

Facilitation of the non-native annual plant *Mesembryanthemum crystallinum* (Aizoaceae) by the endemic cactus *Eulychnia acida* (Cactaceae) in the Atacama Desert

Jaime Madrigal-González · Alex P. Cea ·
Leticia A. Sánchez-Fernández · Karina P. Martínez-Tillería ·
Juan E. Calderón · Julio R. Gutiérrez

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Abstract The Atacama Desert is one of the most stressful environments worldwide and represents a strong barrier for the establishment of native and non-native plants. In this study, we report the establishment of a non-native annual plant through facilitation by a native endemic cactus in a relatively undisturbed coastal area in north-central Chile. Soil collected under *Eulychnia acida* contained more available nutrients (N, P and K), water, and soluble salts than soils collected away from *E. acida*. Co-occurrence analyses showed a strong positive spatial association (facilitation) between the native cactus *E. acida* and the non-native annual, *Mesembryanthemum crystallinum*. The aboveground biomass of *M. crystallinum* individuals was 4-fold higher under the influence of

E. acida. Native halophytes occasionally shared the cactus understory with the non-native species, but dominant native shrubs and perennial herbs did not co-occur with the cactus at scales of 1 and 4 m². All these results support facilitation of the native cactus on the non-native herb. The combination of direct and indirect positive effects could explain the assembly of the non-native annual plant in these undisturbed areas of the Atacama Desert and have major implications on *M. crystallinum* capacity to colonize new areas.

Keywords Facilitation · *Mesembryanthemum crystallinum* · *Eulychnia acida* · Saline soils · Atacama Desert · Direct and indirect interactions

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J. Madrigal-González (✉) · A. P. Cea ·
L. A. Sánchez-Fernández · K. P. Martínez-Tillería ·
J. E. Calderón · J. R. Gutiérrez
Instituto de Ecología y Biodiversidad (IEB), Universidad
de La Serena, Casilla 599, La Serena, Chile
e-mail: ecojmg@hotmail.com

A. P. Cea · K. P. Martínez-Tillería · J. R. Gutiérrez
Universidad de La Serena, La Serena, Chile

J. R. Gutiérrez
Centro de Estudios Avanzados en Zonas Áridas
(CEAZA), Universidad de La Serena, La Serena, Chile

Introduction

How non-native species invade new areas is a central issue in ecology and conservation biology (Lodge 1993; Kolar and Lodge 2001). Competition in the recipient community (i.e., ecological resistance) and abiotic stresses (i.e., physical environment) have been traditionally proposed as major controls of non-native species establishment (Case 1990; D'Antonio 1993; Alpert et al. 2000; Corbin and D'Antonio 2004). However, non-native species may be facilitated by resident species (Simberloff and Von Holle 1999; Badano et al. 2007; Bulleri et al. 2008). Under abiotic stress, facilitation is thought to be important in structuring plant communities, as ameliorated abiotic

conditions allow for many species to establish and persist under the influence of nurse plants (Bertness and Callaway 1994; Brooker et al. 2008; Holmgren and Scheffer 2010). For instance, Cavieres et al. (2005) documented the facilitative effects of native cushions (*Azorella monantha* Clos) on the invasive herb *Taraxacum officinale* L. in the Andes (central Chile) due to ameliorated microclimatic conditions under the influence of nurse individuals. Interestingly, when the physical environment becomes too extreme (e.g. desert ecosystems), scarce resources and prevailing interference among stress-tolerant species determine low rates of non-native species invasions (Alpert et al. 2000; Michalet et al. 2006).

Mesembryanthemum crystallinum L. (Aizoaceae) is an annual plant that has successfully invaded Mediterranean coastal areas in North and South America (Bloom and Troughton 1979; Vivrette and Muller 1977; Winter and Troughton 1978; Winter et al. 1978). In the southern Atacama Desert in Chile, this annual plant is particularly abundant in habitats that have been severely disturbed by native herbivores and humans (Contreras and Gutiérrez 1991). In undisturbed shrublands however, *M. crystallinum* is scarce and commonly occurs in close association with the endemic cactus *Eulychnia acida* Phil. var *procumbens* F. Ritter (Cactaceae, hereafter *E. acida*). This suggests that the native cactus could facilitate the establishment of the non-native annual in undisturbed areas of the Atacama Desert by ameliorating environmental stress and decreasing competition (Levine 1999).

