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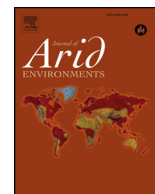
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Influence of microhabitat on functional attributes of two columnar cacti with different distribution ranges

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ABSTRACT

Microhabitat variations condition the ability of plant populations to colonize and recruit. Normally cacti species need nurse conditions for establishment of seedlings, resulting in patches under forest cover and increasing the contrasting conditions between slopes with different solar exposure and humidity percentage. We hypothesize that *Cephalocereus senilis*, a species with restricted range, will have constant functional attributes at each slope and therefore greater sensitivity to environmental variation than *Stenocereus dumortieri*, a species of wide distribution. This study contrasts microhabitat response of two cacti with different distribution ranges using several functional traits: spatial association pattern, variation in morphological attributes, habitat disturbance conditions and community association. The main contributions of this work are: i) use of a multivariate approach that allows observation of variation patterns between different conditions of exposure and ii) contrast of wide and restricted distribution species in response to dry environmental requirements. The functional attributes of *C. senilis* are constant (density, morphology, disturbance conditions and associated vegetation), with the exception of the spatial arrangement of individuals, clumped towards an eastern orientation and regularly spaced on the western orientation. In contrast, *S. dumortieri* has different functional attributes, performing better on unexposed hillsides (aggregation radii smaller, highest density, larger plants, more preserved environment and greater diversity of associated vegetation). Our results are an example of the general response to micro-environmental variation of wide (tolerance) and restricted (avoidance) species in dry environments at both the population and community levels, representing an evolutionary evidence of adaption divergence.

1. Introduction

Microhabitat restrictions and preferences of species are assumed to be adaptive, such that fitness is higher in optimal habitats, causing natural selection to maintain ecological preferences, biological associations and morphological traits with a genetic basis (Martin, 1998). In species with a restricted distribution range, degree of adaptability diminishes, limiting radiation and colonization capacity, there by maintaining restricted ecological niche and distribution area (Boyko, 1947).

In semi-arid environments, opposite slope orientations have different gradients of temperature, aridity, vegetation cover, and humidity, thereby differentially stressing the plants (Ackerly et al., 2002; Harman et al., 2014). This divergence is increased by environmental gradients affecting morphological traits, aggregation, spatial dependence (population level), and the balance between competition and facilitation in plant-plant and animal-plant interactions (community level) (Callaway et al., 2002; Schob et al., 2013). The effect of divergence in microhabitat is highest in plants with a restricted distribution than in more broadly distributed species because fitness of the former depends on optimal conditions located only in particular sites. Functional attributes of the species such as clumped spatial distribution, morphological attributes and biotic-abiotic interactions become homogenized (Holmgren and Scheffer, 2010). In contrast, a broadly ranging colonization strategy requires different approaches, which results in more plastic variation of biological associations, morphological attributes, and flexibility of ecological requirements (Ackerly et al., 2002). A selective, functional trait at the population level confers advantages to certain individuals that guarantee species persistence, e.g.

defense against herbivore attack, space competition, early germination, etc. Selection is important in functional trait evolution and helps explain population differentiation via habitat divergence (Geber and Griffen, 2003). By contrast, at the community level, a functional trait depends on the ecological importance of a species, measured by its interactions and role in the ecosystem (Bocanegra-González et al., 2015). Thus, a particular functional role could be modified by environmental changes, disturbance, or extinction-invasion dynamics (Allen et al., 1999; Lin and Sutherland, 2014).

Both levels are influenced by physical and biotic microhabitat variables such as incidental light or distance to the nearest neighbor. Several studies have shown patch divergence among microhabitat gradients, seedling survival compromised by particular stressful microhabitat conditions, and presence of tree canopies benefiting establishment, density and diversity. Overall, the response of species is related to stress-resistance strategies (either tolerance or avoidance) (Paez and Marco, 2000; Andrade et al., 2015; Ramírez et al., 2015; Silva et al., 2016).

Cephalocereus senilis (Haw.) Pfeiff., is an endemic columnar cactus of Mexico with restricted distribution in Hidalgo and Guanajuato states. Its populations are abundant but limited to small and well conserved areas. It is an endangered species by the IUCN red list (B1ab, iii,v; Guadalupe-Martínez et al., 2013) due to its limited distribution range with an occurrence of $2170 \, km^2$ approximately. It is primarily threatened by over-collection of juvenile plants (Hunt et al., 2006; Guadalupe-Martínez et al., 2013). *Stenocereus dumortieri* (Scheidw.) Backeb, has a wide distribution in México (Aguascalientes, Guanajuato, Hidalgo, Jalisco, Michoacán, México City, Morelos, Oaxaca, Puebla, Querétaro, San Luis Potosí and Veracruz). It is locally abundant; its population growth rate is not declining; and it is classified as of Least Concern by the IUCN Red List (Arias et al., 2013).

