



## Responses of different herb life-history groups to a dominant shrub species along a dune stabilization gradient

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### Abstract

Shrubs play a pivotal role in reversing desertification and in promoting ecological rehabilitation in severe environments. However, how the interactions between shrubs and their understorey species change during restoration remains unclear. Here, we report the results of an observational study conducted in the Mu Us Desert of northern China. This study explored how dune stabilization and the size of individual shrubs affect shrub–herb interactions. In particular, we aimed to determine how different life-history groups and performance indicators (e.g., biomass and richness) of subordinate species respond to shrub–herb interactions during dune stabilization. The shrub *Artemisia ordosica* had positive effects on understorey species in this dune system. The ability of the shrub to promote the growth of understorey species increased with dune stabilization, but decreased from small to large shrubs. This effect was due to an increase in the relative abundance and biomass of perennials and their higher sensitivity to the positive effects of the shrubs. In contrast, the ability of shrubs to improve the richness of understorey species decreased with dune stabilization, but increased from small to large shrubs. This effect occurred because perennials suffered high strain during recruitment in disturbed open patches of the semi-fixed dunes, particularly below small shrubs. Our results support the theory claiming that communities are sets of hidden interaction groups that have contrasting responses (neutral for annuals, but facilitative for perennials) to dominant neighbors in a single community, depending on their functional strategies. Furthermore, our study highlights the high efficiency of *A. ordosica* in facilitating ecological restoration of dry and disturbed sandy communities.

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**Keywords:** *Artemisia ordosica*; Dune stabilization; Facilitation; Life-history groups; Mu Us desert; Shrub size

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## Introduction

Desertification is a process of land degradation that affects arid to dry sub-humid areas, and that is induced by several factors, including changing climate, increasing anthropogenic disturbance, and natural dynamics (Mainguet 2003). A wide variety of techniques have been proposed to improve the physical and biological properties of degraded systems (Andel & Aronson 2012). Among these techniques, ecological restoration uses model species that have positive ecosystem-engineering effects, such as native nurse species, to manipulate the structure of communities and overcome biotic and abiotic barriers simultaneously (Padilla & Pugnaire 2006). Pioneer shrubs often play a key role in ecological restoration, due to their facilitative effects in altering surface wind and fluvial flows, ameliorating stressful micro-environmental conditions, and improving soil fertility (Padilla & Pugnaire 2006; Gómez-Aparicio 2009). However, shrub encroachment might also induce negative effects, such as increase in runoff and soil erosion (Parizek, Rostagno, & Sottini 2002), or reduced soil moisture (Darrouzet-Nardi, D'antonio, & Dawson 2006) and infiltration (Parizek et al. 2002). The balance of these positive and negative biotic effects drives the rate and direction of successional changes. Consequently, knowledge from restoration experiments could be useful to restore degraded systems toward establishing target communities (Siles, Rey, Alcántara, & Ramírez 2008; Gómez-Aparicio 2009). Moreover, understanding how restoration practices differentially affect demographic parameters could help to establish the costs and benefits of restoration actions objectively, enhancing the management of these ecosystems (Gillespie & Allen 2004).

It has been originally proposed that facilitation should increase with increasing environmental stress (Bertness & Callaway 1994). However, the outcome of plant-plant interactions is highly dependent on the functional strategies of interacting species and how the community is positioned within the ecological niche of the species (Liancourt, Callaway, & Michalet 2005; Michalet et al. 2006; Gross, Liancourt, Choler, Suding, & Lavorel 2010; Liancourt, Le Bagousse-Pinguet, Rixen, & Dolezal 2017). Contrasting species responses to neighbors are commonly observed in a single community, consequently, the community-level understorey species response to a dominant foundation species might be null or weakly significant (e.g., Michalet et al. 2015b). Thus, it is important to subdivide understorey species into, at least, distinct life-history groups to advance our understanding on how plant-plant interactions contribute to ecological restoration.