To document a case of facilitation of a non-native annual plant by a native cactus in a relatively undisturbed area of the Atacama Desert, we addressed and tested two central assumptions: (i) there is a spatial positive association between *E. acida* and *M. crystallinum*, and (ii) the aboveground biomass of *M. crystallinum* is higher under the influence of *E. acida*. We forward the hypothesis that higher soil salinity (which is favourable for halophytes to endure arid conditions, Bloom 1979), and water and nutrient availability under the influence of the native cactus explain direct facilitative effects on the non-native herb. Additionally, and taking into account that other species in the native community can affect establishment of the non-native herb, we studied species interactions under the assumption that high competition may determine high resistance to invasion in this

extreme desert (Alpert et al. 2000). If this was true, indirect facilitation by nurse control of potential competitors could also explain the spatial distribution and fitness of the non-native plant (Levine 1999; Callaway and Pennings 2000).

Materials and methods

Study area

This study was conducted in Los Choros, the southern part of the coastal area of the Atacama Desert, 100 km north of La Serena (29°15'19"S–71°24'22"W; see Suppl. Mat. Fig. 1, and Plate 1). Average altitude is 10 m.a.s.l. and the distance to the coastline is 1 km. The climate is arid Mediterranean, with 40 mm of annual average precipitation and an average temperature of 14.7 °C (Di Castri and Hajek 1976; Novoa and López 2001). Coastal fog is frequent and notably contributes to the air and soil humidity, especially in nearby hills where plant composition and cover are often different from that of the lowlands (Muñoz-Schick et al. 2001). The soils are sandy in texture, with neutral-basic pH and low levels of available nutrients for plants (e.g., N, P, and K). Based on biogeographical criteria, this area belongs to the Coastal Desert of El Huasco in the eco-region of the Atacama Desert (Gajardo 1994), which is one of the world's 34 hotspots of biodiversity experiencing a dramatic loss of endemic plant species in the past few decades (Prendergast et al. 1999; Myers et al. 2000).

Vegetation

Vegetation of the southern part of the Atacama Desert is dominated by small shrubs, perennial herbs and the cactus *E. acida*. Dominant shrub species are: *Frankenia chilensis* K. Presl ex Roem. et Schlt., *Chuquiraga ulicina* (Hook. & Arn.) Hook., *Encelia canescens* Lam., and *Heliotropium floridum* (A.DC.) Clos. *Cristaria glaucophylla* Cav. is the most abundant perennial herb. *Eulychnia acida* var. *procumbens* is an endemic cactus to the coastal area of the Atacama Desert (Chile) (Squeo et al. 2001). This cactus has a characteristic procumbent growth form, and is a long-lived species that has the ability to persist for more than 100 years. *Eulychnia acida* is a key species in coastal areas of the Atacama Desert because it provides refuge for many

animals (e.g., reptiles and small mammals) and physical support for epiphytic lichens, and is an important resource for pollinators (e.g., invertebrates and vertebrates).

Mesembryanthemum crystallinum (Aizoaceae) is an annual plant native to South Africa that has invaded large areas in the Americas. It has been reported that the ability of *M. crystallinum* to perform as a facultative Crassulacean Acid Metabolism (CAM) species is critical for its high invasiveness (Vivrette and Muller 1977). However, CAM metabolism requires high levels of inorganic salt for the fixation of substantial amounts of CO₂ (Bloom 1979), which explains why this annual plant preferably distributes over coastal areas in arid environments. As a consequence of the accumulation of salt in above-ground stems, this species usually increases salt concentration in the topsoil. This process has been recognised as a critical attribute of this species' success in outcompeting native plants in invaded areas of North America (Kloot 1983).

