

Enhanced facilitation at the extreme end of the aridity gradient in the Atacama Desert: a community-level approach

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Abstract. Plant facilitation is now recognized as an important process in severe environments. However, there is still no agreement on how facilitation changes as conditions become increasingly severe. The classic stress gradient hypothesis (SGH) predicts a monotonic increase in facilitation, which rises in frequency as conditions approach the extreme end of the environmental gradient. However, few studies have evaluated the validity of the SGH at the community level, the level at which it was formulated. Moreover, few studies have tested the SGH at either extreme of the gradient, and very few have excluded the effect of livestock on community response to stress. In line with the SGH, we hypothesized that several spatial pattern summary statistics would change monotonically from the least to the most arid sites, indicating increasingly aggregated patterns. In this study, we performed an evaluation of the SGH both within communities of shrub species and across a large portion of the Atacama Desert, and we isolated the abiotic component of the SGH. Our environmental gradient covered an extreme aridity gradient (<20–130 mm annual precipitation). To perform point pattern analysis, we established 13 sites with environmental conditions representing four distinct levels of this gradient. Further, we conducted species co-occurrence analyses at 19 sites along the gradient. Both sets of analyses showed stronger positive spatial associations among plants at the most extreme end of the gradient. This was true regardless of whether we included all individuals, only small individuals located around large ones, or individuals in species pairs. Moreover, species tended to show greater co-occurrence as environmental severity increased. This increase in aggregation in the plant community seems to correlate with an increase in the strength of positive interspecific interactions, rather than greater clustering within each species. These monotonic increases in species co-occurrence and spatial association in more severe environments are consistent with some of the predictions of SGH, and collectively these results suggest that as the climate becomes more arid, positive species pairs interactions tend to be prevalent in the community.

Key words: aridity gradient; C-score; deserts; facilitation; plant–plant interactions; spatial patterns; stress gradient hypothesis.

INTRODUCTION

The importance of facilitation as a key determinant of plant community organization is now widely recognized, particularly when this facilitation occurs in communities characterized by environmental severity or stress (e.g., Bruno et al. 2003, Callaway 2007, He et al. 2013, Soliveres et al. 2015). In an influential paper, Bertness and Callaway (1994) postulated that facilitation and competition are inversely correlated along gradients of environmental stress: as sites become more stressful, facilitation increases in frequency and importance. This

“stress gradient hypothesis” (SGH) remains a frame of reference for studies that explore plant–plant interactions along stress gradients.

Tests based on a small number of species pairs have repeatedly supported the hypothesis (e.g., Aguiar et al. 1992, Callaway et al. 2002, Holzapfel et al. 2006, He et al. 2013), but there are some important exceptions (e.g., Kitzberger et al. 2000, Tielbörger and Kadmon 2000, Maestre et al. 2005, 2006). Interestingly, most of the studies that do not support the predictions of the SGH were conducted across aridity gradients. This finding motivated other hypotheses, such as the hump-shaped hypothesis, that predicts that facilitation should be more intense under moderate stress (Maestre and Cortina 2004, Michalet et al. 2006, Holmgren and Scheffer 2010),

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or the refined stress gradient hypothesis (Maestre et al. 2009), which emphasizes that the balance between facilitation and competition is dependent on the life strategy of the plant (stress tolerant and competitor) and/or the type of stress to which it is subjected (e.g., resource/non-resource dichotomy). Although Maestre et al. (2009) paper attempted to reconcile these two points of view, it led to further debate (e.g., He and Bertness 2014, Michalet et al. 2014, Soliveres and Maestre 2014).

In recent years, other studies have tried to provide broader context for the SGH (Brooker et al. 2008, Maestre et al. 2009, Soliveres and Maestre 2014). One of the main conclusions has been that very few studies have tested the SGH at the community level. In their review, Soliveres and Maestre (2014) found that only 18 of 208 studies addressed the balance between competition and facilitation in plant communities along environmental severity gradients; of these, only 10 were conducted in drylands, and seven of these were unpublished data of the authors themselves.

An additional weakness of studies testing the SGH has been the failure to sample across the entire stress gradient (but see, e.g., Baumeister and Callaway 2006, Kawai and Tokeshi 2007, le Roux and McGeoch 2010, Armas et al. 2011). Finally, studies might unintentionally have sampled over more than one stress gradient (Kawai and Tokeshi 2007, Verwijmeren et al. 2014), underscoring the need to separate abiotic and biotic stresses in such studies. The SGH, in fact, was originally conceived as an inverted hump on an axis that polarized biotic vs. abiotic stresses or pressures, with competition being greatest at intermediate levels of this axis (e.g., moderate biotic pressure and moderate abiotic stress) and facilitation dominating at the extremes of biotic and abiotic stresses. Moreover, and following a plant productivity gradient, at the less productive end of the gradient, facilitation is due to protection from harsh abiotic conditions, whereas on the more productive end, it reflects protection from herbivory. At many points on the less productive end, however, herbivory may be present via livestock grazing, which confounds interpretation; this has not been considered by most studies that have addressed the abiotic extreme of the curve.

Spatial pattern analysis is a way to test hypotheses about community organization, although the relationship between pattern and processes may be difficult to pinpoint without experimental manipulations (e.g., McIntire and Fajardo 2009). However, the emergence of new null models has increased the possibility of linking patterns and processes. Finding similar results from different null models may further support a conclusion based on spatial pattern analysis alone (Wiegand and Moloney 2014).