In the present study, we addresses the following questions: a) do the functional traits of cacti vary among micro-environmental conditions in dry environments?, b) Is there an increased micro-environment effect on a narrowly distributed vs a wide-ranging cactus species?

We hypothesize that *Cephalocereus senilis*, a species with restricted range, will have a constant spatial distribution, with specific morphological and functional attributes on each slope orientations where it occurs, and therefore greater sensitivity to environmental variation than *Stenocereus dumortieri*, a species of wide distribution, which presents higher spatial, morphological and functional variation on each orientation.

2. Material and methods

2.1. Study site

This study was conducted in the Metztitlan Ravine Biosphere Reserve (MRBR), Hidalgo, México. The area of the reserve has 2,090,512 ha, between 19°35′52"-21°25′00″ North latitude and 97°57′27"-99°51′51″ west longitude. The predominant climate of the study zone is dry-warm (BS0hw) with winter precipitation not exceeding 700 mm. Crasicaule scrubland covers the north and northeastern slopes, from 1300 to 1700 m asl, with species of *Yucca, Prosopis, Celtis, Bursera* and *Acacia* in the upper layer. The understory has species of Leguminosae, Compositae, Labiatae and Gramineae. These scrublands are dominated by cactus species, such as *S. dumortieri* and *Myrtillocactus geometrizans* although *Opuntiaficus-indica, Cylindropuntia tunicata* and *Echinocereus cinerascens* are also common.

2.2. Sample design

Four quadrats of variable size according to the slope topography, two per species, were placed on slopes with opposite orientation (East or West) in the Metztitlan valley during the dry season (Table 1). All individuals on each slope were mapped on XY coordinates for the

evaluation of the aggregation pattern. In addition, 15 plants were selected randomly per plot, each one designated as centroid within a circumference of 5 m radius ($3701 \, m^2$ evaluated area per plot), for the evaluation of chronic disturbance metrics (Martorell and Peters, 2009) and vegetation community composition (alpha and beta biodiversity index). Finally, morphological attributes of the selected plants were taken for the evaluation.

2.3. Spatial distribution

To determine the plant spatial distribution, the *Kt* function was used according to Ripley (1981) with the Spatial Analysis program (Duncan, 1990). These functions use a Poisson distribution of individuals with respect to 99 random points on each quadrat in ascending intervals of 0.5 m within the 5 m radius, the limit proposed by De la Cruz (2006) corresponding to less than a third of the quadrat lengths in order to diminish border effects. However, if the data exceed or do not reach the expected values generated by the *Kt* function, then an aggregated or random pattern is inferred, respectively. When the calculated data are within the expected range by the model, the distribution pattern is regular (Peter, 1995).

2.4. Morphological analysis

Four morphological-functional traits were measured on 15 individuals: height and width at 1.3 m, overall number of columns per individual (stems) and number of secondary branches for comparison between east and west slopes (James and McCulloch, 1990). The height was obtained using an electronic altimeter and width by a diametric clamp (Haglöf® both). A Generalized Discriminant Function Analysis (GFDA) was used to analyze the morphological traits. The GFDA was made twice, one by each species contrasting both slopes.

2.5. Disturbance state

Eleven environment-functional traits (Table 2) were used to measure disturbance and habitat variation according to the method of Martorell and Peters (2009), considering an average of the 15 circumferences by quadrat. A Multidimensional Scaling Analysis (MSA) based on Morisita's distances (Linares, 2001) of all metric measurements was made to observe association between exposure condition and data sets (StatSoft, 2011).

2.6. Diversity assessment

A complete identification of the vegetation community was made based on taxonomic lists and dichotomous keys (Rzedowski and Rzedowski, 2003). On the basis of abundance and richness of other species placed in the 5 m radius around each *Cephalocereus senilis* and *Stenocereus dumortieri* individual, we estimated the Hill's number (effective number of species) of order ^1D (Jost, 2006) to measure diversity for botanical communities on each orientation. Additionally, the β-diversity was calculated using the Whittaker's index (Whittaker, 1960) to evaluate the distance decay in similarity between plant species composition. Finally, a Multidimensional Scaling Analysis (MSA) was used to show the dissimilarity between slope communities based on Jaccard's distance matrix (StatSoft, 2011).

3. Results

3.1. Spatial distribution

The total number of *Cephalocereus senilis* located on the two orientations was 205 individuals (East: 75 individuals on $2400 \, m^2$, West: 130 individuals on $1225 \, m^2$) and the total *Stenocereus dumortieri* plants located on the two orientations was 135 (East: 55 individuals on

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Table 1
Micro-environmental conditions on East and West slope orientation.

