

## Living where others dare not: Microhabitat distribution in *Chorizanthe rigida*, a serotinous desert annual



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### ABSTRACT

We studied the small scale distribution pattern of *Chorizanthe rigida*, a serotinous desert annual, in a shrub-mound-to-desert-pavement gradient. Two sites were established in the Mojave Desert and two sites were established in the Sonoran Desert. We placed transects along a soil surface gradient from shrub mounds to desert pavements, and measured land surface properties, soil characteristics, and *C. rigida*'s small scale distribution. A Principal Components Analysis was done on the resulting site  $\times$  soil variables matrix. *C. rigida* established preferentially in desert pavements outside shrub canopies. Pavements showed finer soil textures and higher electrical conductivities, while shrub mounds had sandy textures, low surface rockiness, higher nitrogen, and higher cover of annuals. We discuss a probable relationship between seed retention and the establishment on desert pavements: timing seed release allows this species to avoid wind- or animal-induced seed dispersal into shrub mounds and establish outside the nurse mounds, where most annual plants concentrate. The seeds encased in the serotinous involucre, released after rains, are dispersed by run-off into the desert pavements and transition zones where, once developed, the dead seed-retaining structures of adult *C. rigida* plants persist for years releasing seeds to subsequent rain events.

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## 1. Introduction

The distribution of plants across landscapes results from life history traits interacting with environmental conditions at a local scale. In deserts, dispersal and establishment play a major role in plant distribution and in the clumped structure of desert communities (Shmida and Whittaker, 1981; Silvertown and Wilson, 1994; Yeaton and Manzanares, 1986). Although most desert plants germinate and establish below the protective shade of “nurse” shrubs (Valiente-Banuet et al., 2006), some species are able to establish successfully in open spaces. For example, the globose cactus *Mammillaria pectinifera* is able to colonize gravelly surfaces in the arid Tehuacán Valley in Mexico through its ability to (a) retain seeds in specialized serotinous fruits and release them after strong rains, and (b) to germinate and establish in the microhabitat provided by the protective shade of pavement rocks (Peters et al., 2008). Similarly, in the Sonoran and Mojave deserts most annual plants

establish under the protective shade of shrubs, but some species seem to preferentially establish in open pavements. One of the most common cases of these non-nursed species are serotinous annual plants of “basicarpic” morphology: small ephemeral plants that produce flowers and seeds near ground level and retain them for long periods in hard, lignified, structures (Ellner and Shmida, 1981). Basicarpic plants with delayed seed dispersal occur in many deserts throughout the world and in different families. Some examples are *Anastatica hierochuntica* (Brassicaceae, “rose of Jericho”) and *Anthemis melampodina* (Asteraceae, “Negev chamomile”) in Israel, *Torulularia torulosa* (Brassicaceae, “torularia”) in Pakistan, *Plantago coronopus* (Plantaginaceae, “minutina”) throughout Eurasian deserts, *Glossonema boveanum* (Apocynaceae) in the Sahara (Steinberger et al., 1991), as well as *Blepharis grossa* (Acanthaceae, “desert thistle”), and *Geigeria alata* and *G. ornativa* (Asteraceae) in the Namib (Günster, 1992). Most of these species seem to prosper well in open pavements, and do not seem to need the protective shade of nurse shrubs in order to survive harsh desert conditions (Gutterman, 1994, 2002).

In the Sonoran and Mojave deserts the most common basicarpic plant is *Chorizanthe rigida* (Polygonaceae), a serotinous

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winter desert annual distributed from the southern Great Basin Region to the Mojave, Sonoran, and Baja Californian Deserts (Baldwin et al. 2002; Felger, 2000). *C. rigida*'s dead spiny plants persist for several years firmly anchored to the ground by their tap roots. The species' dispersal units (i.e., the seed-bearing involucre) remain attached to the dried mother plant, which thus retains seeds after maturation and death. The dry involucre become loose at their base when the plant is rehydrated by rain and can get detached from it. This process is followed by tissue dehydration causing unreleased involucre to re-attach to the mother plant for months to years until another rain event occurs. Like in many other basicarpic desert annuals, the seed-retention system of *C. rigida* demands the allocation of sizeable amounts of the plant's photosynthetic budget toward the construction of the plant's rigid, lignified structures. The adaptive significance of this dispersal syndrome seems related to the ability to retain an above-ground seed bank in the dry maternal tissues, instead of releasing the seeds to the ground at the end of the life cycle.

