsula of Baja California. Sarcocaulescent trees possess morphological traits of both woody desert plants and cacti: They have true deciduous leaves and their external morphology resembles that of a tree, but the presence of chlorenchyma in their stem surface, the large amounts of radial and axial parenchyma in their trunks, and their capacity to store water and nutrients resembles in many aspects the morphology of cacti (Humphrey, 1935; Bullock, 1936; McVaugh and Rzedowski, 1965; Rzedowski and Kruse, 1979; Wiggins, 1980; Carlquist, 2001). Moreover, while the origin of cacti is monophyletic, sarcocaulescent plants belong to different, non-related families such as Anacardiaceae (genera *Cyrtocarpa* and *Pachychormus*), Burseraceae (*Bursera*), Euphorbiaceae (*Jatropha* and *Pedilanthus*), and Fouquieriaceae (*Fouquieria*). This suggests the existence of strong selective pressures during the evolution of the peninsula in favour of this particular life-form.

Finally, our results suggest that in these deserts functional morphology of the stem seems to be the leading factor determining the abundance and distribution of desert perennials, by regulating their capacity to capture light, store water and nutrients, survive droughts, and explore their immediate environment. This, in turn, suggests that Shreve's classification of desert communities using the external morphology of the dominant plants as a main descriptive does indeed reflect a significant underlying pattern. The Sonoran and Baja California Deserts' large variation in winter/summer rainfall patterns, continentality, temperature regime, and landbridge connections, have all contributed not only to its large floristic diversity, but also to its wondrous

wealth of life-forms and adaptations (Shreve, 1937; Shreve and Wiggins, 1964; Wiggins, 1980; Rzedowski, 1991).

Appendix A

Listing of species used in the analysis, with their labelling code for the ordination plots.

Species	Family	Code
Adelia virgata Brandegee	Euphorbiaceae	AVI
Agave datylio F.A.C. Weber	Agavaceae	ADA
Brickellia coulteri A. Gray	Asteraceae	BCO
Bursera epinnata (Rose) Engl.	Burseraceae	BEP
Bursera microphylla A. Gray	Burseraceae	BMI
Bursera odorata Brandegee	Burseraceae	BOD
Caesalpinia placida Brandegee	Fabaceae	CPL
Capparis atamisquea Kuntze	Capparaceae	CAT
Castela peninsularis Rose	Simaroubaceae	CPE
Cercidium praecox (Ruíz & Pav. ex Hook. & Arn.) Harms	Fabaceae	CPR
Cochemiea poselgeri Britton & Rose	Cactaceae	CPO
Colubrina glabra S. Watson	Rhamnaceae	COG
Condalia globosa I. M. Johnst.	Rhamnaceae	CGL
Cyrtocarpa edulis Standl	Anacardiaceae	CED
Encelia palmeri Vasey & N.E. Rose	Asteraceae	EPA
Ferocactus peninsulae Britton & Rose	Cactaceae	FPE
Fouquieria digueti (Tiegh.) I. M. Johnst	Fouquieriaceae	FDI
Hibiscus denudatus Benth	Malvaceae	HDE
Hyptis laniflora Benth	Lamiaceae	HLA
Ibervillea sonorae (S. Watson) Greene	Cucurbitaceae	ISO
Jatropha cinerea Müll. Arg.	Euphorbiaceae	JCI
Jatropha cuneata Wiggins & Rollins	Euphorbiaceae	JCU
Krameria parvifolia Benth	Krameriaceae	KPA
Larrea tridentata Coville	Zygophyllaceae	LTR
Lophocereus schottii Britton & Rose	Cactaceae	LSC
Lycium berlandieri Dunal	Solanaceae	LBE
Mammillaria dioica K. Brandegee	Cactaceae	MDI
Maytenus phyllanthoides Benth	Celastraceae	MPH
Melochia tomentosa L.	Sterculiaceae	MTO
Olneya tesota A. Gray	Fabaceae	OTE
Opuntia cholla F. A. C. Weber	Cactaceae	OCH
Pachycereus pringlei Britton & Rose	Cactaceae	PPR
Pedilanthus macrocarpus Benth	Euphorbiaceae	PMA