Species	Aspect	Geographic location	Altitude (m asl)	Mean temperature (°C)	Slope (°)	Relative humidity (%)	Coverage (%)
Cephalocereus senilis	East	20°27′55.66″N 98°39′58.48″O	1351	38.5 ± 4.3	28 ± 14.6	2 ± 8.5	4.6 ± 2.3
	West	20°28′2.77″ N 98°39′58.9″O	1347	36.4 ± 6.2	35 ± 21.3	2.1 ± 9.3	5.4 ± 2.8
Stenocereus dumortieri	East	20°26′45.38″N 98°40′29.52″O	1608	38.7 ± 12.3	14.5 ± 37.8	14.2 ± 12.5	28.7 ± 16.8
	West	20°26′48.1″N 98°40′31.1″O	1612	34.4 ± 16.7	24.3 ± 53.2	17.3 ± 22.6	33 ± 28.7

Table 2
Evaluated disturbance measures, modified from Martorell and Peters (2009).

Type	Key	Measure
Human activities	PC	Fraction of plant cut: plants with machete cuts divided by the total number of plant in the circumference.
	WE	Fuel wood extraction: evidence of harvesting, proportional to circumference.
	HA	Adjacency to areas of human activity: proximity in meters to houses, cornfields, mines, chapels or other cultures.
	TUP	Cover of trails used by people: proportion of the circumference covered by trails.
	FE	Fire evidence: evidence of carbonized areas over trunks or soil within the circumference, this metric was recorded as presence-one or absence-zero.
Cattle activities	TUC	Cover of trails used by cattle: proportion of the circumference covered by livestock trails.
	CD	Frequency of cattle dung: both bovine and equine dung, registered as presence-absence
Environmental degradation	ESS	Percentage of eroded-soil surface: proportion of areas with removal of material by water within the circumference.
	STM	cover of surface totally modified: proportion of paved roads, houses, artificial waterways or old cultures within the circumference
Micro-environmental characteristics	S	Inclination in degrees: measured with SmartTool® clinometers.
	VC	Percentage of vegetation cover: measured with Forest® Spherical densitometer.

Table 3
Ripley's function $K(t)$ and functional traits of two columnar cacti species in the Metztitlan valley using 95% confidence interval (99 simulations) with a 0.5 m step. Plus sign indicates a clumped distribution and empty cell indicates a regular distribution. Ind/ha: Density of individuals per hectare, N: Total individuals, Plot: Evaluated area (m²), H: height (m), W: width (cm), He: number of heads, P: peaks,* significant contribution to GDFA.

Species	Slope	Distance										Ind/ha	N	Plot	H	D	He	P
		0.5	1	1.5	2	2.5	3	3.5	4	4.5	5							
Chepalocereus senilis	East					+	+	+	+	+		541.67	75	2400	5.56 ± 2.36	22.18 ± 5.47	3.13 ± 1.64	14.77 ± 10.16
	West											612.24	130	1225	6.18 ± 1.33	25.09 ± 3.22	3.46 ± 1.84	14.8 ± 13.7
Stenocereus dumortieri	East			+	+	+	+	+	+		+	550	55	1000	3.53 ± 1.13	38.59 ± 12.85	3.47 ± 1.96	14.67 ± 10.35
	West		+	+	+	+	+					1777.77	80	450	4.32 ± 1.35*	31.2 ± 9.1	4.1 ± 1.43	12.8 ± 8.56

1000 m², West: 80 individuals on 450 m²). The slope conformation, accessibility and density of individuals in the evaluated areas were different, so the evaluated quadrant does not show complete correspondence (Table 3).

Cephalocereus senilis exhibits a different distribution pattern between orientations with an aggregation pattern in a radius of 2.5–4.5 m on the east slope (Table 3, Fig. 1a) and a regular distribution in the west slope (Fig. 1b). *Stenocereus dumortieri* has a clumped distribution on both slopes, but with a different radius (Table 3), higher on the east (2–5 m, Fig. 1c) versus west orientation (1.5–3.5 m, Fig. 1d). Both species showed a greater density on the west than east hillsides, but with the highest difference between slope orientations in *S. dumortieri* (Table 3).

3.2. Morphological analysis

The GDFA show that *C. senilis* individuals do not differ morphologically ($F_{(4,25)}$: 0.828, p = 0.519) but *S. dumortieri* individuals are significantly different between orientations ($F_{(4,25)}$: 2.856, p = 0.045, Fig. 2). These differences are explained exclusively by height in a unique discriminant function (Wilk's lambda of height: 0.82, $F_{(1,25)}$: 6.154, p: 0.02; eigenvalue: 1.139, cumulative variance: 100%), with tallest plants on the west slope (Table 3).