Desert landscapes are often formed by a spatial mosaic composed of a matrix of barren pavements and mounds with shrubs growing on them (Evenari, 1985; Musick, 1975). Open pavements and shrub mounds differ in soil texture and surface rockiness, which result in varying micro-topographic properties (Wood et al., 2002). Desert pavements develop on flat, gently sloping, landforms and are covered by coarse gravel and cobble-sized clasts (Musick, 1975). The tightly-packed clasts trap fine particles and, consequently, the rocky surface overlays fine textured soils with low infiltration rates, resulting in salt accumulation in the upper horizons (Wood et al., 2005).

In contrast, the adjacent shrub mounds show more bare soil (Wood et al., 2002) and low surface rockiness formed by sparse and heterogeneous clasts. The microtopography of mounds and the occurrence of shrubs promote eolian sand deposition (Abrahams et al., 1995; Parsons et al., 1992). These sandy soil patches have high infiltration rates and deep leaching of salts, which result in ameliorated growth conditions for annual plants compared to the adjacent, generally barren, desert pavements (Musick, 1975; Wood et al., 2005).

The preference of basicarpic plants for pavements, an unfavorable environment avoided by most other annual plants, is intriguing. Shrubs enhance water infiltration (Berndtsson and Larson, 1987; Schlesinger and Pilmanis, 1998) while their canopy shading decreases evaporation and reduces high soil surface temperatures (Franco and Nobel, 1989; Valiente-Banuet and Ezcurra, 1991), which results in higher water availability and more suitable growth conditions under nurses. Decomposition of plant litter is carried out under shrubs by bacterial activity while in open pavements it is mostly caused by photo-degradation. Hence, shrubs also increase soil nutrient content from organic decomposition in the soil (García-Moya and McKell, 1970; Lajtha and Schlesinger, 1986). Granivorous rodents preferentially dig their burrows under shrubs, further contributing to water infiltration and the incorporation of organic matter into the soil profile (Neave and Abrahams, 2001; Whitford and Kay, 1999).

As part of a broader study on the functional ecology of serotiny and delayed dispersal in desert plants, in this paper we explore the hypothesis that *C. rigida*, like other lignified basicarpic plants, is able to colonize desert pavements, occupying a micro-niche contrastingly different from that of the most common, nurse-dependent annual desert plants. To test this hypothesis, we analyzed the small scale distribution pattern of *C. rigida* along the pavement-to-shrub-mound desert gradient, and characterized soil properties along these microhabitats.

## 2. Methods

### 2.1. Study species

*C. rigida* is a short, erect desert annual, normally 2–10 cm high. It has a single main taproot and stout stems covered by stiff, spiny bracts. As the stem grows, the soft, long-petioled basal leaves are shed, and give place to linear, rigid bracts (or cauline leaves) armed with a terminal spiny awn that becomes hard and thorn-like in age. The single flowers, with a diminutive yellow perianth, are subtended by a 3-segmented involucre with hard spiny bracts. The fruit is an achene that matures inside the involucre.

### 2.2. Study sites

Field work was conducted at desert pavement and bare-ground mosaic landscapes (*sensu* Wood et al., 2002) where *C. rigida* populations occur. All sites had creosote (*Larrea tridentata*) scrub associations. The creosote bush was the dominant shrub occupying the desert mounds, and well-developed desert pavements were found between mounds. In order to cover the distributional and environmental range of the species, two sites were established in the colder, winter-rain-fed Mojave Desert, and two in the bi-seasonal Sonoran Desert, which receives both winter Pacific fronts and summer monsoon rains. Because the surface characteristics of desert pavements may vary according to geologic age, clast lithology, and local geomorphology (Al-Farraj and Harvey, 2000), we also selected our four sites in order to cover as much variation as possible in micro-topographic pavement traits that could be relevant in explaining the small scale distribution pattern of *C. rigida*. Two sites were established at the Mojave Desert National Preserve, California; the first one was located on an alluvial fan skirt with dolomite limestone deposits located in the Clark Mountains Wilderness Area (35° 31' 32" N/115° 35' 19" W, 1065 m elevation, 144 mm mean annual precipitation, and 24.8 °C mean annual temperature, NOAA, Mojave, CA, Weather Station), and the second one was established on volcanic lava deposits located in the Cima Volcanic Field (35° 12' 0.4" N/115° 52' 11.6" W, 700 m elevation, reported mean annual precipitation and temperature 70 mm and 17 °C, respectively; Wood et al., 2002). A third site was established on rhyolitic alluvial deposits located in the Arizona Upland portion of the Sonoran Desert in Organ Pipe National Monument, Arizona (32° 07' 49.4" N/112° 45' 56.4" W, 550 m elevation, 240 mm mean annual precipitation and 20.3 °C mean annual temperature, NOAA, Organ Pipe Cactus National Monument, AZ, Weather Station), and, finally, a fourth site was located near the southeastern edge of the plant's distribution, on volcanic lava deposits in the Lower Colorado Valley portion of the Sonoran Desert, in the Pinacate Biosphere Reserve, Sonora, Mexico (31° 51' 48.8" N/113° 26' 45.8" W, 322 m elevation, 140 mm mean annual precipitation and 21 °C mean annual temperature (Coll-Hurtado, 2007; Ezcurra and Rodrigues, 1986).