We developed a field study to evaluate the SGH that avoids three main concerns outlined above (i.e., scarcity of community level approaches, sampling along incomplete gradients, and presence of livestock). First, we sampled entire desert plant communities (e.g., all shrub species at a given locality) in one of the most arid places

on Earth, the hyperarid Atacama Desert. Second, our samples were taken over a very broad aridity gradient, extending to the hyperarid extreme of this gradient, where positive plant interactions would be expected to collapse (Michalet et al. 2014). Third, we controlled for the effect of livestock. Thus, our objective was to test the SGH according to the original assumptions of the hypothesis and along one of the most representative environmental gradients: aridity. Specifically, we asked if the strength of (1) intraspecific aggregation, (2) interspecific association, (3) the aggregation of all individuals regardless of species, and (4) the distribution of small (young) individuals around larger (old) ones, all increase as they approach the arid end of the gradient. We addressed these objectives by employing two different approaches to spatial pattern analysis: point pattern analysis and null model analysis of species co-occurrence. The former approach includes specific null models to test specific questions, and it may be complemented by the statement of a priori hypotheses (Schurr et al. 2004, McIntire and Fajardo 2014, Wiegand and Moloney 2014). Point pattern analysis has not been employed before to test the SGH. The later approach, the null model analysis of species co-occurrence, emphasizes identification of non-random species associations in presence-absence community matrices. This observed matrix is then randomized, the metric of interest (e.g., co-occurrence) is recalculated for the null assemblage and the process is repeated many times (usually 1000 times) to provide a distribution of expected values. If the observed value lies in the extreme tail of this distribution, it is considered to be significant (e.g., co-occurrence among species is more frequent than expected by chance).

We predicted that the strength of association (plant-plant co-occurrence) should increase monotonically as a positive function of aridity across this gradient, both at the level of individual species and for the entire assemblage. Furthermore, the association should have the same monotonic trend in small (young) individuals surrounding large (older) ones. Finally, we predicted that measures of inter- and intraspecific associations should be stronger and more positive in more arid sites. By applying two distinct approaches to these predictions, we believe that our study provides a robust test of the SGH among plant communities over a compelling gradient of stress. Moreover, if these approaches reveal a similar pattern, this will provide important insight into the response of plant communities to abiotic stress.

MATERIALS AND METHODS

Study area

For our point pattern analysis, based on mapping of individuals, field work was conducted in the coastal desert of Chile, along a wide geographic area ranging from the hyperarid Pan de Azúcar National Park (26° S) to the semiarid Bosque Fray Jorge National Park (31° S; Fray

Jorge, hereafter). In our study, latitude can be used as a proxy for environmental harshness, because in the Atacama Desert there is an increasing aridity gradient from south to north between the latitudes 25° and 30° S (DGA 1987, Arroyo et al. 1988). The former two regions represent the extremes of the gradient at which observations were made. Two other regions were Quebrada El Romeral (29.5° S) and, further north, Llanos de Challe National Park (28° S; Fig. 1). Although there are no specific precipitation data for Pan de Azúcar, nearby localities are notably xeric (e.g., Chañaral, 7 mm/yr; Taltal, 21 mm/yr; both sites are within a few kilometers of Pan de Azúcar [di Castri and Hajek 1976]). Rainfall at Fray Jorge (~130 mm/yr) is one order of magnitude higher than in Pan de Azúcar. Considering that Pan de Azúcar constitutes the most arid limit of growth for shrubland communities, while the Fray Jorge is a transition to dry Mediterranean environments, the gradient includes what could be considered the extremes in the region of the Atacama Desert for shrub communities. Following a gradient of more to less arid conditions, we sampled 13 sites at the four regions as follows Pan de Azúcar ($n = 3$), Llanos de Challe ($n = 4$), Romeral ($n = 2$), and Fray Jorge ($n = 4$; Fig. 1, Table 1).

We also conducted a null model analysis of species co-occurrence, for which we visited the same regions and sites as those used for spatial pattern analysis, with a few exceptions. In Llanos de Challe, we only sampled two of the four sites, and at Fray Jorge we sampled three of the four sites. We added a site (Flamenco), geographically located between Pan de Azúcar and Llanos de Challe. Furthermore, we analyzed seven additional sites that had been sampled previously. Four of these were inside national parks (two sites in Fray Jorge and two in Llanos de Challe), while another three sites were located outside these parks. The final three sites were impacted by domestic livestock, but were included nonetheless to increase sample size; results did not change qualitatively if these were excluded, however. Hence, a total of 19 localities was included in our analysis. For null model analysis, we also used latitude as a proxy for environmental harshness.

Plant cover is frequently used as a surrogate for environmental severity, and some authors believe it represents the integrated response of vegetation to the entire set of stressful conditions of a given locality (Lortie and Callaway 2006, Dullinger et al. 2007, Maestre et al. 2009, Soliveres et al. 2010). Following this logic, we also defined our gradient on shrub cover, the dominant life form in our study area. Specifically, the locality (site) with the greatest environmental severity was defined as that with the least absolute shrub cover (total shrub cover [m^2]/whole surface of the plot). Cover decreased monotonically with decreasing latitude, i.e., from Fray Jorge to Pan de Azúcar.

Since the goal of the present study was to analyze the abiotic component of the SGH, and thus, how spatial patterns in these communities are influenced by those