Facilitation may also switch back to competition or collapse in extremely stressful conditions (Maestre & Cortina 2004; Michalet et al. 2006; Kéfi et al. 2007; Xiao, Michalet, Wang, & Chen 2009; Holmgren & Scheffer 2010; Michalet, Le Bagousse-Pinguet, Maalouf, & Lortie 2014; Soliveres,

Smit, & Maestre 2015). It has been proposed that such deviation from the Stress Gradient Hypothesis proposed by Bertness and Callaway (1994) may be due to either the types of stress gradient (resource vs. direct stress gradients) and/or the species involved in the interactions (Michalet 2007; Saccone, Delzon, Brun, & Michalet 2009; Maestre, Callaway, Valladares, & Lortie 2009). Ecological restoration sometimes fails in dry or disturbed environments, because the only locally available target species are too shade-intolerant and drought-tolerant to benefit from neighbors (Pennings, Selig, Houser, & Bertness 2003; Noumi, Chaieb, Michalet, & Touzard 2015). Furthermore, in highly disturbed environmental conditions, the role of plant-plant interactions becomes insignificant, as has been shown for both competition (Grime 1973; Huston 1979; Tilman 1982; Maalouf, Bagousse-Pinguet, Marchand, Touzard, & Michalet 2012) and facilitation (Kéfi et al. 2007; Forey, Touzard, & Michalet 2010; Le Bagousse-Pinguet et al. 2014b; Michalet et al. 2014). Therefore, the potential of using shrubs as tools to facilitate ecological restoration in highly disturbed and dry ecosystems requires careful evaluation.

The collapse of facilitation model predicts that facilitation should vanish in particular in disturbed ecosystems, because decreasing plant size reduces the beneficial effects of shading on understorey species (Michalet et al. 2006; Le Bagousse-Pinguet, Forey, Touzard, & Michalet 2013). Plant size is a common predictor of plant performance under a range of ecological conditions (Miriti 2006), and could be used to indicate plant age and for mediating plant-plant interactions (Lamb & Cahill 2006; Schiffrers & Tielboerger 2006). Most studies on plant-plant interactions have focused on the age of protégé species, rather than the nurse species (Miriti 2006; Schiffrers & Tielboerger 2006; Sthultz, Gehring, & Whitham 2007; but see Allegranza et al. 2016; Amghar et al. 2016). Depending on species strategies, plant-plant interactions might become increasingly positive, collapse or switch to negative, with the performance ability of different nurses varying in magnitude and direction depending on size. Such effects need detailed investigation to detect the optimal size of nurse shrubs for ecosystem rehabilitation.

Dunes are ubiquitous landforms in deserts and sandy soil areas, particularly in northern China. Historical desertification and recent rehabilitation practices have created landscapes composed of a mosaic of sand dunes with different degrees of dune stabilization. Xerophytic shrub species have been widely selected for use in ecological restoration, due to their ability to fix mobile sand, sequester carbon, and contribute nutrients to the soil (Zhou, Li, Chen, Zhang, & Li 2011). Due to these restoration and conservation efforts, mobile dunes may be transformed into semi-fixed ones, and, ultimately, to fixed dunes (Wang, Yang, Dong, & Zhang 2009). Community composition and soil properties change along this dune stabilization gradient (She et al. 2015), reflecting the amelioration of surface disturbance. Changes in plant-plant interactions and patterns of associations between

dominant and understorey species along dune stabilization gradients have been already assessed in coastal sand dunes (e.g., Forey, Lortie, & Michalet 2009, 2010); however, few studies have been conducted in continental dunes, despite their importance for ecological restoration in desert areas. Additionally, variation in plant–plant interactions along gradients of dune stabilization may strongly differ between coastal and continental dunes due to the absence in the latter of environmental changes related to increasing distance from the beach that may confound the effect of decreasing physical disturbance in the former (Forey et al. 2010). Thus, continental dunes are a well-suited system to study the effect of physical disturbance on plant–plant interactions.

Here, we focus on a sandy shrubland in northwest China, where desertification has been occurring over the last several decades. In recent years, an ecological restoration program has been in progress, facilitating vegetation recovery. We aim to determine how shrub–herb interactions vary along a dune stabilization gradient and with shrub size, and to examine whether contrasting life-history groups within the dependent community respond differently to the shrub along treatments. We hypothesized that: (i) shrub facilitative effects on the biomass and richness of understorey species vary at the community level across the dune stabilization gradient and with shrub size; (ii) contrasting facilitative responses of different life-history groups are induced by different positions of annuals/perennials along the dune stabilization gradient; and (iii) perennial species are more sensitive than annuals to the varying effects of the dominant shrub along the dune stabilization gradient and with shrub size. To test these hypotheses, we assessed the pattern of associations of understorey herbs with different plant size of the dominant shrub species *Artemisia ordosica* along a dune stabilization gradient.