Prosopis articulata S. Watson	Fabaceae	PAR
Ruellia peninsularis (Rose) I. M. Johnst.	Acanthaceae	RPE
Solanum hindsianum Benth.	Solanaceae	SHI
Stenocereus gummosus (Engelm.) A. Gibson & K. E. Horak	Cactaceae	SGU
Stenocereus thurberi (Engelm.) Buxb.	Cactaceae	STH
Viguiera deltoidea A. Gray	Asteraceae	VDE
Wilcoxia striata Britton & Rose	Cactaceae	WST
Ziziphus obtusifolia (Hook ex Torr. & A. Gray) A. Gray	Rhamnaceae	ZOB

Electronic Appendix. Morphological and functional traits used in the analysis. [*]Life-forms follow Raunkiaer (1934): Microphanerophytes: trees and shrubs 2–8 m high; Nanophanerophytes: shrubs 0.5–2 m; Chamephytes: perennials <0.5 m. [**]Leaf size also follows Raunkiaer (1934): Leptophyllous <25 mm^2; Nanophyllous 26–225 mm^2; Microphyllous 226–2025 mm^2. Flower size: small, <1 cm length, intermediate 1–4 cm; large >4 cm. Fruit size: small <1 cm; intermediate 1–4 cm; large >4 cm. Fruit quantity of fruits: few <50; many >50. Seed size: small <4 mm; intermediate 4–10 mm; large >10 mm. Seed quantity: few <10; many >10.

Vegetative traits		Reproductive traits		Functional traits
Stem	Leaf	Flower	Fruit	
Consistency	*Type*	*Size*	*Size*	*Propagation*
Woody	Simple	Small	Small	Sexual
Sarcocaulescent	Compound	Intermediate	Intermediate	Vegetative
Succulent	Aphyllous	Large	Large	Both
Position	*Size*[**]	*Perianth*	*Quantity*	*Foliage*
Erect	Leptophylles	Single	Few	Perennial
Creeping	Nanophylles	Double	Many	Deciduous
Decumbent	Microphylles	Null	*Type*	*Flowering*
Hardness of wood	*Form*	*Colour of corolla*	Capsule	Only in drought
Hard	Obovate	Red	Legume	Only with rains
Soft	Ovate	Yellow	Berry	Independent of rains
Specific function	Lanceolate	Various	Drupe	*Pollination*
Photosynthetic	Tapering	*Condition of the piece*	Achene	Annemofilous
Storage	Cordate	Dialypetalous	*Indumentum*	Entomofilous
Indumentum	*Border*	Gamopetalous	Hair	Ornitofilous
Thorn	Entire	*Disposition*	Gland	*Dispersion*
Hair	Wavy	Cyclic	Thorn	Wind
Gland	Crenated	Hemicyclic	Smooth	Insects

Smooth	Serrated	*Symmetry*		Rodents
Canopy	Revoluted	Zygomorphic	*Seed size*	Birds
Open	Involuted	Actinomorphic	Small	Reptiles
Closed	*Indumentum*	*Sex separation in flowers*	Intermediate	Vertebrates
*Life-form**	Thorn			
Hermaphroditic	*Large*	Explosives		
Microphanerophyte	Hair	Unisexual	*Seed quantity*	*Protection*
Nanophanerophyte	Gland	*Arrangement*	Few	Needs nurse
Chamephyte	Smooth	Solitary	*Much*	Nurses
Climber	*Consistency*	Inflorescence	*Seed annex structures*	
Arrangement	Succulent	*Indumentum*	Arile	
Trunk and branch	Normal	Thorn	Wing/Hair	
Brachyblasts	*Position*	Hair		
Branching angle	Alternate	Gland		
More 45°	Opposite	Smooth		
Less 45°	Fasciculate	*Rewards*		
Bark	*Composed*	Nectar/Other		
Hard	*Chemical*			
	Resin/Latex	*Sex separation in individual plants*		
Soft		Monoecious		
Decorticating		Dioecious		
Chemical defenses				
Resin				
Latex				

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