3.3. Disturbance state

The MSA of disturbance traits comparing slope populations of *C. senilis* (N: 30, stress: 0.00079, dimensions: 9, alienation: 0.0011, Fig. 3a) corresponds to similar disturbance conditions between slopes. In contrast, *S. dumortieri* shows a contrast between slopes with major disturbed conditions on the east orientation (N: 30, stress: 0.00236, dimensions: 9, alienation: 0.0034, Fig. 3b) explained by two sets of contrasting traits (N: 9, stress: 0.00000038, dimension: 7, alienation: 0.0000038, Fig. 3c). East slope populations of *S. dumortieri* have a positive association with FE, PC, STM, WE and TUC; but a negative association with ESS, S, VC and TUP. There was no variation among areas of human activities (HA) and frequency of cattle dung (CD) on 30 radii of *S. dumortieri*; these variables were eliminated from the analysis.

3.4. Diversity assessment

The total area of the 15 random circumferences on each quadrat showed that *Selaginella lepidophylla* (Hook. & Grev.) Spring (East 72%, West 69%) and *Agave xylocantha* Salm-Dyck (East 18.7%, West 8.9%) were the principal floristic elements associated with *C. senilis* on both slope orientations. In contrast, different dominant composition between slope orientations were observed for *S. dumortieri*. On the east slope *Muhlenbergia tenuifolia* Kunth (74%), *Acacia subangulata* Rose (5.5%) and *Senna pringlei* (Rose) Irwin & Barneby (3.3%) were dominant; on
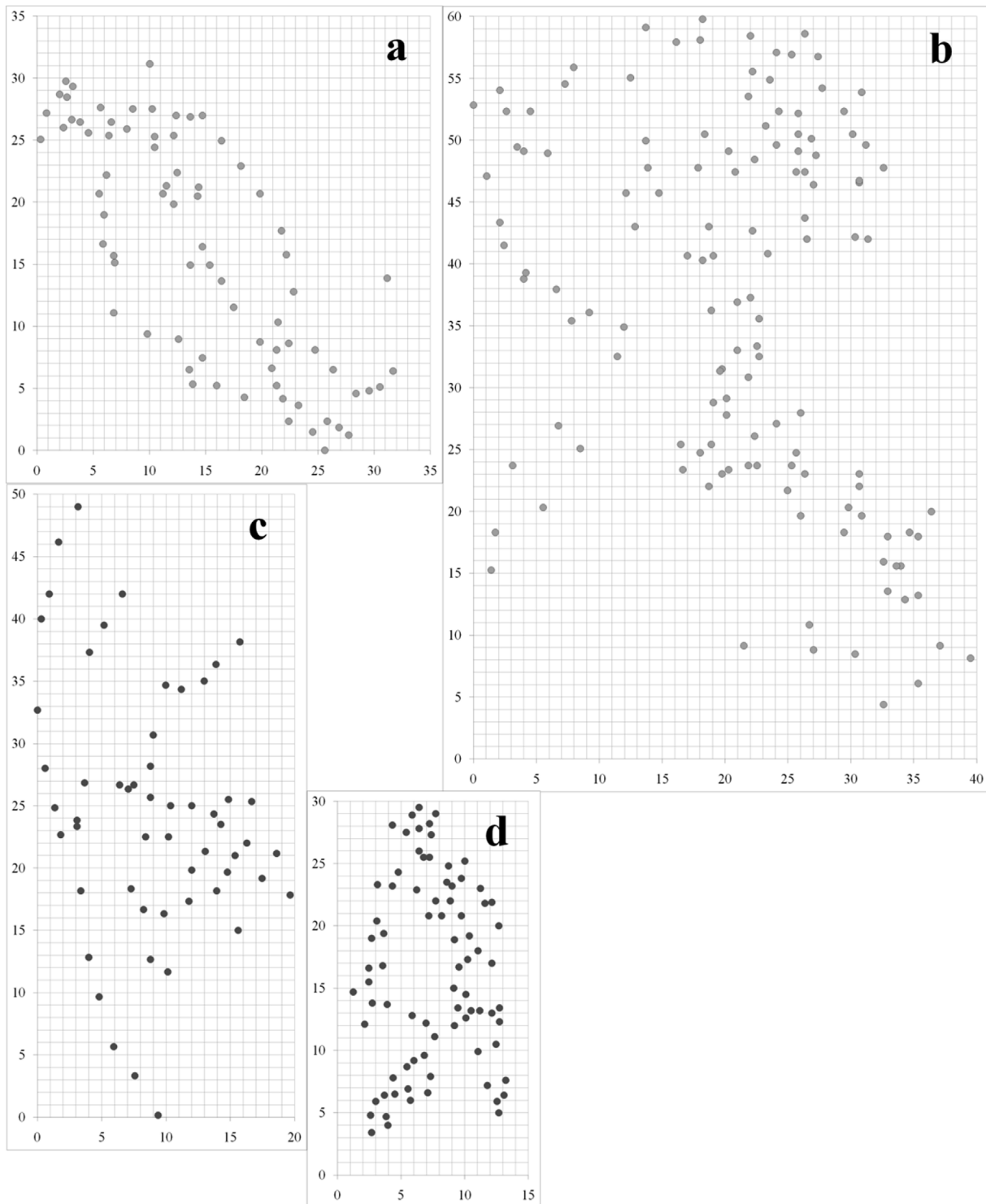
Fig. 1. Spatial distribution of two columnar cacti species in the Metztitlan valley (scale in meters). a) *Cephalocereus senilis* east slope, aggregation pattern between 2.5 and 4.5 m² of radius, b) *C. senilis* west slope, regular distribution, c) *Stenocereus dumortieri* east slope, aggregation pattern between 2 and 5 m² of radius, d) *S. dumortieri* west slope, so clumped aggregation pattern between 1.5 and 3.5 m² of radius.