Spatial association between *E. acida* and *M. crystallinum*

To determine the spatial association of *M. crystallinum* and *E. acida*, we surveyed the occurrence of both species in 100 1.5 × 1.5 m plots along a 3 km transect that was established 1 km inland parallel to the coastline. Environmental conditions were assumed to be homogeneous along the entire sampling transect. We analysed the spatial association of *M. crystallinum* and *E. acida* using the checkerboard unit index (CU) which is a pair-wise co-occurrence index computed as $(r_i - S)(r_j - S)$, where r_i and r_j are the total number of occurrences of the species i and j , respectively, and S is the number of sites shared by both the i and j species (Stone and Roberts 1990). To test the hypothesis that the CU was not significantly different from that expected by chance, we created a null model through 10,000 permutations of data, maintaining that the occurrence of each species in the simulation was identical to the original data and that each sample was equally likely to be represented. We used the software Ecosim 700 for this analysis (Gotelli and Enstminger 1999).

Individual above-ground biomass in *M. crystallinum*

To test the influence of *E. acida* on *M. crystallinum* above ground biomass, we randomly recorded 53

individuals of *M. crystallinum* under and outside the influence of *E. acida* (total of 106 individuals) during the stage of maximum biomass production in this plant (November). The number of *M. crystallinum* plants chosen for analysis was limited by the individuals found outside the influence of *E. acida*. Individual plants were oven-dried at 60 °C for 7 days and then weighed in the lab. We tested differences in the individual above ground biomass (g) of *M. crystallinum* under and outside the influence of *E. acida* using generalized linear models (GLM). We assumed a gamma distribution of the error term in the dependent variable (individual above-ground biomass) given the deviation from normality shown by above ground biomass error in a Q-Q plot (Supp. Mat. Fig. 2). A log link function was used. The Wald χ^2 statistic was calculated using software SPSS 17.0 (IBM, USA).

Direct mechanisms of facilitation: soil properties

A total of 20 soil samples under and outside the influence of *E. acida* were collected at a depth of 30 cm. Since *M. crystallinum* can increase salt content in the topsoil, soil samples under the influence of *E. acida* were taken from individuals not colonized by *M. crystallinum*. Each soil sample was transported to the lab and the water content (% soil weight), nutrients (N, P, and K) and electrical conductivity (EC, soil salinity) were determined. Before chemical determination, the soil samples were sieved (2 mm) and oven dried at 60 °C for 2 days for water content determination. Nitrogen was determined using Kjeldahl digestion, and available phosphorous was determined by using Olsen's method. Exchangeable potassium was determined using atomic absorption spectrophotometry. The pH was measured with a digital pH meter (model Q-400M2, QUIMIS, Diadema, Sao Paulo, Brazil) and electrical conductivity was measured with a digital conductivity meter (model SC-12, Suntext, Taipei, Taiwan). All methods for soil chemical determination followed that described by Sadzawka et al. (2006) and were performed at the Instituto Nacional de Investigaciones Agropecuarias of Chile (INIA-La Platina, Santiago de Chile).

We used multivariate analysis of variance (MANOVA) to test the null hypothesis of no significant differences in soil properties between soils under and outside the influence of the cactus. All variables were log transformed to meet parametric assumptions (e.g.,

homogeneity of variance and normality). An F ratio based on Pillai's trace was calculated using SPSS 17.0 statistical software (SPSS Inc., Chicago, IL, USA). A test of between-subjects effects to test differences independently for each soil variable was used. The threshold for rejecting the null hypothesis of non-significant differences among treatments was set at $p < 0.05$.

Indirect mechanisms of facilitation: species co-occurrences in the native community