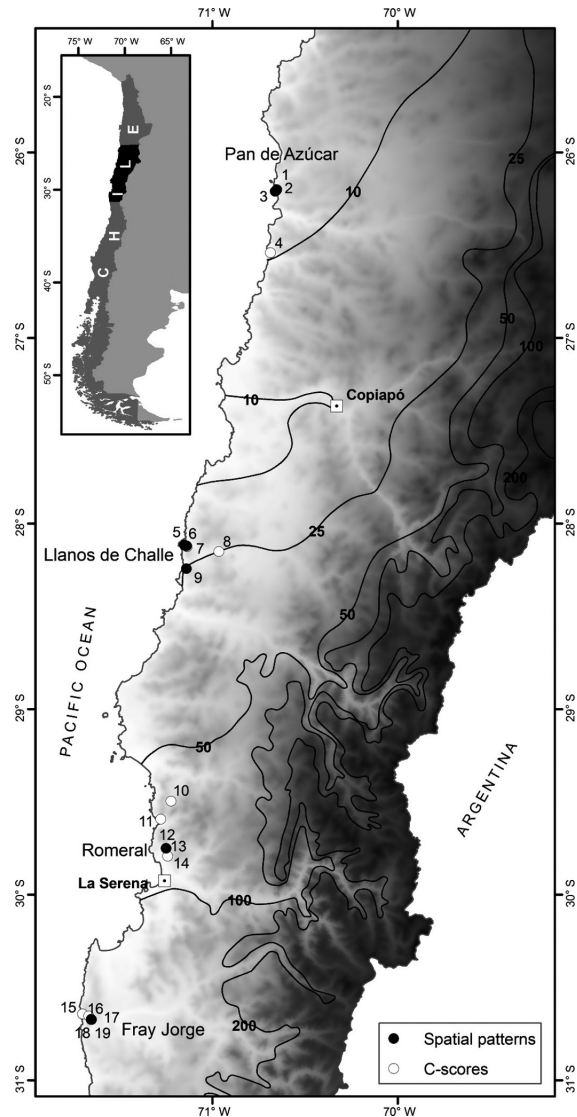


FIG. 1. Location of sites along the Atacama Desert region (black area in inset). Black dots indicate plots where point pattern analysis was performed while white dots indicate those sites where plant co-occurrence (checkerboard score [C-score]; Stone and Roberts 1990) was measured. Squares indicate major cities. Different shading indicates different altitudes (the darker, the higher). Numbered lines represent isohyets (mm).

conditions, we worked in protected areas where biotic influences such as those due to domestic animals (e.g., goats, cattle, sheep, and horses) were absent or minimal. As noted above, our results were not altered by the inclusion of three sites outside Fray Jorge and Llanos de Challe, which were exposed to livestock grazing.

Soil samples

At Pan de Azúcar (Lobera and Alluvial Fan) and Llanos de Challe (Hill Slope and Dunas) we collected three ~15 cm deep soil samples (~1 kg each) from open spaces, and three similar soil samples beneath dominant

TABLE 1. Localities studied and site characteristics for (a) point pattern analysis and (b) null model analysis.

Region and site	Geographic position	Plot size (m)	No. individuals mapped	No. dead individuals	No. shrub species	Shrub cover (%)	C-score SES
a) Point pattern analysis							
Fray Jorge							
Plot 3	30°40'24.02", 71°39'2.16"	30 × 25	580	130	8	44.9	
Plot 2	30°40'22.31", 71°39'4.64"	30 × 30	391	72	5	65†	
Plot 4	30°40'20.85", 71°39'9.03"	30 × 30	403	48	6	61.5	
Plot 1	30° 40' 17.28", 71° 39' 9.04"	30 × 30	407	137	9	49	
Romeral							
Romeral 1	29°44'59.57", 71°14'57.60"	30 × 23	482	112	13	57.3	
Romeral 2	29°44'58.47", 71°14'57.60"	30 × 30	300	77	13	44.9	
Llanos de Challe							
Hill slope	28°14'32.79", 71°08'22.93"	30 × 20	487	102	10	25.2	
Copiapoal	28°07'10.8", 71°08'18.1"	30 × 30	389	40	8	15.7	
Dunas	28°06'53.97", 71°09'0.07"	30 × 30	366	60	10	30.9	
Dunas 2	28°06'53.9", 71°09'0.09"	30 × 30	408	51	11	26.9	
Pan de Azúcar							
Alluvial fan	26°12'17.95", 70°39'17.81"	30 × 20	360	184	2	3.7	
Lobera	26°12'33.22", 70°39'38.06"	30 × 25	311	107	4	4.9	
Old river bed	26°11'57.99", 70°39'9.56"	20 × 15	191	46	3	3.3	
b) Null model analysis							
FJ_plot3	30°40'24.02", 71°39'2.16"					44.9	3.32
FJ_plot2	30°40'22.31", 71°39'4.64"					65	3.51
FJ_plot4	30°40'20.85", 71°39'9.03"					61.5	1.49
Site6_FJ.LasVacas	30°39'10.83", 71°39'56.77"					50	3.08
Site7_FJ.platform	30°38'31.25", 71°41'58.18"					53	-1.37
Site1_Romeral	29°47'33.3", 71°14'25.0"					13	3.97
Romeral1	29°44'59.57", 71°14'57.60"					57.3	3.10
Romeral2	29°44'58.47", 71°14'57.60"					44.9	2.63
Site5_Temblador	29°35'32.5", 71°16'40.6"					18	0.45
Site4_Higuera	29°29'42.9", 71°13'20.4"					19	3.40
BaseCerro	28°14'32.79", 71°08'22.93"					25.2	2.25
Site2_Challe	28°09'02.7", 70°57'53.6"					12	-0.78
Site3_Copiapoal	28°07'28.5", 71°08'09.8"					21	1.86
Copiapoal	28°07'10.8", 71°08'18.1"					15.7	3.89
Dunas	28°06'53.97", 71°09'0.07"					28.9	1.02
Flamenco	26°32'23.90", 70°41'11.84"					5	0.83
Lobera	26°12'33.22", 70°39'38.06"					4.9	-0.04
Alluvial fan	26°12'17.95", 70°39'17.81"					3.7	-2.90
Old river bed	26°11'57.99", 70°39'9.56"					3.3	-0.82

Notes: In (a), we show the four regions studied; the localities from each region; the geographic position along the gradient; the size of the plots laid out for mapping of individuals; the numbers of individuals mapped (dead and alive); the number of the dead individuals mapped; the number of shrub species inside the plot; and the cover of shrubs inside the plot. In (b), we show the locality; the geographic position; the cover of shrubs; and the standardized effect size (SES) calculated as (observed C-score—mean of simulated C-scores)/(standard deviation of simulated C-scores). The C-score (checkerboard score) is an index of co-occurrence (negative values indicate aggregation). In both (a) and (b), the sites are ordered by latitude, a good proxy for aridity in the Atacama Desert (the lower the latitude, the more arid the site). †Includes cover of subshrubs and perennial herbs.

shrubs. At Romeral, we took four soil samples from open spaces and eight from beneath canopies (four underneath *Flourensia thurifera* and four beneath *Pleocarpus revolutus* shrubs). Soil analyses included organic material, pH, texture, and total N, P, and K. Analyses were performed in the Technological Center for Soils and Crops of the University of Talca (Talca, Chile).