### 2.3. Sampling

Three 5 m × 1 m transects were set up parallel to each other at three identified land surface mosaics: desert pavement zone, bare-ground shrub mounds and the transition zone between those two surfaces (Figs. 1 and 2). These transect triads were replicated five times at each site, totaling 15 transects per site, except for Pinacate, which had three replicates and hence only 9 transects in total. Transects were subdivided into ten subplots, 0.5 m × 1 m in size. Soil and land surface variables were sampled on the even-numbered subplots; the number of dry, seed-bearing individuals of *C. rigida* was recorded in each transect on the odd-numbered

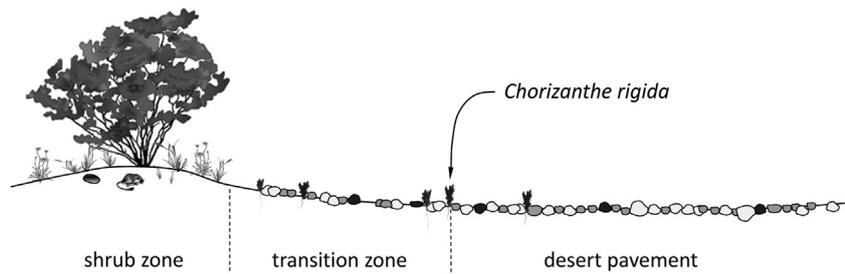


Fig. 1. Profile diagram of the desert plain microhabitats: desert pavement, transition area, and shrub mound.

subplots (total sub-plot area per transect = 2.5 m<sup>2</sup>). Changes in plant tissue color caused by weathering allowed to identify plants belonging to 2011, 2010 and previous years.

Land surface properties were characterized by measuring surface roughness, surface cover, and surface clast dimensions. Surface roughness was obtained by placing a 1 m bicycle chain on the ground and measuring its shortened length ( $L_s$ ) and comparing it to the original length ( $L_0 = 100$  cm). A roughness index (RI) was calculated using the following formula ( $RI = 100 (1 - L_s/L_0)$ ; Saleh 1993). Surface cover was characterized by placing a grid with 36 intersections on five of the 0.5 m × 1 m subplots along the transects of each land mosaic. The ground surface below each intersection

was categorized according to their soil surface as bare soil, gravel (2–6 mm), and rocks (>6 mm), and according to their biological cover as soil crust, annuals (forbs and grasses) and shrubs. A 1 m tape was placed on three even numbered 0.5 × 1 m plots, and all of the clasts intersecting the meter were collected and measured to obtain its projected area, and SE was calculated as a measure of clast size heterogeneity (Wood et al., 2002).

A total of 54 composite soil samples were obtained by taking five 6-cm-deep core soil samples from each transect. Soil samples were air dried and sieved to remove coarse fragments (>2 mm). Percentages of gravel and finer soil particles were calculated gravimetrically. Particle-size distribution was determined through