## Materials and methods

### Study site

We conducted the experiment at the Yanchi Research Station of the Chinese Terrestrial Ecosystem Research Network (37°42′37″ N, 107°13′37″ E; 1530 m above sea level), Ningxia, China. The site is located on the southwestern fringe of the Mu Us Desert and has a typical mid-temperate semi-arid continental climate (Fig. 1). The mean annual air-temperature (1954–2004) is 8.1 °C, with mean monthly temperatures ranging from −8.7 °C in January to 22.4 °C in July. Mean annual precipitation was 275 mm for the 1954–2013 period and mean pan evaporation was an order of magnitude higher than precipitation (2100 mm). Rainfall events mainly occur during summer and fall and show large interannual variation (133–572 mm year<sup>−1</sup>). Mean sunshine time reaches 2800 h (Jia et al. 2016).

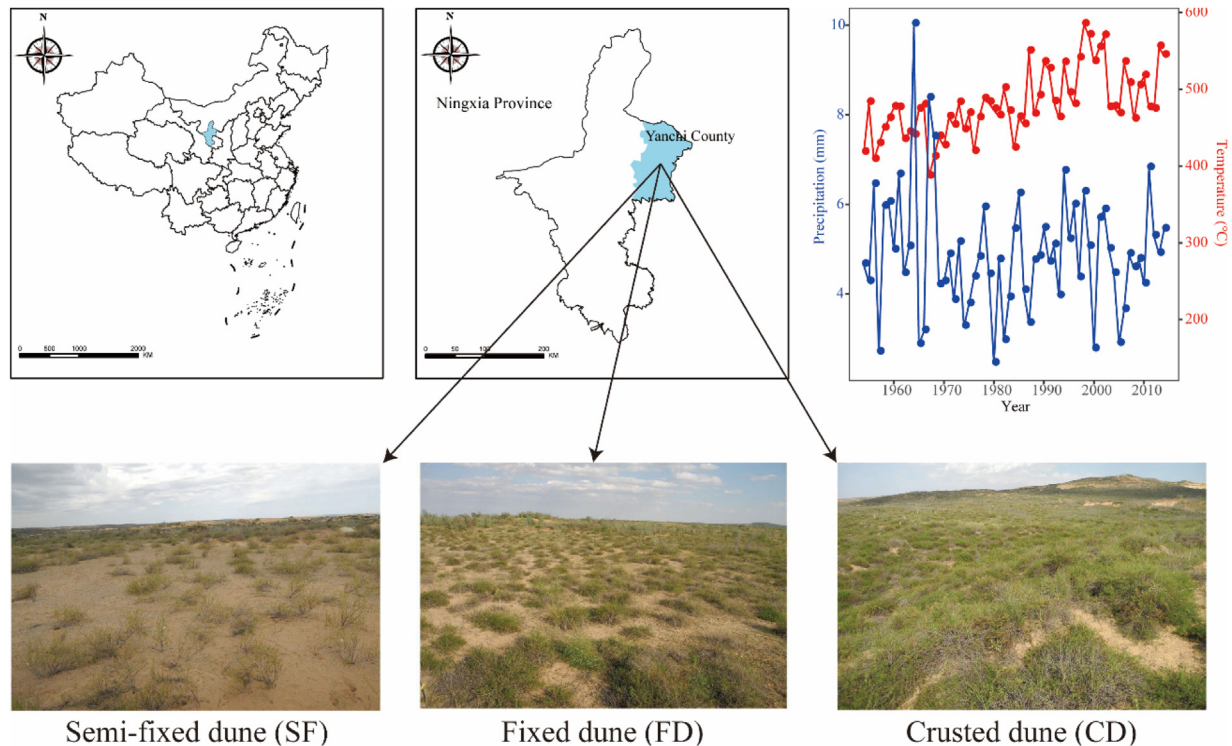
Historically, a dry steppe covered this region, and then desertification occurred, mainly due to human activities, in particular unregulated land conversion to cropland, overgraz-