the west slope *Anredera ramosa* (Moq.) Eliasson (12%), *Mammillaria crinita* DC. (9%), *Acacia subangulata* Rose (7.6%), *Celtis pallida* Torrey (7.4%), *Sedum dendroideum* Moc. & Sesse ex DC. (6.5%) and *Myrtillocactus geometrizans* (Mart. ex Pfeiff.) Console (5.4%), were the most abundant, showing a greater heterogeneity on the western than eastern slope.

The effective number of species was higher on west slopes for the communities of both species, but highest for *S. dumortieri* on the west slope (*C. senilis* east: 2.8, west: 4.2; *S. dumortieri* east 12.4, west: 29.8). β-diversity index suggests a higher similarity in plant species composition between slopes for *C. senilis* (3.5) than for the *S. dumortieri* community (4.2).

A clear dissimilarity between the associated community of *C. senilis* on each slope cannot be seen (N: 30, stress: 0.04, dimensions: 7, alienation; 0.05, Fig. 4a). In contrast, *S. dumortieri* communities differed by slope in the MDS analysis (Fig. 4b). In particular, we note three focal
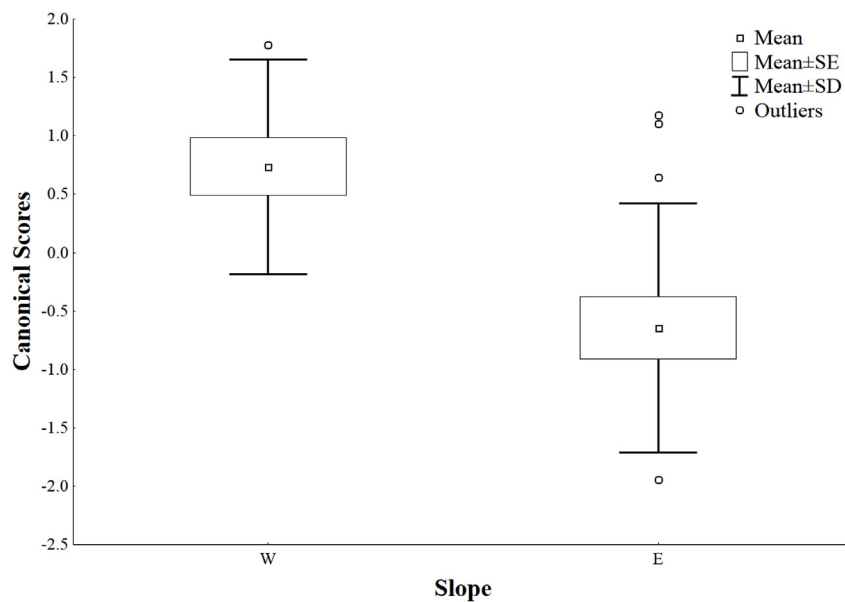
Fig. 2. GDFA with morphological traits of *Stenocereus dumortieri* individuals of different slope orientations. W: west, E: east. (Wilk's lambda of height: 0.82, $F_{(1,25)}$: 6.154, p: 0.02; eigenvalue: 1.139, cumulative variance: 100%).

radius groupings on the west slope with less diversity (Fig. 4b).

4. Discussion

The functional attributes of *Cephalocereus senilis*, the cactus with restricted distribution, on slopes with different orientations were constant (density, morphology, disturbance conditions and associated vegetal community) with the exception of spatial arrangement of individuals, which were clumped on the east (exposed) orientation and regular on the west (unexposed) orientation. In contrast, *Stenocereus dumortieri*, with wide distribution had different functional attributes, better on the west (unexposed) compared to the east (exposed) slope (aggregation radius smaller, highest density, higher plants, a more preserved environment, and greater vegetation diversity).