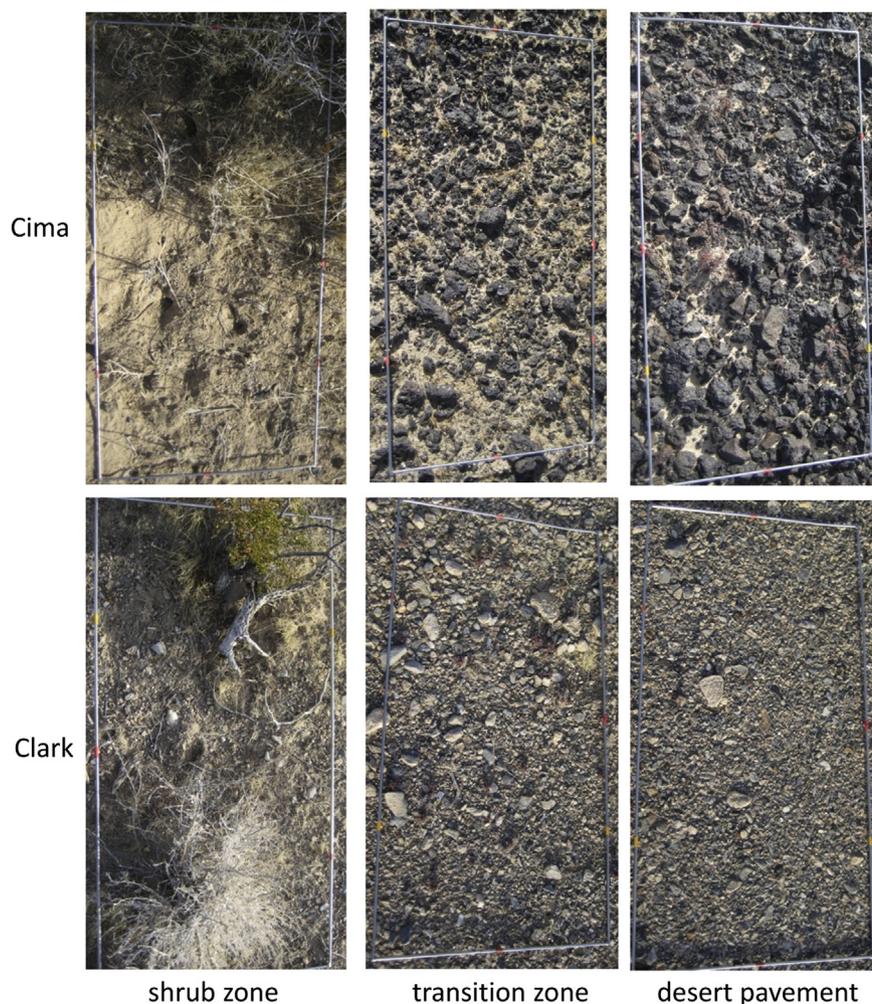


Fig. 2. Photographs of the three land surface mosaics in two of the sites located in the Mojave Desert. Field of view of each photograph is approximately 100 cm × 50 cm.

**Table 1**

Log-linear contingency-table analysis for the effect of site (Pinacate, OPNM, Cima and Clark), gradient (desert pavement, transition, shrub zone) and the interaction on the number of individuals of *C. rigida* (see Fig. 3 for the corresponding plot).

Source	$\chi^2$ deviance	df	<i>P</i>	$r^2$
Site	10.41	3	0.0150	0.08
Gradient	14.24	2	0.0008	0.11
Site $\times$ gradient	55.69	6	<0.0001	0.41
Error	53.96	42		
Total model	134.29	53		0.60

the Bouyoucos hydrometer method (Gee and Bauder, 1986). Surface soil aggregates were collected for soil bulk density determination by the paraffin-coated clod method corrected for gravel content (Hirmas and Furquim, 2006). Electrical conductivity and pH values were recorded from a 1:1 soil/water extract (Rhoades, 1982). Total carbon and nitrogen of the composite soils were obtained by the combustion method using a CE Elantech Nitrogen Carbon Analyzer (Nelson and Sommers, 1996).

#### 2.4. Statistical analyses

Log-linear contingency table analysis models with  $\chi^2$  deviance was used to study the effect of site (Pinacate, OPNM, Cima and Clark) and landscape mosaic (pavement, transition, shrub zone) on the number of individuals of *C. rigida*. In order to reduce the dimensionality of the soil surface data and to simplify the effect of correlated variables, a Principal Components Analysis (PCA) was performed on the soil data, using the following 18 environmental variables as descriptors of the transect soils: (1–6) soil cover (% bare soil, gravel, rock, biological soil crusts, annual plants, and shrubs), (7) surface roughness, (8) mean clast area, (9) SE of mean clast area, (10) soil bulk density, (11–14) soil texture (% gravel, sand, silt, and clay), (15) electrical conductivity, (16) pH, (17) total carbon and (18) total nitrogen. Variables were standardized prior to analysis given that they are measured in different units. We used a Varimax rotation on the PCA results (following Noy-Meir and Whittaker, 1977) to maximize the association between our axes and external environmental factors such as site or position along the landscape mosaic gradient, thus rendering the data more directly interpretable ecologically without losing any of the variance extracted by the component axes. The broken stick test was used to select the