ing, and the unregulated use of water resources. Recently, ecological restoration programs were conducted, with long-term protection measures resulting in the current landscape consisting of fixed dunes (vegetation cover >40%), semi-fixed dunes (vegetation cover of 15–40%), and mobile dunes (vegetation cover <15%) (Wang et al. 2009). The vegetation was established via aerial seeding after setting checkerboard sand-barriers in 1998 and prohibiting grazing until now. The vegetation in the study site is dominated by desert shrubs (e.g., *A. ordosica*, *Salix psammophila*, *Hedysarum scoparium*, and *Hedysarum mongolicum*), with scattered distributions of herbaceous species (e.g., *Leymus secalinus*, *Setaria viridis*, and *Stipa glareosa*). The *A. ordosica* community includes up to 20 species. The most common perennial herbaceous species are *Heteropappus altaicus*, *Cynanchum thesioides*, *L. secalinus*, *S. glareosa*, and *Ixeridium chinens*. The most common annuals are *Euphorbia esula*, *Chenopodium aristatum*, *Corispermum puberulum*, *S. viridis*, *Eragrostis pilosa*, *Incarvillea sinensis*, and *Salsola collina*.

At the study site, *A. ordosica* (Asteraceae) is the dominant shrub, due to its strong tolerance to sand deposition and ability to stabilize dunes. Mature plant height is  $0.63 \pm 0.04$  m, canopy size is  $0.96 \pm 0.19$  m<sup>2</sup>, shrub volume is  $0.64 \pm 0.14$  m<sup>3</sup>, average leaf area is  $26.59 \pm 3.61$  cm<sup>2</sup> per branch, and the specific leaf area is  $160.37 \pm 7.84$  g m<sup>−2</sup> (n = 30, data from She et al. 2015). Its tap roots can reach 1–3 m depth, while the lateral roots are mainly distributed in the upper soil layer (0–40 cm) (Li, Yu, Werger, Dong, & Zuidema 2011). Approximately 70% fine roots are concentrated in the 0–40 cm soil layer (Lai et al. 2016).

### Experimental design, sampling, and index of interaction

All sampling was completed at the end of the growing season (early September) in 2015. At the study site, we selected sampling plots covered by *A. ordosica* shrubs that had not been subject to anthropogenic disturbance. This region is covered with semi-fixed dunes (SF), fixed dunes (FD), and fixed dunes covered with biocrusts (crusted dunes hereafter; CD). In semi-fixed dunes, the surface has no biocrusts, and there is low vegetation cover (mean ± se:  $24.50 \pm 2.79\%$ ). In fixed dunes, there is very low cover of biocrusts (<20%) and low vegetation cover ( $27.50 \pm 2.74\%$ ), with a biocrust thickness of  $2.43 \pm 0.16$  mm. In crusted dunes, the biocrusts were largely developed (>50% for cover and  $6.73 \pm 0.37$  mm for thickness), with significantly greater vegetation cover ( $56.78 \pm 3.46\%$ ) (see Table 1 and Appendix A: Table S1 for details). Within each stage of dune stabilization, we randomly selected 15 plots containing shrubs of two different sizes (SF:  $1.76 \pm 0.51$  m<sup>2</sup> for large shrubs and  $0.72 \pm 0.18$  m<sup>2</sup> for small shrubs; FD:  $1.42 \pm 0.49$  m<sup>2</sup> for large shrubs and  $0.69 \pm 0.21$  m<sup>2</sup> for small shrubs; CD:  $1.57 \pm 0.48$  m<sup>2</sup> for large shrubs and  $0.69 \pm 0.19$  m<sup>2</sup> for small shrubs; Appendix A:



**Fig. 1.** Location and climatic diagram (blue represents precipitation and red represents temperature) of the study site in northern China, and photographs of the three stages of dune stabilization. SF; semi-fixed dunes; FD, fixed dunes; and CD, crusted dunes. All photographs were taken in July 2014. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1.** Vegetation and soil characteristics of the three stages of dune stabilization (SF, semi-fixed; FD, fixed dune; and CD, crusted dune; Mean  $\pm$  se, N = 30).