To test whether competition is the prevailing force structuring the native plant community we determined the presence of perennial plants (small shrubs, perennial herbs, and the cactus) within a fixed 1,000 m² plot and conducted co-occurrence analyses. Since a co-occurrence analysis is sensitive to distances, at which species likely interact, and interactions among plants in desert ecosystems preferentially take place below ground, we conducted two independent co-occurrence analyses at 1 and 4 m² scales. For community analyses, we used the C-score index, which is the average value of all possible pair-wise CUs in the species matrix. This index has suitable properties regarding statistical errors in hypothesis testing (Gotelli 2000). We applied null models to species co-occurrence analyses using the software Ecosim 700 (Gotelli and Enstminger 1999). A total of 10,000 simulations of C scores from random permutations of the original species presence/absence data were computed. We maintained the occurrence of each species identical to the original matrix (fixed), and each sample was equally likely to be represented in the simulation (colonisation potential of species was equiprobable). When the observed C-score was higher or lower than 95 % of the expected values, a significant spatial segregation or association of the species was assumed, respectively. Ecologists interpret such a significant spatial segregation or association of species to be the result of predominant negative or positive

interactions, respectively (Purves and Law 2002; Tirado and Pugnaire 2005).

Results

Effects of *E. acida* on *M. crystallinum*

Co-occurrence analysis revealed a significant positive spatial association of *M. crystallinum* and *E. acida* ($CU_{\text{observed}} = 36.00$, $p < 0.0001$; Fig. 1). Of the 100 1.5 × 1.5 m² sampling quadrats, *E. acida* and *M. crystallinum* occurred in 42 and 37 quadrats, respectively. Both plants shared 33 quadrats, and 89 % of the *M. crystallinum* occurrences were in association with *E. acida*. None of the simulated CUs obtained by random permutation of the original data were equal to or exceeded the observed CU (Suppl. Mat. Fig. 3).

Generalized linear models suggested a significant effect of *E. acida* on the above ground biomass of the non-native species (Wald $\chi^2_{(1)} = 97.098$, $p < 0.0001$).



Fig. 1 *Mesembryanthemum crystallinum* growing in association with the native cactus *Eulychnia acida* var. *procumbens* in the study area (Los Choros, north-central Chile)

Table 1 Parameter Estimates for GLM applied to individual above ground biomass

	Parameter	B	SE	95 % Wald confidence interval		Wald Chi square	Hypothesis Test	
				Lower	Upper		df	Sig.
Dependent variable:	(Intercept)	0.269	0.0885	0.095	0.442	9.204	1	0.002
biomass	Cactus	1.233	0.1252	0.988	1.479	97.098	1	0.00001
Model: (Intercept), Cactus	(Scale)	0.415	0.0536	0.322	0.535			

This effect was positive (Table 1), being individual above ground biomass under the influence of the cactus up to fourfold higher than outside its influence (Fig. 2).

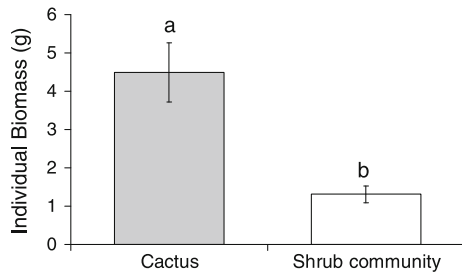


Fig. 2 Mean \pm 95 % confidence intervals of individual dry biomass of *M. crystallinum* under the influence of *E. acida*, and beyond its influence. *a*, *b* Differences at $p < 0.01$