4.1. Spatial distribution

Landscape strongly influences microclimate on a local scale, in particular air and soil temperatures, and soil moisture and availability of nutrients (Ackerly et al., 2002, 2010). The dry condition on exposed orientations negatively affects seedling establishment and subsequent spatial aggregation patterns due to high mortality of seedlings and a heterogeneous mosaic of ideal microhabitat conditions (Kutiel, 1997). *Cephalocereus senilis* has a clumped distribution on the exposed orientation in restricted radius between 2.5 and 4.5 m, supporting the idea of a restricted environmental mosaic with optimal conditions for seedling establishment (Table 1). The regular distribution of plants in the protected orientation suggests a more homogenous microhabitat which promotes a higher density and low seed dispersal by bats, because them do not need find other food sources. Previous studies on *C. columna-trajani* in Tehuacan valley, showed that the seeds are rarely ingested by bats, which instead spit them out as they fly or perch to eat the fruits (Godinez-Álvarez and Valiente-Banuet, 2000; Rojas-Martínez et al., 2012). On the MRBR a healthy population of frugivorous bats are present, facilitating dispersal but with a differential efficiency (clumped on exposed hillside, related with poor dispersal) between orientations according to our results.

In the case of *Stenocereus dumortieri*, patch amplitude varies on unexposed slopes with the densest clumps of plants suggesting an unrestricted spatial competition. In contrast, on the exposed hillside, the species has an aggregate distribution with a greater radius, suggesting

plasticity in colonization capability of diverse microhabitats (Table 1). This capability is an advantage for the radiation of this cactus with respect to *C. senilis*. This radiation capacity has been associated with the preference of bats (same dispersers for *S. dumortieri*) for ingesting the seeds and defecating them in distant places at a distance greater than 3.5 km (Godinez-Álvarez et al., 2002; Rojas-Martínez et al., 2012, 2015).

4.2. Morphological analysis

Plant functional trait variability is a response to environmental factors, life history and, in some cases, healthy demographic structure (Martin, 1998; Ackerly et al., 2002; Callaway et al., 2002; Drezner, 2006; Andrade et al., 2015). Normally the observed variability of morphological traits within populations is not spatially structured, but differences among populations can correlate with environmental heterogeneity and genetic variation (Albert et al., 2010). In *C. senilis* there is morphological homogeneity between contrasting orientations, suggesting cohorts of similar age, poor recruitment (unhealthy demographic structure) and probably genetic homogeneity, although this assumption needs further analysis to prove.

In the case of *S. dumortieri*, we expected large differences between slope orientations due to a plastic environmental response, but only height varied significantly. This measure is correlated with plant age suggesting a demographic variation between orientations and a dominant adult population on the unexposed hillside. It has been suggested that plastic attributes can be adaptive because they allow radiation, colonization and competition (Leffler et al., 2014). The low allocation efficiency of GDFA on the west hillside (66%) suggests plasticity in height and therefore adaptive potential.