Data collection for point pattern analysis

In each of the four study regions, one plot was established per site (there were two to four sites per region, Table 1), except for one locality in Llanos de Challe, where two plots were laid out in the same locality (Dunas and Dunas 2). Thirteen plots were studied in total. Most

plots were 30×30 m in size (Table 1), which was large enough to include several individuals of the dominant shrub species across different size classes. Plots were chosen to be as internally homogeneous as possible, i.e., they lacked obvious relief, stream beds, etc., they presented similar aspect, soils, and slopes throughout, and did not include large boulders or gullies. All shrubs inside the plots, from sapling to adult size, were mapped and measured to the nearest decimeter. Plant size was quantified using plant height and largest and smallest crown diameters (see *Point pattern analysis*). Many species in all four regions employ vegetative propagation, but for most of the mapped points, it was easy to identify distinct individuals. In cases where it was not, we registered seemingly dependent shoots as part of a single individual. When in doubt, we excavated the soil to determine if there were underground connections. When it was clear that several branches represented a single individual, the main shoot (the larger one) was considered the central point to be mapped; otherwise, when there was no dominant branch, the location of the centroid was used.

Data collection for null model analysis

At each site, shrub species presence was recorded in at least 100 1×1 m quadrats that were established at 5-m intervals along 10 parallel, 50-m transects. This scheme was sometimes modified to adapt to topographic heterogeneities. In each quadrat, shoot frequency was determined by recording the presence of all woody plants (shrubs) that had shoot projections inside the quadrat; dead individuals were also included if they could be identified. In one case, a species of subshrub presented large cover inside the plot (Site7_FJ.Platform) and was included. Plant specimens were collected for identification when required.

Point pattern analysis

Point pattern analysis was conducted with the *Programita* software (Wiegand and Moloney 2004, 2014, Wiegand et al. 2013). We used the pair correlation function, $g(r)$ (Stoyan and Stoyan 1994), which is regarded as one of the best indexes for the detection of spatial patterns at different distances (Wiegand et al. 2013, Wiegand and Moloney 2014). The univariate pair correlation function, $g_{11}(r)$, is a non-cumulative neighborhood density function that estimates the density of neighbors within a class or group at distance r from the typical point of the pattern, divided by the overall density λ of the pattern (λ = number of points/ area; Wiegand et al. 2013). In this case, a class is operationally defined to comprise a group of plants of interest; this may be all individuals of a selected species, all living shrubs, etc. If plants (and hence neighbors) are distributed randomly, then the value of the pair correlation function yields $g(r) = 1$. Values greater than 1 indicate aggregation, and those lower than one indicate segregation or regularity.

In contrast to the univariate pair correlation function, the bivariate pair correlation, $g_{12}(r)$, characterizes spatial relationships between two classes, e.g., young vs. adult plants of a given species, living vs. dead shrubs, etc. This is defined as the expected density of neighbors of one class at a distance r from the typical individual of the second class, divided by the overall density λ_1 of the pattern of the first class. As with the univariate pair correlation function, values greater and lower than 1 indicate attraction and repulsion, respectively.

One way to quantify the strength of an interaction at small distances (which are of greatest interest given the objectives of our study) is to record the value of $g(r)$ using small radii around focal shrubs (Barot et al. 1999, Getzin et al. 2008). We therefore conducted four different analyses using a radius of 2 m around focal shrubs. Inside that radius we expected strong shrub-shrub interactions. These $g(r)$ scores were used to determine the strength of aggregation along the aridity gradient. These four analyses were addressed: (1) all individual shrubs (of all species), (2) intraspecific interactions (using only the two or three most dominant species), (3) interspecific interactions (pairwise species-species interactions between the two or three most dominant species), and (4) small individuals around large individuals (regardless of species).

For the first of these tests (the univariate pair correlation function for all individuals regardless of species), we compared the observed pattern to a null model assuming complete spatial randomness (CSR). This allowed us to determine if a given pattern was aggregated, regular, or random. If the pattern was aggregated, CSR permitted us to determine the degree of aggregation (e.g., based on deviation from CSR). We expected the degree of aggregation to be greater in more arid regions. For the second test (the univariate pair correlation function for intraspecific aggregation), we again compared observed patterns to a CSR null model. In contrast, for the third test (the bivariate pair correlation function for interspecific aggregation), we compared observed patterns against an independence null model (toroidal shift), which allowed us to discern if a given species pair was associated, and how strong that association was. Finally, for the distribution of small individuals around big ones (thus, a bivariate pair correlation function), the antecedent condition null model was considered; this analysis tests whether there are more points of a given class (in this case, small individuals) in the vicinity of points of another class (here, adults). This model is the one most directly related to facilitation, given that this positive interaction usually involves nurses (adult shrubs) and seedlings/saplings distributed near those nurses. Because we did not map the locations of seedlings, the small individuals were those of the smallest sizes, many of which were true saplings (1–3-yr-old individuals, based on personal observations). Size was calculated from three measurements: height and largest and smallest crown diameters. These values were inserted into the formula of an elliptical cone ($1/3 \times 3.1416 \times \text{height} \times \text{largest crown diameter} \times \text{smallest crown diameter}$). We favored this

synthetic metric over any single linear measurement since a single size parameter may be biased for a myriad of reasons, including accidents, droughts, and herbivory.