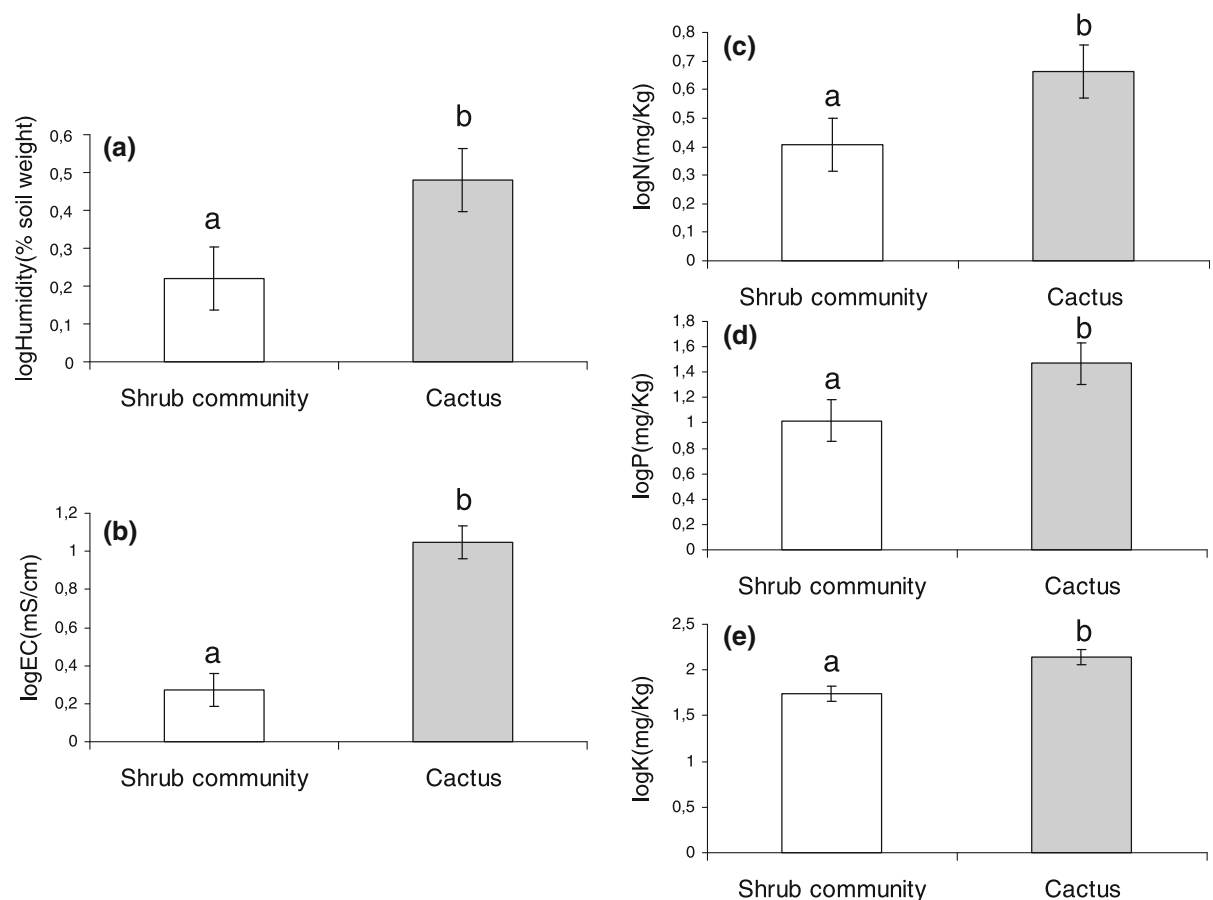


Fig. 3 Means \pm 95 % Confidence Intervals of soil properties (log-scale) under *E. acida* and outside its influence. Humidity–water as % of soil weight; *EC* electrical conductivity, *N* Nitrogen, *P* Phosphorus, *K* Potassium. *a*, *b* Differences at $p < 0.01$

Soil properties under and outside the influence of *E. acida*

Soil properties, including water content, available nutrients, and electrical conductivity, were significantly higher under the influence of the cactus than outside its influence (Pillai's trace = 0.934, $F_{(5,14)} = 39.656$, $p < 0.0001$; Fig. 3). This was confirmed by the outcomes of the corrected model in the univariate tests (Table 2). Electrical conductivity was 11-fold higher under the cactus than outside it ($F_{1,18} = 186.452$, $p < 0.0001$). Although the soil water content was extremely low in both microhabitats, it was as much as three-fold higher under the influence of the cactus compared to outside of the influence ($F_{1,18} = 21.46$, $p < 0.001$). Similarly, available N, P, and K were on average 1.7, 2.9, and 2.5 times higher under *E. acida* than outside ($F_{1,18} = 17.158$, $p < 0.001$;

Table 2 Univariate tests (corrected model) for each dependent variable

Dependent variables	SS	gl	MS	F	<i>p</i> value
log humidity					
Test	0.334	1	0.334	21.46	0.0001
Error	0.28	18	0.016		
log CE					
Test	3.019	1	3.019	186.452	0.0001
Error	0.291	18	0.016		
log N					
Test	0.331	1	0.331	17.158	0.001
Error	0.347	18	0.019		
log P					
Test	1.014	1	1.014	17.422	0.001
Error	1.047	18	0.058		
log K					
Test	0.821	1	0.821	55.823	0.0001
Error	0.265	18	0.015		
pH					
Test	2.198	1	2.198	61.273	0.0001
Error	0.646	18	0.036		

$F_{1,18} = 17.422$, $p < 0.001$; and $F_{1,18} = 55.823$, $p < 0.0001$, respectively).