Dune stabilization stage	SF	FD	CD
Vegetation cover (%)	24.50 $\pm$ 2.79	27.50 $\pm$ 2.74	56.78 $\pm$ 3.46
Shrub biomass (g m <sup>2</sup> )	76.98 $\pm$ 56.27	144.9 $\pm$ 75.05	500.4 $\pm$ 88.44
Biocrust cover (%)	0	10	45
Bulk density (g cm <sup>-3</sup> )	1.50 $\pm$ 0.05	1.38 $\pm$ 0.02	1.43 $\pm$ 0.05
pH	7.57 $\pm$ 0.02	7.48 $\pm$ 0.06	7.55 $\pm$ 0.04
SOC (g kg <sup>-1</sup> )	0.82 $\pm$ 0.07	1.33 $\pm$ 0.12	2.74 $\pm$ 0.17
TN (g kg <sup>-1</sup> )	0.05 $\pm$ 0.00	0.07 $\pm$ 0.00	0.20 $\pm$ 0.03
TP (g kg <sup>-1</sup> )	0.16 $\pm$ 0.01	0.18 $\pm$ 0.01	0.26 $\pm$ 0.01

Table S1 for details) and the same number of plots in open areas as in sampling plots for each stage. Distance between shrub plots was at least 5 m. To obtain comparable samples for assessing species in surrounding ‘open areas’ (areas not influenced by shrubs), areas matching the size of the shrub sample were surveyed away from each sampled shrub (at least 1 m). A wire hoop was shaped to match the size of sampled shrubs in the adjacent open area. In total, 90 pairs of under canopy and open area plots were surveyed (3 dune stabilization stages  $\times$  2 shrub sizes  $\times$  15 pairs).

We also measured the length and width of the shrub crown, which was approximately ellipsoidal. The performance of all understorey species was expressed as per unit surface area

using the surface of the individual shrub calculated as ellipses:

$$CA = \frac{\pi \times C_1 \times C_2}{4}$$

where  $CA$  is the shrub crown area, and  $C_1$  and  $C_2$  are the values of shrub crown length and crown width, respectively. For the understorey species, in each plot, the number of individual plants of each species was recorded. The above-ground biomass of each species was sampled separately in all plots, by cutting individual plants at ground level with scissors. Plant material was oven-dried for 72 h at 70 °C and was then weighed.



To quantify the net effect of each individual shrub on its understorey community, we calculated the relative interaction index (RII; [Armas, Ordiales, & Pugnaire 2004](#)) for aboveground biomass (RII<sub>Biomass</sub>) and species richness (RII<sub>Richness</sub>) using the following equation:

$$RII = \frac{X_w - X_0}{X_w + X_0}$$

where  $X_w$  and  $X_0$  are the values of the performance variable of the targets (biomass or richness) with and without neighbors. RII is symmetrical around zero (no significant interaction), and has defined limits between  $-1$  and  $+1$ ; negative values indicate competition, and positive values indicate facilitation. We calculated RII for biomass and richness for species at the community level and for perennials and annuals separately.

## Data analysis

To test our first hypothesis, community-level RIIs (RII<sub>Biomass</sub> and RII<sub>Richness</sub>) of understorey species were analyzed using a two-way ANOVA model (followed by Tukey HSD tests when necessary), using dune stabilization and shrub size as factors. Then, to assess the different distribution of life-history species along the dune stabilization gradient for shrub plots of different sizes in absence of shrubs, we used a three-way ANOVA model (followed by Tukey HSD tests, when necessary), with dune stabilization, shrub size, and life-history groups as factors, and the performance of species (biomass, abundance, and richness) in open areas as dependent variables. To test the third hypothesis, the RIIs on the biomass and richness of the two life-history groups were analyzed using a three-way ANOVA model (followed by Tukey HSD tests, when necessary), with dune stabilization, shrub size, and life-history groups as factors. Furthermore, to explore how the intensity of interactions on the performance of different species groups varied with increasing shrub size, linear regression was used to analyze the relationship between the size of the shrub canopy and RII<sub>Richness</sub> and RII<sub>Biomass</sub> of the two life-history groups, separately and for both groups pooled. One-sample  $t$  test was used to analyze significant deviations of RII values from zero. Species performance data were log transformed to improve normality. All analyses were completed using R software ([R Core Team 2014](#)).