Plant size was used as a proxy for age. For each species, we divided all the individuals in two halves. Those in the upper half were considered to be adults, and those in the lower half were considered juveniles. Maximum values of $g(r)$ at small distances (<2 m) in each of the four analyses were used to determine the strength of aggregation along the aridity gradient. To make results comparable, we standardized the $g(r)$ values using the standardized effect size (SES) (observed $g(r)$ – mean of 199 randomizations)/(standard deviation of simulated $g(r)$ values). A $g(r)$ value of 5 at a 1-m distance, for example, means that the average neighborhood density 1 m away from a given shrub is five times higher than that expected under a random pattern. We expected the value of $g(r)$ to covary positively with aridity across the four regions studied.

To have a single value that represented the regional strength of the interaction, we averaged the $g(r)$ values for each of the dominant species from each of the sampling sites. Since we aimed to assess average community response, we also averaged the values from all interactions between species pairs, regardless of whether they deviated significantly from randomness. These two values were employed to compare the strength of intraspecific vs. interspecific aggregation. This comparison can indicate whether competition was greater within or among species.

Null model analysis

For each locality, species were organized into a presence-absence matrix (species in rows, quadrats in columns), generating 19 matrices. Matrices were analyzed using null models that randomize the matrices, and co-occurrence was quantified using the checkerboard score (C-score; Stone and Roberts 1990) as a summary statistic. The C-score, which measures how often different species pairs appear in the same quadrats, is considered one of the best indexes to determine species co-occurrence patterns for sample lists (Gotelli 2000); the higher the C-score, the less co-occurrence between all of the species pairs in the community. An observed C-score was calculated for each locality and all 19 indices were compared to indices derived from 5000 randomly assembled matrices (null matrices). The null model used to generate null matrices was based on the fixed-equiprobable algorithm, which has low Type I error, good power to detect non-random patterns, and is recommended when the data matrix has many zeros and sampled communities are considered homogeneous (Gotelli 2000). In this algorithm, row totals are fixed, whereas column totals may vary but remain equally probable.

We chose the fixed-equiprobable algorithm instead of the more widely used fixed-fixed (rows and columns fixed) algorithm because we considered that all the plots within a matrix were equally suitable to all species (hence

our systematic sampling; see López et al. 2013 for a similar approach). In this sense, our analysis assumes the sample plots are homogeneous. We registered shrub patches and open spaces as variants of the same community. Thus, our sampling resulted in some degenerate matrices (samples without species records); all our localities had some empty sites.

Because raw C-score values vary depending on species number, incidence, and co-occurrences observed at each locality, a standardized effect size (observed C-score – mean of simulated C-scores)/(standard deviation of simulated C-scores) was calculated for each matrix so as to compare results across sites (see, e.g., Dullinger et al. 2007). The SES measures the number of standard deviations that the observed index is above or below the mean index of the simulated communities. If values are positive, then there are fewer co-occurrences than expected by chance, whereas if they are negative, then there are more co-occurrences. Fewer co-occurrences are interpreted to be indicative of competition, whereas more co-occurrence suggests facilitation. Assuming a normal distribution of deviations, approximately 95% of the SES values should fall between -1.96 and 1.96 standard deviations from the mean, provided that co-occurrences are not different from that expected by chance alone. The SES analysis was performed with EcoSim7 (Gotelli and Entsminger 2005).

The SGH was tested by modeling co-occurrence as a function of aridity using regression analysis. We regressed the SES from all localities against their respective latitude or cover values (Table 1). A positive relationship would provide evidence for the SGH (i.e., the higher the value on the aridity gradient the more positive the SES of the C-score). In all cases, we employed first-, second-, and third-order polynomial regressions in order to identify linear and nonlinear relations, and to assess the best fit of the data. Fitted models were compared using an information-based theory framework. The best model for each type of predictor (aridity–latitude or cover) was then selected according to the lowest Akaike information criteria (AIC) value and results from the likelihood ratio test to select the best model (Lehmann 1989, Pinheiro and Bates 2000). All these statistical analyses were performed using the `gls` function in R software (R Development Core Team 2014) by way of the interface implemented in InfoStat-Statistical software (Di Rienzo et al. 2014). Finally, we carried out an empirical Bayes approach aimed at detecting if specific pairs of species are influencing the matrix wide results (Gotelli and Ulrich 2010). For this we used the program Pairs (Ulrich 2008).

RESULTS

Soil samples

Soils in all studied regions were sandy (the great majority with sand contents in soils $>75\%$), and included varying amounts of loam. Levels of N, P, and K were

higher underneath shrubs, especially K and P. This was particularly true in Pan de Azúcar (Table 2).

Plant–plant associations

An examination of the global (community level) pair-correlation $g_{11}(r)$ values (all individuals regardless of species; CSR null model) reveals a trend in the values from Llanos de Challe (second most arid region in the

TABLE 2. Soil characteristics in three of the studied regions.