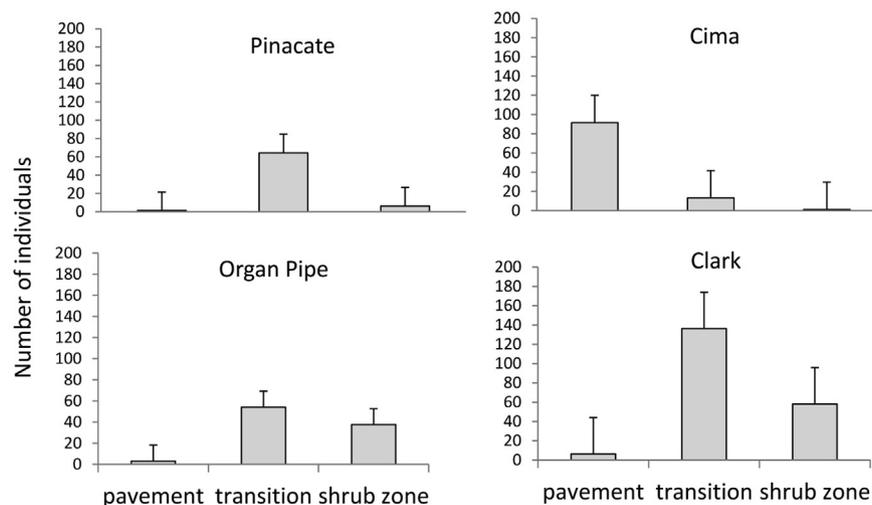
**Table 2**

Principal Component Analysis of soil traits: (a) Eigenvalues, percent of variance, and cumulative percent of variance explained by PC1 and PC2. (b) Loadings/correlation coefficients for each environmental variable in each eigenvector. Bold numbers indicate significant ( $P < 0.01$ ) loading values.

	PC 1	PC 2
<i>a) Axis values</i>		
Eigenvalue	4.65	4.51
Percentage	25.81	25.04
Cumulative %	25.81	50.85
<i>b) Environmental variables</i>		
Roughness	0.106	<b>0.818</b>
Bare soil	<b>-0.627</b>	-0.109
Gravel	0.577	-0.709
Rock	0.498	<b>0.731</b>
Crust	-0.539	0.319
Annuals	<b>-0.710</b>	0.292
Shrub	-0.285	-0.063
Clast area	0.330	<b>0.792</b>
SE(area)	0.049	<b>0.785</b>
Bulk_density	0.376	<b>0.646</b>
pH	0.539	0.480
EC	<b>0.591</b>	0.529
%TN	<b>-0.629</b>	-0.285
%TC	-0.133	-0.381
% gravel	0.247	-0.434
% sand	<b>-0.789</b>	-0.057
% clay	<b>0.595</b>	-0.096
% silt	<b>0.668</b>	0.044

principal components axes that explained more variance than could be expected under a random null model. Because in a standardized-data PCA the loadings of the variables on each axis are correlation coefficients, we identified the soil variables that were significantly associated with each axis at  $P = 0.01$ . We also performed a two-way ANOVA on the variables that had highest PCA scores (roughness, clast area, SE of clast area, % rock cover, and soil bulk density) to test their differences among sites and among transects, or the interaction of both factors.

Finally, a response function model was fitted to the abundance data of *C. rigida* along PC1 to model the species distributional niche along the environmental micro-topographic gradient and to identify the preferred soil microhabitat for the species. Given that abundances are measured in number of individuals (a frequency count), in order to model the species response to the multivariate



**Fig. 3.** Total number of individuals (mean  $\pm$  s.e.) of *C. rigida* on the land surface (pavement, transition, and shrub zone) in each site (Pinacate, OPNM, Cima and Clark). A highly significant interaction term ( $P < 0.0001$ ) was found in the corresponding log-linear model (Table 1), highlighting the fact that while the highest densities in the Cima site were found in open pavements, in all other sites the highest densities occurred in transition areas.