## Results

Our results showed that dune stabilization and shrub size differently influenced community-level RII on biomass and richness, thus supporting our first hypothesis ([Table 2](#) and [Fig. 2](#)). RII<sub>Biomass</sub> increased with increasing degree of dune stabilization ( $F = 4.53$ ,  $P = 0.01$ ), but decreased by 30% from small shrubs ( $0.49 \pm 0.04$ ) to large shrubs ( $0.35 \pm 0.02$ ) on average ( $F = 7.75$ ,  $P < 0.01$ ). There was also no difference in RII<sub>Biomass</sub> between large and small shrubs in areas with high

**Table 2.** Results of the two-way ANOVAs for the effects of dune stabilization, shrub size, and their interactions on community-level RII<sub>Biomass</sub> and RII<sub>Richness</sub> of the understorey species. Significant results are indicated in bold.

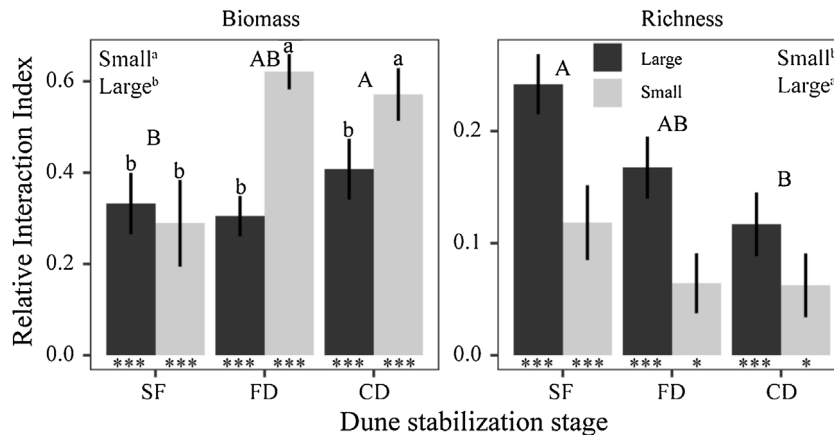
Factor	DF	RII <sub>Biomass</sub>		RII <sub>Richness</sub>	
		F	P	F	P
Dune stabilization	2	4.19	<b>0.02</b>	5.37	<b>&lt;0.01</b>
Size	1	9.18	<b>&lt;0.01</b>	16.26	<b>&lt;0.01</b>
Dune stabilization $\times$ size	2	3.87	<b>0.02</b>	0.79	0.46

disturbance. Differences were only detected for the two most fixed dunes (significant  $D \times S$  interaction;  $F = 3.96$ ,  $P = 0.02$ ). In contrast, RII<sub>Richness</sub> decreased with increasing dune stabilization ( $F = 5.30$ ,  $P < 0.01$ ), but increased by 115% from small shrubs ( $0.08 \pm 0.01$ ) to large shrubs ( $0.18 \pm 0.01$ ) on average ( $F = 16.14$ ,  $P < 0.01$ ).

In the open plots (without *Artemisia*), there were contrasting variations in the performance of the two species groups along the dune gradient and with shrub size ([Fig. 3](#) and [Appendix A: Table S2](#)), supporting our second hypothesis. Aboveground biomass and abundance of perennials were highest in the two fixed dunes. In comparison, for annuals, the highest values for the performance of both groups were observed in the semi-fixed dune, particularly in the small shrub plots (highly significant  $D \times S \times G$  interaction;  $F = 25.58$ ,  $P < 0.01$  for biomass, and  $F = 15.18$ ,  $P < 0.01$  for abundance). In contrast, species richness of perennials was higher than that of annuals in almost all treatments ( $F = 95.86$ ,  $P < 0.01$ ).