Region and site	N† (mg/ kg)	P (mg/ kg)	K (mg/ kg)	OM (%)	pH
Romeral					
Open_4	4	16	134	1.14	7.73
Open3	10	8	60	0.54	8.53
Open4	8	5	36	0.21	8.41
Open5	11	7	43	0.18	8.38
Flourensia1	10	26	513	1.94	7.62
Flourensia2	15	25	408	0.9	7.46
Flourensia3	17	43	448	0.73	7.86
Flourensia4	68	86	528	2.61	7.19
Pleocarphus3	12	31	180	1.11	8.61
Pleocarphus3	11	13	233	0.12	8.97
Pleocarphus3	8	11	56	0.31	8.75
Pleocarphus_S/N	12	29	475	1.09	8.71
Llanos de Challe					
Hill.slope01	6	75	438	1.6	8.9
Hill.slope02	4	14	605	1.23	8.39
Hill.slope03	4	22	523	0.79	8.71
Hill.slopeS1	24	28	743	1.06	7.05
Hill.slopeS2	15	55	685	4.83	5.72
Hill.slopeS3	12	73	397	5.59	6.78
Dunas.Open1	5	19	95	0.33	8.94
Dunas.Open2	3	11	91	0.56	8.94
Dunas.Open3	5	192	144	1.27	9.04
Dunas.Shrubs1	15	140	395	1.27	9.87
Dunas.Shrubs2	8	169	299	1.77	9.68
Dunas.Shrubs3	11	245	391	2.65	9.83
Pan de Azúcar					
Lobera 1	6	3	193	0.36	8.18
Lobera 2	4	5	124	0.43	8.49
Lobera 3	24	4	365	0.43	9.19
Lobera S1	23	82	541	2.79	8.70
Lobera S2	5	84	654	9.30	7.73
Lobera S3	18	42	591	5.53	7.89
Alluvial.fan01	3	5	220	0.43	7.69
Alluvial.fan02	4	8	186	0.57	6.33
Alluvial.fan03	3	3	154	0.19	8.18
Alluvial.fanS1	5	45	882	3.46	8.29
Alluvial.fanS2	11	254	878	3.53	8.19
Alluvial.fanS3	15	153	1546	16.41	7.9

Notes: N, total nitrogen; P, phosphorous; K, potassium; OM, organic matter. Values are shown for soil samples collected beneath shrub canopies (boldface type) and away from shrubs. A few replicates were taken from each locality for each microhabitat.

TABLE 3. Results for the complete spatial randomness (CSR) null model, considering all individuals regardless of species.

Region	Average $g_{11}(r)$ by region	Average $g_{11}(r)$ by region, SES
Fray Jorge	1.30	4.96
Romeral	1.44	4.02
Llanos de Challe	1.30	1.94
Pan de Azúcar	2.47	10.09

Notes: The average pair-correlation function, $g_{11}(r)$, indicates the average $g_{11}(r)$ value of all the localities in a given region. The second column shows the unstandardized $g_{11}(r)$ for the dominant species; the third column shows standardized effect sizes (SES).

gradient) toward both the less arid and the more arid extremes (Table 3, SES values). However, the $g_{11}(r)$ value for Pan de Azúcar, the most arid region, is markedly greater, indicating significantly stronger aggregations (Table 3 and Appendix S1: Table S1).

The $g_{11}(r)$ values for the dominant species vary slightly from region to region (CSR null model for each species), but they do not show a latitudinal trend (Table 4 and Appendix S1: Table S2). This is not the case for the $g_{12}(r)$ values of the interactions (toroidal shift null model), the average value of which increases monotonically from Fray Jorge to Pan de Azúcar (Table 5 and Appendix S1: Table S3).

TABLE 4. Results for the complete spatial randomness (CSR) null model considering all individuals within the dominant species.

Region and site	Average $g_{11}(r)$ by locality	Average $g_{11}(r)$ by region, SES
Fray Jorge		6.41
Plot 1	3.59	
Plot 2	2.37	
Plot 3	1.55	
Plot 4	1.69	
Romeral		5.06
Romeral 1	1.8	
Romeral 2	3.63	
Llanos de Challe		5.16
Copiapoal	1.7	
Dunas	1.71	
Dunas 2	1.89	
Hill slope	1.86	
Pan de Azúcar		6.21
Lobera	1.66	
Alluvial fan	2.82	
Old river bed	2.03	

Notes: The average pair-correlation function, $g_{11}(r)$, by locality indicates the unstandardized, average $g_{11}(r)$ value of the dominant species in each locality. The $g_{11}(r)$ by region shows the standardized effect size (SES) of $g_{11}(r)$ values averaged across all localities from a given region.

TABLE 5. Results for the independence null model (inter-specific association), considering the pairwise interaction among the dominant species in each locality.

Region and site	Average $g_{12}(r)$ by locality	Average $g_{12}(r)$ by region	Average $g_{12}(r)$ by region, SES
Fray Jorge		1.27	0.22
Plot 1	1.39		
Plot 2	0.8		
Plot 3	1.06		
Plot 4	1.22		
Romeral		1.39	0.32
Romeral 1	1.03		
Romeral 2	1.6		
Llanos de Challe		2.15	2.42
Copiapoal	1.08		
Dunas	3.75		
Dunas 2	1.18		
Hill slope	1.64		
Pan de Azúcar		2.7	7.28
Lobera	3.71		
Alluvial fan	2.32		
Old river bed	2.08		

Notes: The average pair-correlation function, $g_{12}(r)$, by locality indicates the average $g_{12}(r)$ value of all the species \times species associations in each locality; the average pair-correlation function, $g_{12}(r)$, by region indicates the average $g_{12}(r)$ value from all localities within a given region. The last column is the same as the second-to-last column, but with the values standardized (SES).

Finally, the antecedent condition null model (model for the bivariate pair-correlation test for small individuals around large individuals) produced a pattern similar to the global model, with SES values increasing from Llanos de Challe toward both extremes. As with the global model, values at Pan de Azúcar indicated greater sapling aggregation around adults in this region (Table 6 and Appendix S1: Table S4).

Null model analysis

Species aggregation measured by C-score analysis increased with higher aridity (significant for the

TABLE 6. Results for the antecedent condition null model considering all individuals within the dominant species (small individuals around large individuals; the larger the value, the more aggregated small individuals are around large ones).