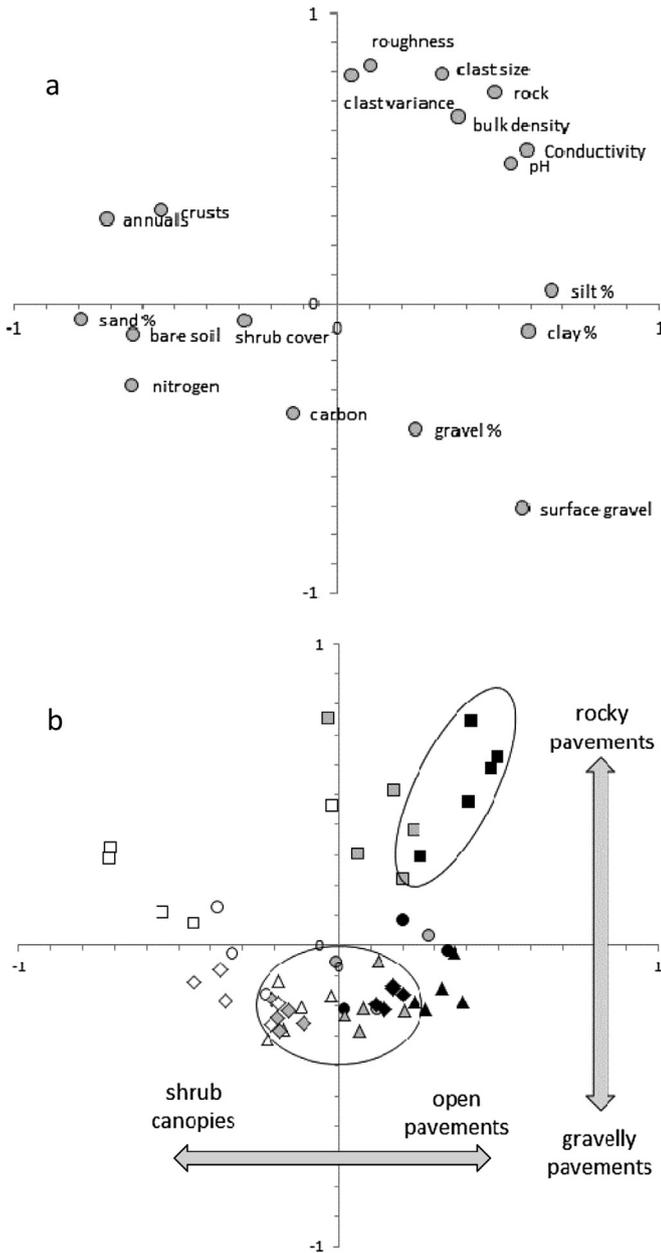
soil gradient we fitted a bell-shaped, quadratic log-linear model with Poisson error using Generalized Linear Models, taking PC1 as the independent predictor and species abundance in each transect as the dependent variable. For each modeled response curve we calculated the predicted point of maximum abundance along the gradient ( $x_{max}$ ) by calculating the first derivative of the fitted model and solving it for the point that makes the slope equal to zero (the function's maximum).

**3. Results**

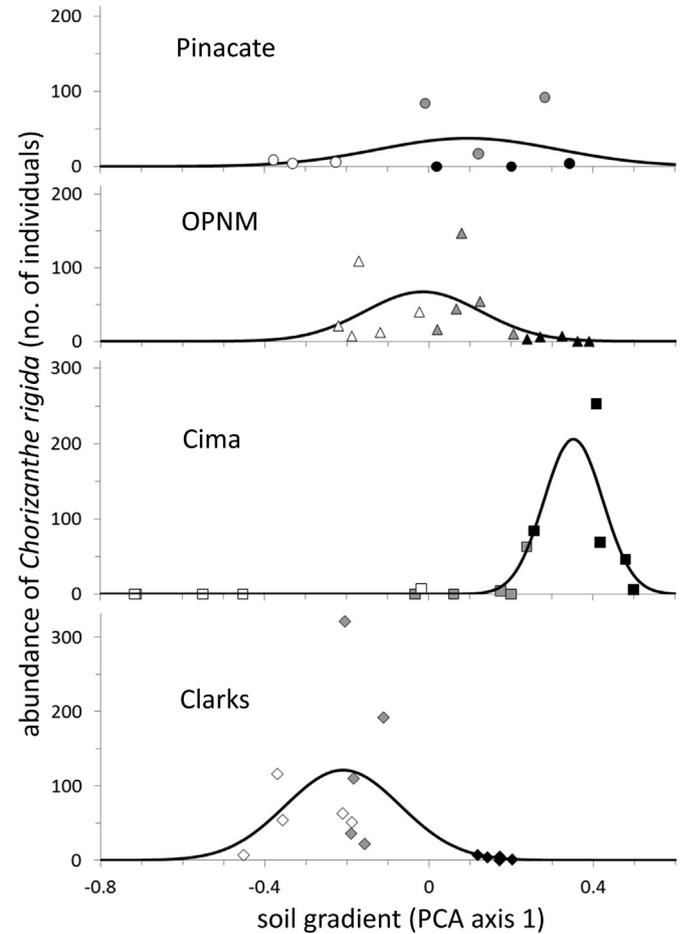
We found significant differences in the number of individuals of *C. rigida* as a result of the effect of site ( $\chi^2 = 10.41$ ,  $df = 3$ ,  $P = 0.015$ ), landscape mosaic ( $\chi^2 = 14.24$ ,  $df = 2$ ,  $P = 0.0008$ ), and their

interaction ( $\chi^2 = 55.69$ ,  $df = 6$ ,  $P < 0.0001$ , Table 1). In most sites (Clark, OPNM, and Pinacate), *C. rigida* established preferentially in the transition zone. In the Cima site, however, maximum counts were observed in the open pavements (Fig. 3).