Interactions structuring the native shrubland community

Co-occurrence analyses showed significant spatial segregation of species in both 1 and 4 m² cells (C-score = 12,067.22, $p = 0.0010$ and C-score = 1,372.51, $p = 0.0007$, respectively). Of the 10,000 simulated C scores that corresponded to the 1 × 1 m cells, 10 were higher than the observed index and 9,990 were lower (Suppl. Mat. Fig. 4a). In the 2 × 2 m cells, seven simulated C scores were higher than the observed and 9,993 were lower (Suppl. Mat. Fig. 4b). Pair-wise co-occurrences among dominant shrub species (e.g., *Frankenia chilensis*, *Encelia canescens*, *Cristaria glaucophylla*, *Heliotropium floridum*, and *Eulychnia acida*) showed high observed CU values, suggesting a generalised spatial segregation of dominant species (Table 3a, b). The halophytes *Atriplex mucronata*, *Suaeda foliosa*, and *Nolana divaricata* showed low CU values, which reflect a spatial association with *E. acida*. However, this result should be

analysed with caution, since these species were present in <1 % of the 1 m² and 4 % of the 4 m² cells.

Discussion

In undisturbed areas of the southern part of the Atacama Desert the non-native herb *M. crystallinum* colonizes and invades native plant communities only where the cactus *E. acida* is present. Direct and indirect positive effects may explain this positive interaction. Soils under the influence of the cactus had significantly more water and nutrients than soils outside its influence. Similar direct impacts of certain species (usually shrub species) on critical aspects of the environment positively affect the performance of other species in arid and semiarid ecosystems (Flores and Jurado 2003). Since the study site is close to the Pacific Ocean, the atmosphere has high moisture content (>80 %) and provides nutrients and water in addition to salt (Barbosa et al. 2010). The air moisture is trapped by the cactus and deposited in the ground. Because of high water evaporation, salts then accumulate on the soil surface. Accordingly, soils under the influence of *E. acida* had 11-fold higher salinity than soils outside its influence. Under this condition, only halophytic plants can establish and benefit from higher soil fertility and water. *Mesembryanthemum crystallinum* performs as a C₃ herb in mesic environments, but change to CAM metabolism under drought stress, which can induce additional demands for the uptake of inorganic salts (Bloom 1979). Tolerance to salinity may allow this and other halophytes to establish under the influence of *E. acida*. In contrast, most dominant shrubs and perennial herbs present in this community cannot establish in this saline micro-environment as supported by our results on species co-occurrence.

Native species showed a checkerboard spatial distribution at the two scales observed within the fixed 1,000 m² plot (1 and 4 m²). Such non-random spatial pattern is interpreted as a consequence of prevailing negative interactions among species, which is in accordance with the niche-based assumptions of Diamond's assembly rules (Gotelli and McCabe 2002). Plants in the southern Atacama Desert, as in other deserts, deplete water from shallow soil profiles because extensive root systems (i.e. shallow and dimorphic) are common in the majority of functional types (e.g., xerophytes, succulents, and perennial herbs; Squeo et al.