Region	Average $g_{12}(r)$ by region	Average $g_{12}(r)$ by region, SES
Fray Jorge	1.46	4.55
Romeral	1.61	3.46
Llanos de Challe	1.27	2.94
Pan de Azúcar	2.54	6.19

Notes: The average pair-correlation function, $g_{12}(r)$, indicates the average $g_{12}(r)$ value for all the localities in each region. The last column is the same as the middle column, except that the values are standardized (SES).

latitudinal gradient, marginally significant for the cover gradient; Appendix S1: Tables S5 and S6, Fig. 2). For the latitudinal gradient, the relationship was best described by a quadratic model (adjusted $r^2 = 0.33$, $P = 0.017$, although the improvement in fit compared to a linear model was small). For the analysis of cover as a proxy for stress, the regression models are either not significant or marginally significant (Appendix S1: Table S6; $r^2_{\text{adj}} = 0.27$, $P = 0.053$ for the cubic model, $r^2_{\text{adj}} = 0.19$, $P = 0.074$ for the quadratic model, and, $r^2_{\text{adj}} = 0.11$, $P = 0.089$ for the linear model). If one apparent outlier (Site7_FJ.Platform, highlighted in Fig. 2) is omitted, regressions are highly significant and there are large increases in r^2 (Appendix S1: Table S6). Based on AIC values and the likelihood ratio test and with this site outlier omitted, the best model was the linear regression in the case of latitude, whereas the best model was the quadratic one for shrub cover (Appendix S1: Table S6b). This apparent site outlier is a shrubland with an important dominant component of subshrubs in the community; it is dominated by a large woody rosette species (*Puya chilensis*), which has a life form not present in the other 18 communities sampled.

The empirical Bayes approach showed that very few species pairs yielded significant associations (Appendix S1: Table S7). The percentage of species pairs positively associated ranged between 0% and 11% of all species pairs found in their respective sites, and was not related to latitude or plant cover; hence, there was no tendency for aggregated pairs to be in the more stressful part of the gradient. There were some species pairs appearing in different sites along the gradient, but frequently they had neutral associations and did not influence the matrix wide results. A functional group frequently related with positive associations with other species was that of cacti (several species).

DISCUSSION

This study evaluated whether spatial patterns of Atacama Desert plant communities varied according to theoretical predictions along a sharp aridity gradient. We documented a clear tendency for directional, monotonic, positive change toward stronger interspecific associations as aridity increases. This trend was documented with two distinct approaches, which is particularly important since the conceptual bases of these two types of spatial pattern analyses are different; mapping of individuals is based on inter-plant distances, while co-occurrence analysis assesses whether different categories (e.g., species, size classes) occur more frequently than expected. It is noteworthy that interspecific aggregation increased monotonically along the aridity gradient, while intraspecific association did not; moreover, the relative importance of interspecific vs. the intraspecific associations indices changed over the gradient, such that the inter-specific $g_{12}(r)$ value became higher than the intra-specific $g_{11}(r)$ value as aridity increased.

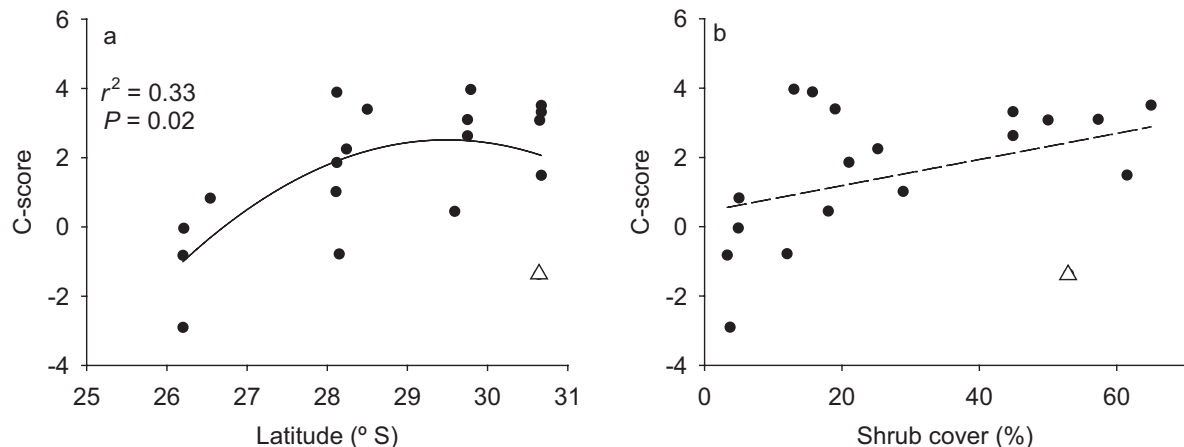


FIG. 2. C-score values as a function of (a) latitude and (b) plant cover in the coastal desert of Atacama. In this desert, as latitude decreases, aridity increases. Trend lines are the result of linear regressions (significant for latitude, marginally significant for shrub cover; $n = 19$ sites, i.e., including an apparent outlier site in the Fray Jorge region, which is indicated in the graph by an open triangle).

Causes of aggregation and attraction

Aggregated patterns can arise from five main causes. The first cause is environmental heterogeneity (e.g., a patchy distribution of favorable sites). In this case, plants would tend to aggregate in a limited number of favorable sites. Seed trapping is a second potential cause of aggregation patterns, especially in plant communities in arid shrublands that usually form a mosaic of perennial plant patches interspersed within a matrix of soil with low plant cover (Aguiar and Sala 1999); here, shrubs may act as true obstacles for seeds. A third reason can be dispersal limitation, which might also explain contagious distributions. A fourth cause of aggregated patterns may be vegetative propagation, which is the main reproductive strategy of woody species in some dry regions (Bond and Midgley 2001, Torres et al. 2014). True facilitation is the last potential process generating aggregation (Callaway 1995, 2007).