We only found two PCA axes for soil variables that differed from the random expectation of the broken stick model. These two principal components jointly explained 50.8% of the soil variation in the data (PC1 = 25.8%, PC2 = 25.0%). PC1 was negatively associated with % sand, cover of annuals, total nitrogen, and the presence of bare soil, and positively associated with electrical conductivity and finer soil particles (% clay and % silt). PC2 was negatively associated with surface gravel, and positively associated with bulk density, rockiness, clast area, clast variance, and surface roughness (Table 2, Fig. 4a). Clearly, PC1 depicts the land surface gradient: bare ground areas with shrub mounds are distributed on the left hand of the axis while desert pavements appear at the right hand of the axis. PC2, separated our plots into two groups: Pinacate, OPNM and Clark, all of which have gravelly pavements, are on the negative side of this axis, while, the transects from Cima, which have a much higher rockiness, larger clasts, and a rougher ground surface, appear on the positive side of PC2 (Fig. 4b). This visual interpretation was statistically confirmed by a simple ANOVA on each axis: 69% of the variance in PC1 was explained by the position of the plot along the topographic gradient ( $F_{2,51} = 105.6$ ,  $P < 0.0001$ ), while the effect of sites only explained 6% of the variance on this axis ( $F_{3,50} = 6.6$ ,  $P = 0.001$ ). Variance in PC2 was largely (81%) explained by the effect of sites ( $F_{3,50} = 82.3$ ,



**Fig. 4.** PCA bi-plot showing (a) the loadings of environmental variables along PC1 and PC2, and (b) the site scores on PC1 and PC2. Sites are shape coded as follows: Pinacate ○, OPNM △, Cima □, and Clark ◇. Sample points are color coded as follows: black – desert pavement, gray – transition, white – shrub zone. Ellipses around the symbols encircle replicate sets in which *C. rigida* is distributed.



**Fig. 5.** Distribution of *C. rigida* along the composite soil axis (PC1). Data points coded as in Fig. 3. The bell-shaped lines show the functional response model of species density against the soil axis.

**Table 3**Roughness and clast values for each land surface mosaic for each site (mean  $\pm$  SE).

		Roughness index (%)	Clast area (mm <sup>2</sup> )	SE clast area	Rock (% cover)	Bulk density (g/cm <sup>3</sup> )
Desert Pavement	Pinacate	2.00 $\pm$ 0.45	262.7 $\pm$ 55.05	28.2 $\pm$ 8.00	9.26 $\pm$ 4.04	1.20 $\pm$ 0.08
	OPNM	1.16 $\pm$ 0.23	232.4 $\pm$ 29.28	22.8 $\pm$ 4.32	7.44 $\pm$ 1.33	1.23 $\pm$ 0.06
	Cima	4.16 $\pm$ 1.05	504.3 $\pm$ 51.69	82.3 $\pm$ 11.14	53.78 $\pm$ 5.11	1.59 $\pm$ 0.01
	Clark	0.68 $\pm$ 0.04	165.7 $\pm$ 23.26	13.4 $\pm$ 1.63	5.37 $\pm$ 2.02	1.45 $\pm$ 0.07
Transition	Pinacate	2.45 $\pm$ 0.57	237.7 $\pm$ 90.38	27.1 $\pm$ 11.20	8.02 $\pm$ 4.29	1.08 $\pm$ 0.23
	OPNM	1.57 $\pm$ 0.36	199.5 $\pm$ 24.14	23.0 $\pm$ 4.52	7.33 $\pm$ 2.97	1.16 $\pm$ 0.02
	Cima	3.66 $\pm$ 0.65	507.3 $\pm$ 19.86	103.5 $\pm$ 41.28	27.56 $\pm$ 6.17	1.56 $\pm$ 0.02
	Clark	1.58 $\pm$ 0.28	143.8 $\pm$ 15.20	12.9 $\pm$ 1.25	1.67 $\pm$ 0.61	1.19 $\pm$ 0.08
Shrub Zone	Pinacate	1.49 $\pm$ 0.41	113.8 $\pm$ 20.58	57.8 $\pm$ 42.67	2.78 $\pm$ 1.41	1.05 $\pm$ 0.03
	OPNM	1.50 $\pm$ 0.36	192.9 $\pm$ 27.68	21.8 $\pm$ 3.47	4.00 $\pm$ 1.45	1.08 $\pm$ 0.04
	Cima	3.08 $\pm$ 0.61	253.0 $\pm$ 63.79	47.0 $\pm$ 11.69	8.22 $\pm$ 5.66	1.31 $\pm$ 0.04
	Clark	1.34 $\pm$ 0.21	155.4 $\pm$ 28.28	18.9 $\pm$ 3.15	2.87 $\pm$ 1.39	1.12 $\pm$ 0.05

$P < 0.0001$ ) while the effect of the topographic gradient was non-significant on this axis.