4.3. Disturbance state

Morphological traits and plant-plant interactions are functional attributes correlated with environmental variation (Schob et al., 2013). The incorporation of scaling relationships between morphological traits, vegetation models and community assembly allow the assessment of the combined effect of microhabitat attributes such as solar incidence, water, and disturbance regimes. Reduction of vegetation cover is the main disturbance, the effect of which increases drought stress by increased exposure to the sun due to loss of vegetation cover
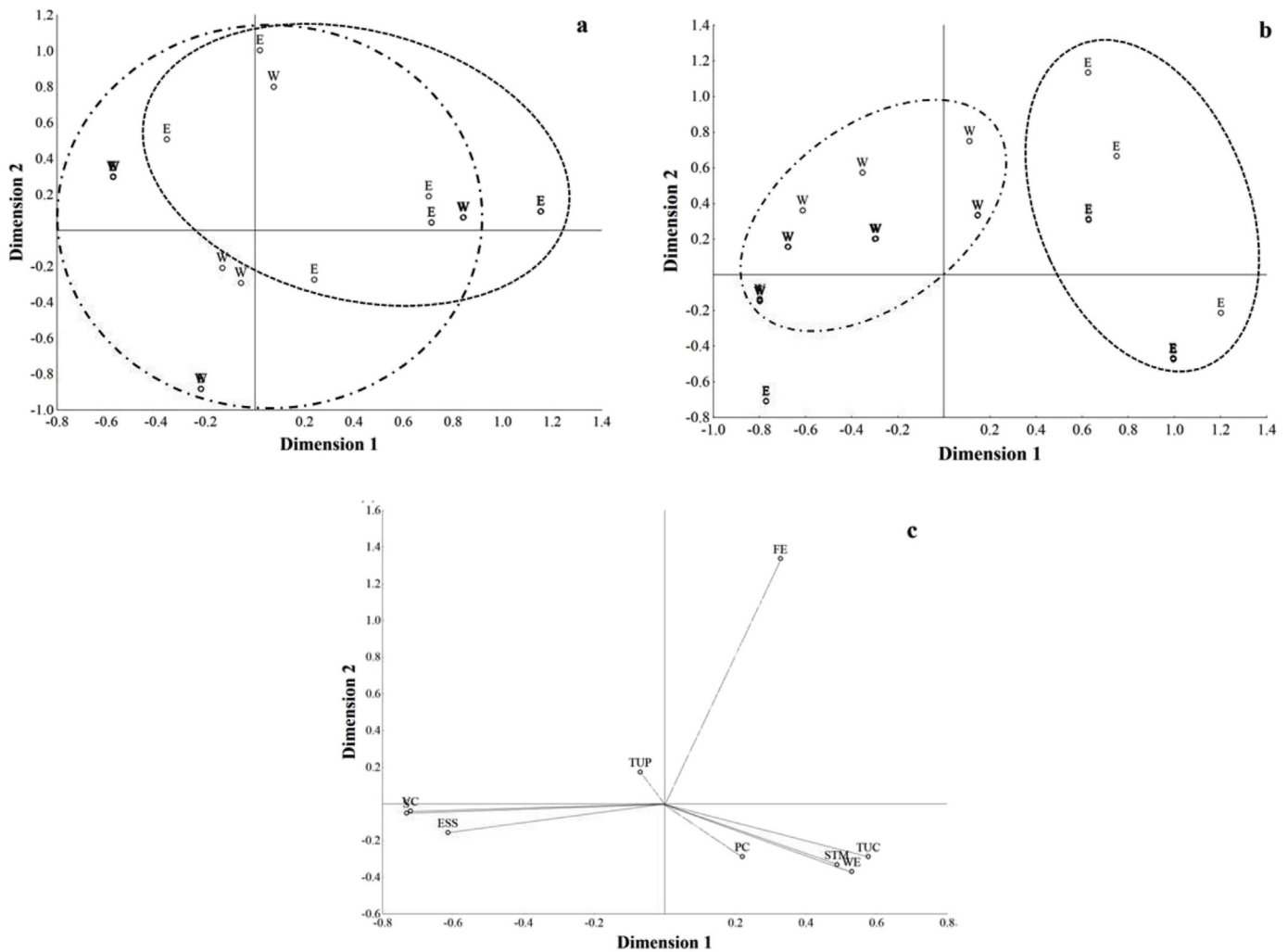
Fig. 3. MSA based on Morishita's distances of disturbance traits proposed by Martorell and Peters (2009), a) *Cephalocereus senilis* comparison between slope orientations, b) *Stenocereus dumortieri* comparison between orientations, c) Variable array dimensions of MSA with disturbing traits. W: west slope, E: east slope, S: inclination in degrees, VC: vegetation coverage percentage, ESS: eroded-soil surface, TUP: trails used by people, FE: fire evidence, PC: fraction of plant cut, STM: surface totally modified, WE: wood extraction, TUC: trails used by cattle.

(De Bello et al., 2012). *Cephalocereus senilis* persists on contrasting slope orientations but with stable microhabitat conditions without loss of vegetation coverage, thus maintaining moderate levels of sunlight, which protect young individuals from drought. *Stenocereus dumortieri* can persist under disturbed conditions but decreases in height. Moreover, community diversity is reduced and individuals become spatially isolated, which explain the patch amplitude. The most important disturbance traits for the maintenance of healthy populations are percentage of vegetation cover (VC), inclination (S) and percentage of eroded-soil surface (ESS), proportionally resulting in better fitness on unexposed hillsides.

4.4. Diversity assessment

Disturbance has important effects that cause reduction of native plant recruitment by competition and substitution (Álvarez and Cushman, 2002; Heleno et al., 2010; Meers et al., 2012). The effects are strongest on long-lived species with restricted distribution, normally associated with similar habitat conditions. In this way, vegetation community composition depends on constant interactions such as facilitation by nurse tree canopy shape. Cactus species need the presence of a canopy for establishment (Drezner, 2006, 2007, 2010), although some species show high radiation capacity and resistance and establish

on covered or exposed areas indiscriminately (e.g., *Mammillaria carnea*; Golubov et al., 2010). Cacti of restricted distribution are adapted to local conditions although facilitation could play a larger role in more sensitive individuals than those found under harsher overall conditions (Holmgren and Scheffer, 2010). Additionally, variation in survival capability depends on phenotypic plasticity and richness of the genetic base. *C. senilis* persists only in similar plant communities, while *S. dumortieri* has wide amplitude of associations with different species of plants.