In the present study, most of the 19 communities exhibited aggregated patterns. If environmental heterogeneity were responsible for the pattern detected, we should expect increasing levels of abiotic patchiness as aridity increases. We might envisage that possibility for soil water. But if that was the case, we could also have expected some degree of intraspecific aggregation besides interspecific aggregation, unless we assume that niche complementarity enables the association. But for niche complementarity, patchiness of resources is not a requirement. On the other hand, if seed trapping were the mechanism behind the aggregation, we should not expect that these mosaics of shrubs would become more effective traps in more stressful regions; they may simply constitute more discrete foci for seed trapping, thus generating the observed pattern. However, in this case, we would also expect greater intraspecific aggregation, and that did not happen. Finally, because the primary aggregation patterns we documented were interspecific but

intraspecific aggregation did not vary across the gradient, we also exclude dispersal limitation and vegetative propagation from further consideration. Thus, true facilitation is the potential process we consider as the most plausible explanation generating the species aggregation we found in this study.

Facilitation at the edge

Debate is ongoing on whether facilitation declines or increases at the extreme of a stress gradient. The classic SGH predicts a monotonic increase, and several studies support this (e.g., Armas et al. 2011; see He et al. [2013] for a recent worldwide meta-analytical review). In contrast, Michalet et al. (2006, 2014) propose a decline of facilitation at the extreme end of a gradient; the loss of positive relationships between plants would thus be the result of a collapse of facilitation or a switch to competition. Nonetheless, these authors acknowledge that such a collapse of facilitation may be more common at the extreme end of a disturbance gradient as opposed to an abiotic stress gradient. Our study was conducted along an aridity gradient of stress and our results support the existence of facilitation in high-stress environments. Similar patterns have been found in extremely cold environments, such as those in the Antarctic (Molina-Montenegro et al. 2013) or the Tibetan plateau (Pugnaire et al. 2015).

Other recent critics to the SGH come from a meta-analysis of studies conducted at the community level, where Soliveres and Maestre (2014) argued that the SGH only holds at the most xeric end of gradients, and/or when there are few species, when a single environmental factor prevails (both characterize the Atacama Desert), or when the gradient is short (i.e., involving a similar flora). They also reported that communities dominated by woody species (as in our study) are more sensitive to the environmental changes along such stress gradients.

Our results are in agreement with these findings, except in relation to gradient length. Our study documents a clear correlation between facilitation and aridity over a particularly long aridity gradient.

We documented aggregation between certain species pairs in each locality. Interspecific positive interactions thus constitute a subset of all possible pairwise interactions in the region. For the point pattern case in Pan de Azúcar, we conducted analyses in communities that contained only one pair of species: an extreme situation. It would seem that as aridity increases, those subsets in which there are positive (or at least less negative) interactions persist. This could in part explain the increase in facilitation at the most severe end of environmental gradients.

Mechanisms of facilitation

Having documented that facilitation may occur across this gradient, we return to the question of mechanism. Although our study cannot confirm any single mechanism, it provides important insight to which potential mechanisms warrant further consideration.

Facilitation has generally been attributed to the local presence of conditions suitable for plant growth or establishment when a benefactor species is present; in arid regions one such condition is shade, and associated reduction in evapotranspiration, beneath shrubs (e.g., Valiente-Banuet and Ezcurra 1991, Flores and Jurado 2003). This is perhaps best exemplified by many cacti that require the shade of nurse shrubs for establishment (Valiente-Banuet and Ezcurra 1991, Flores and Jurado 2003). In Pan de Azúcar, plant–plant associations may not be particularly related to shade, as plants do not necessarily grow in very close proximity to each other.

Facilitation may also be provided by improved soil conditions, as spaces beneath and around shrubs have more nutrients and organic matter than open spaces. The pattern of higher soil nutrient levels under plants is well-known in arid communities globally (Whitford 2002). In our study, nutrient levels beneath shrubs were higher than in inter-shrub areas across the gradient; however, differences between open spaces and beneath shrubs were particularly sharp in the most arid site, Pan de Azúcar, where nutrients beneath *Heliotropium* shrubs are much higher than in the open (especially P and K; Table 2).

Another potential role of nurse plants, however, has to do with the process of hydraulic lift or hydraulic redistribution (Caldwell and Richards 1989, Prieto et al. 2012), whereby shrubs transport water from deep soil horizons to the surface (and in some cases horizontally as well), where it is passively liberated to the soil and can be used by other plants. Hydraulic redistribution has been documented for several coastal desert species in our studied gradient (Muñoz et al. 2008), and is a plausible explanation for patterns of aggregation. Further promoting this is the fact that roots usually extend farther away from the shrub centroid than the crown perimeter;

this is the case for the dominant shrub in our study sites in Pan de Azúcar (*Heliotropium pycnophyllum*), which has a root system that may extend up to 4 m away from the center of the shrub. It is also the case for the subdominant plant (*Gypothamnium pinifolium*), which has an even more widespread root system, extending up to 10 m away from the shrub (Rundel et al. 1980). Moreover, *H. pycnophyllum* is the species of Pan de Azúcar that can attain the most negative values in osmotic potential (−3 to −6 MPa; Rundel et al. 1980). As such, it should be able to absorb water when, for example, the cactus *Copiapoa cinerea* does not; additionally, *C. cinerea*, as most cacti, has a very shallow root system (Gulmon et al. 1979), which may render it dependent on rain water or hydraulically redistributed water from neighbors.

In summary, we have documented increased interspecific aggregation among plants at the xeric end of an extensive aridity gradient in the hyperarid Atacama Desert, but no such pattern within species. Thus, interspecific aggregation varied according to SGH predictions that states more frequent and important positive plant–plant interactions with increasing stress. In the most basic terms, these results are also consistent with classic niche theory; when abiotic conditions become particularly challenging, only those species whose niche space is relatively complementary (and not redundant or competitive) can co-occur. This may promote facilitative relationships. Of issue now is why this is the case—we present three mechanisms that invoke the role of shade, locally favorable soil conditions, and hydraulic lift. Further efforts should focus on distinguishing which of these is the dominant influence, or if more than one of these operate in concert.

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