Consistent with our third hypothesis, RII clearly varied between the two species groups along the dune stabilization gradient and with respect to shrub size ([Fig. 4](#) and [Appendix A: Table S3](#)). For the RII of each species group, the most significant effect was observed for the life-history group effect and biomass ( $F = 99.23$ ,  $P < 0.01$ ), with much higher facilitation for perennials than for annuals. With increasing dune stabilization, RII<sub>Richness</sub> increased for annuals, but decreased for perennials, particularly for large shrubs (significant  $D \times S \times G$  interaction;  $F = 9.64$ ,  $P < 0.01$ ). RII<sub>Biomass</sub> was highest for perennials at the two extremes of the dune stabilization gradient and the lowest at the intermediate position. The opposite pattern was observed for annuals, particularly for small shrubs (significant  $D \times S \times G$  interaction;  $F = 8.49$ ,  $P < 0.01$ ).

The RII of each life-history group responded differently with increasing shrub size, supporting our third hypothesis ([Fig. 5](#) and [Appendix A: Table S4](#)). When pooling all dune stabilization stages, RII clearly varied with increasing shrub size, depending on performance. RII<sub>Biomass</sub> decreased with increasing size of individual shrubs ( $R^2 = 0.12$ ,  $P < 0.01$ ), whereas RII<sub>Richness</sub> increased ( $R^2 = 0.18$ ;  $P < 0.01$ ). When each group was analyzed separately, for perennials, facilitation of biomass significantly decreased with increasing



**Fig. 2.** Relative interaction indices (RIIs, mean  $\pm$  SE,  $N = 30$ ) for the community-level biomass, and richness of understorey species under large (dark grey) and small (light grey) *A. ordosica* shrubs across the stages of dune stabilization. Significant results of the Two-way ANOVA for the effects of dune stabilization (D), shrub size (S) and their interactions are shown in the upper part of each panel: \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ . Asterisks below bars represent significant deviations of mean RII values from zero (one-sample t-tests: \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ). SF; semi-fixed dunes; FD, fixed dunes; and CD, crusted dunes.

shrub individual size ( $R^2 = 0.17$ ,  $P < 0.01$ ), but increased for richness ( $R^2 = 0.05$ ,  $P = 0.03$ ). There was no significant variation in facilitation with size of individual shrubs for annuals ( $R^2 = 0.01$ ,  $P = 0.31$  for biomass and  $R^2 = 0.03$ ,  $P = 0.13$  for richness).

## Discussion

*A. ordosica* had positive effects on understorey species in this dune system. Overall, facilitation for growth, particularly biomass, decreased with increasing disturbance and shrub size, with the converse being observed for species richness. These contrasting facilitative effects at the community-level might be explained by important variations in the relative dominance of annuals and perennials along the dune stabilization gradient and by the contrasting responses of the two life-history groups to shrub facilitation at different positions along the dune stabilization gradient.