In all sites we found a bell-shaped response function to the multivariate soil gradient as measured by PC1 (Fig. 5). The fit for the Pinacate site was only marginally significant ( $P = 0.04$ ), possibly due to the lower number of transect units. In all other sites, the model fit was highly significant ( $P < 0.01$ ) but the optimum of the distribution varied according to the site: While the modeled abundance of *C. rigida* peaked near the center or the left of PC1 in Pinacate, OPNM, or Clark (where the function's maximum  $x_{\max}$  was, respectively, 0.09,  $-0.02$ , and  $-0.21$ ), in Cima it peaked toward the right of PC1 ( $x_{\max} = 0.35$ ). In short, the response-function model replicated the results of our first analysis: *C. rigida* shows maximum densities in the transition zone between shrubs and pavements, but in the more rocky environments of the Cima volcanic field it establishes better in full pavements.

All selected soil variables (roughness, clast area, SE of clast area, rock cover, and bulk density) varied significantly between sites. As a general rule, in the ANOVAs the Cima site showed significantly ( $P < 0.0001$ ) higher surface roughness, and larger and more variable clasts, as well as higher rock cover and bulk densities, while the other three sites did not differ significantly among themselves (Table 3). On the other hand, only two variables—% rock cover, and soil bulk density—showed significant ( $P < 0.0001$ ) differences among transects: rock cover was lowest under shrubs, highest in pavements, and intermediate in the transition areas, while bulk density was significantly lower under shrubs and did not differ between pavements and transition areas.

#### 4. Discussion

*C. rigida* establishes preferentially in the transition zones along the shrub-to-pavement micro-topographic gradient. However, in surfaces with a high degree of rockiness and large clast size, as in the Cima site, it is also able to colonize open pavements. The establishment of *C. rigida* seems to be associated with a combination of surface roughness and rock cover, as captured in the PCA axes: In three of our studied sites (Pinacate, OPNM, and Clark) pavements are relatively homogeneous, formed mostly by densely-packed small rocks and gravel, while the transition zones maintain a high surface roughness but show a lower rock and gravel cover, leaving small patches of exposed soil between clasts (Table 3). In Cima, in contrast, the pavement is formed by larger rocks, and the maximum degree of roughness was found in the pavements, where the large surface rocks leave small patches of bare soil between them. Thus, in all sites *C. rigida* established preferentially on those surfaces that had rocks and gravel combined with open soil spaces. These micro-topographic traits seem to play an important role in the establishment and distribution of

*C. rigida*, possibly because a higher number of runoff-dispersed propagules get trapped in surfaces with higher roughness (Chambers and MacMahon, 1994; Harper et al., 1964). In agreement with our results, it has been well reported that the aggregation patterns of basicarpic species in other deserts depend on rainfall and runoff conditions (Friedman and Stein, 1980; Günster, 1992, 1993; Hegazy and Kabiell, 2007).

The distribution of *C. rigida* is negatively correlated to the cover of other annual forbs and grasses. This highlights the fact that, while most desert annuals tend to establish preferentially under shrub canopies, as the nurse-shrub paradigm predicts, *C. rigida* is consistently using a microhabitat markedly different from that of most other annuals; it established chiefly in rocky transition zones and desert pavements, two microenvironments that are more saline, less fertile, and more impermeable than the mounds. This distinct microhabitat differs from that used by other desert annuals, which release their seeds at the end of the growing season and are dispersed by faunal activity and wind into shrub mounds where they form a soil seed bank (Pake and Venable, 1996; Venable, 2007). In sharp contrast with most desert ephemerals, *C. rigida* delays seed dispersal retaining the achenes in its lignified stems, timing release with incoming rains and allowing seeds to reach the ground at a time when runoff accumulates on desert pavements (Turk and Graham, 2011). By preferentially establishing on stable geomorphic surfaces, such as desert pavements, where underlying highly aggregated soils provide a suitable substrate for long-term anchoring, *C. rigida* seems to achieve the persistence necessary to release seeds during several rain events, in contrast with dynamic shrub mound areas with low soil aggregation and high bioturbation activity (Ellner and Shmida, 1981). Furthermore, as in the previously discussed case of *Mammillaria pectinifera* (Peters et al., 2008), in *C. rigida* surface rocks seem to provide seedling protection during establishment. Our study provides microhabitat data in support of the hypothesis that the ecological significance of serotiny in desert annuals lies in allowing the seed-retaining, lignified plant skeletons, to repeatedly release seeds after rain events, at an adequate time to establish and develop in normally inhospitable desert pavements.

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