Table 3 Species matrices for pair-wise C scores obtained by random permutation of species presence-absence data. (a) 2 m² cells, (b) 4 m² cells

(a)	<i>Euac</i>	<i>Chul</i>	<i>Atmu</i>	<i>Chfr</i>	<i>Crgl</i>	<i>Enca</i>	<i>Frch</i>	<i>Hefl</i>	<i>Nodi</i>	<i>Sufo</i>
<i>Euac</i>		11,440	749	7,560	32,572	21,870	20,086	16,380	206	840
<i>Chul</i>			672	7,452	27,900	21,004	20,230	20,680	678	1,130
<i>Atmu</i>				518	3,102	1,820	1,590	1,673	42	70
<i>Chfr</i>					14,220	13,255	15,748	15,844	444	740
<i>Crgl</i>						49,923	45,628	43,290	1,545	2,565
<i>Enca</i>							39,592	39,690	1,560	2,600
<i>Frch</i>								29,574	1,325	1,841
<i>Hefl</i>									1,190	2,142
<i>Nodi</i>										45
<i>Sufo</i>										
(b)	<i>Atmu</i>	<i>Chfr</i>	<i>Chul</i>	<i>Crgl</i>	<i>Enca</i>	<i>Euac</i>	<i>Frch</i>	<i>Hefl</i>	<i>Nodi</i>	<i>Sufo</i>
<i>Atmu</i>		220	504	209	608	301	584	552	2	18
<i>Chfr</i>			2,070	1,416	1,722	1,558	2,898	3,000	264	184
<i>Chul</i>				2,175	3,675	2,923	3,332	4,400	588	252
<i>Crgl</i>					1,600	885	1,720	1,656	208	212
<i>Enca</i>						2,948	3,960	4,047	918	462
<i>Euac</i>							1,680	2,088	294	126
<i>Frch</i>								3,348	882	294
<i>Hefl</i>									690	278
<i>Nodi</i>										12
<i>Sufo</i>										

Species acronyms: *Euac* *Eulychnia acida*, *Chul* *Chuquiraga ulicina*, *Atmu* *Atriplex mucronata*, *Chfr* *Chorizanthe franquenoides*, *Crgl* *Cristaria glaucofila*, *Enca* *Encelia canescens*, *Frch* *Franquenya chilensis*, *Hefl* *Heliotropium floridum*, *Nodi* *Nolana divaricata*, *Sufo* *Suaeda foliosa*

1999). Hence, rapid depletion of available water from the upper soil layers by adult individuals may impose strong limits to plant establishment in sites with episodic rainy events (León et al. 2011). In addition, some studies have reported that allelochemicals in *Chuquiraga ulicina*, *Encelia canescens*, and *Frankenia chilensis* may prevent seed germination and seedling survival (Montenegro et al. 1978; Flagg et al. 1999; Facknath and Lalljee 2000; Pons-Cabezas 2002). Therefore, competition and allelopathy in dominant plants may confer high resistance to invasions, and this could partly explain why this non-native species is so scarce outside the influence of the cactus. Although not directly tested in this study, there is support for a relevant role of indirect positive effects as part of the facilitative interaction: (i) the spatial segregation of dominant plants in the recipient community including shrubs, perennial herbs and the cactus support a prevailing role of competition and therefore high resistance to invasion;

(ii) *Mesembryanthemum crystallinum* is abundant in highly disturbed areas nearby, such as roadsides, overgrazed areas, and human settlements (Suppl. Mat Plate 2), but is very scarce in undisturbed communities. Contreras and Gutiérrez (1991) found that *M. crystallinum* in Chile, as an opportunistic alien plant, was indirectly favoured by micro-disturbances due to activities of the subterranean herbivorous rodent *Spalacopus cyanus* in shrublands of the Atacama Desert. Disturbance is one of the primary factors favouring the establishment of alien plants in ecosystems where prevailing negative interactions structure native communities (D'Antonio et al. 1999; Chytrý et al. 2008). In the particular case of *M. crystallinum*, Vivrete and Muller (1977) and Vivrette (1999) observed such pattern of establishment in Mediterranean California.

Facilitation therefore may be crucial to incorporate *M. crystallinum* to the native community by means of direct amelioration of soil conditions and prevention

of direct competition by native species. Eventually, this positive interaction could lead to invasion. Some authors have observed that, once established, *M. crystallinum* may hamper the establishment of native species by increasing salt content in the topsoil (Vivrette and Muller 1977). Future research should determine whether the non-native annual plant is able to spread into the undisturbed communities of the Atacama Desert after its establishment associated with the native cactus.

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