Regarding disturbance, in all plots established in the Metztitlan Valley reserve, a wide divergence of disturbance states is not expected, however the results show greater variation based on human activities including fire events, presence of human settlements, wood extraction for fuel etc. The Martorell and Peter's (2009) method is suitable for the study of contrasting cacti populations to identify those attributes with greater impact on the persistence of the species. In addition, biodiversity in the Metztitlan Valley cannot be preserved by protection only of habitats at the core area of the reserve, where human activities have been limited or eradicated, because each species has a particular response to habitat degradation and some interactions are more affected than others by environmental alterations (Moreno et al., 2007).

In conclusion, we show that the functional traits of cacti vary among micro-environmental conditions in dry environments, but only in the
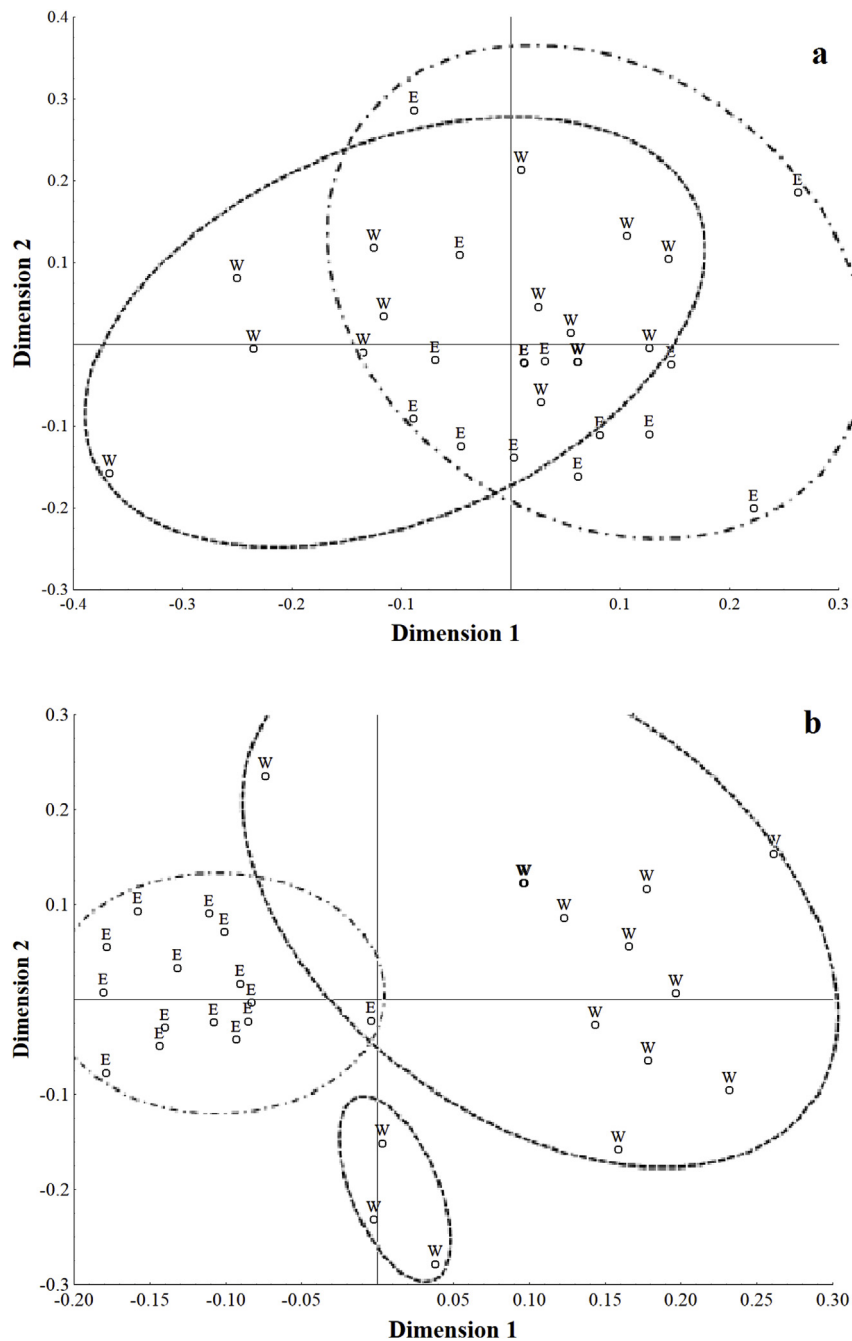
Fig. 4. MSA based on Jaccard's distances of communities composition. a) *Cephalocereus senilis* comparison between slope orientations, b) *Stenocereus dumortieri* comparison between orientations. E: east, W: west.

widely distributed *Stenocereus dumortieri*. By contrast, a cactus of limited distribution *Cephalocereus senilis,* requires stable microenvironment conditions due to its environmental sensitivity and dependence on habitat consistency. Our results are an example of the general response to micro-environmental variation of wide (tolerance) and restricted (avoidance) species in dry environments at population and community levels, representing evolutionary evidence of adaption divergence.

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