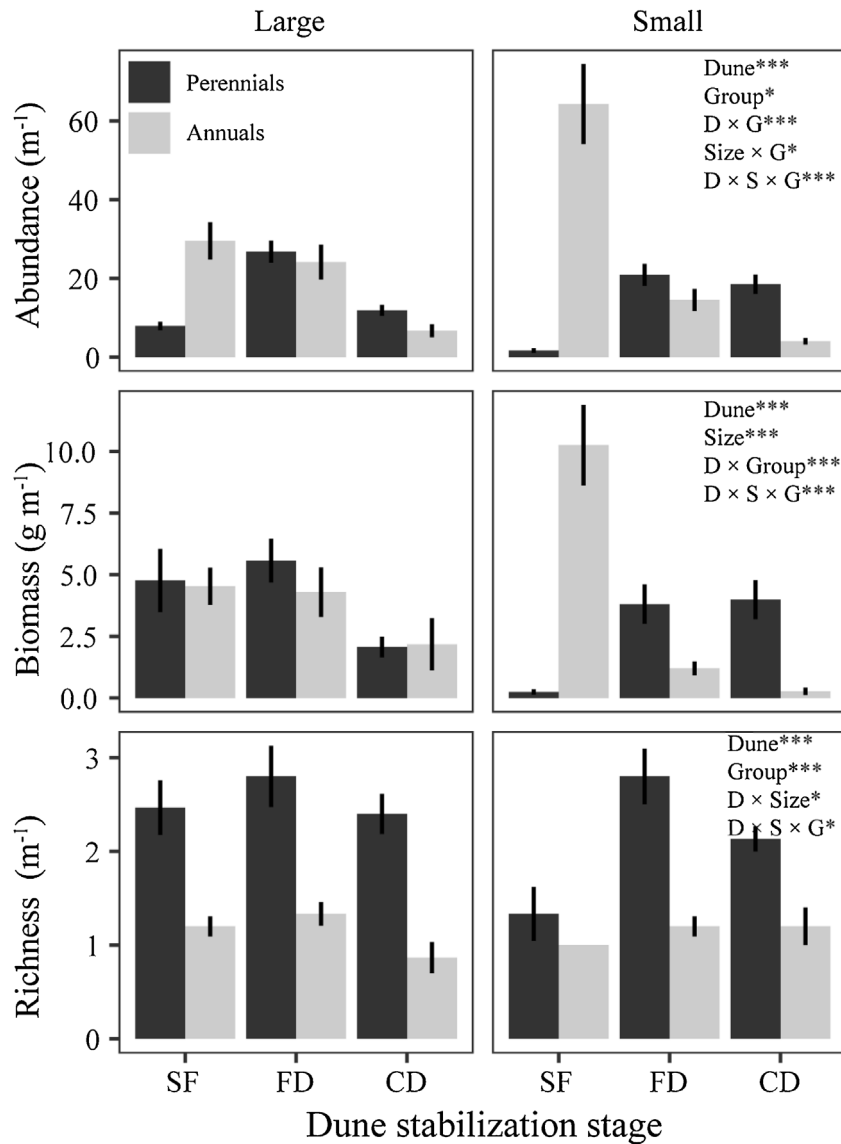
### Facilitative effects of *A. ordosica* on the biomass of understorey species

Facilitation for biomass increased with dune stabilization, from the semi-fixed dune to the crusted dunes (Fig. 2). This pattern was associated with a decrease in biomass (and abundance) of annuals, and an increase in perennials with increasing dune stabilization (Fig. 3). This turnover in biomass and abundance of different life-history groups across the dune stabilization gradient was possibly attributable to changing environmental conditions, because it even occurred in the open spaces between *A. ordosica* patches. However, facilitation for biomass was much stronger for perennials than for annuals along the entire dune stabilization gradient. These latter results demonstrate that the increase in facilitation

for growth at the community level with increasing dune stabilization was caused by an increase in relative abundance and biomass of perennials and their higher sensitivity to the positive effects of shrubs.

Most studies on sand dunes have highlighted that disturbance due to sand burial is the main driver of vegetation structure and composition in these ecosystems (Moreno Casasola 1986; Maun & Perumal 1999; Forey et al. 2008). In particular, an increase in relative abundance of annuals at the expense of perennials with increasing disturbance is a commonly observed pattern in disturbed systems (Grime 1973; Seabloom, Harpole, Reichman, & Tilman 2003; Suding, Goldberg, & Hartman 2003). Functional strategies contribute strongly to explaining species responses to the effects of neighbors in plant communities (Liancourt et al. 2005; Michalet et al. 2006; Forey et al. 2010). For instance, ruderal annuals are highly adapted to tolerate disturbance, and are negatively affected by neighbors, due to their low shade-tolerance (Tielbörger & Kadmon 2000; Seabloom et al. 2003). In contrast, perennial herbs are less tolerant to disturbance (Grime 1974), and are more likely to be facilitated by neighbors than annuals, as shown in the sand dune communities analyzed by Tielbörger and Kadmon (2000) and Forey et al. (2010).

Facilitation for biomass decreased from small to large shrubs in the two fixed dunes. In addition, when all dune stabilization stages were pooled, facilitation for growth performance decreased from small to large shrubs for perennials, but not for annuals. Thus, the presence of shrubs was beneficial for the growth of perennial species until a certain threshold of shrub size. This conversion from facilitation to competition likely occurred due to increasing interference effects related to higher stem density with shrub age, as well as higher competition for light between shrubs and perennials. Variation in the effects of shrubs on understorey species

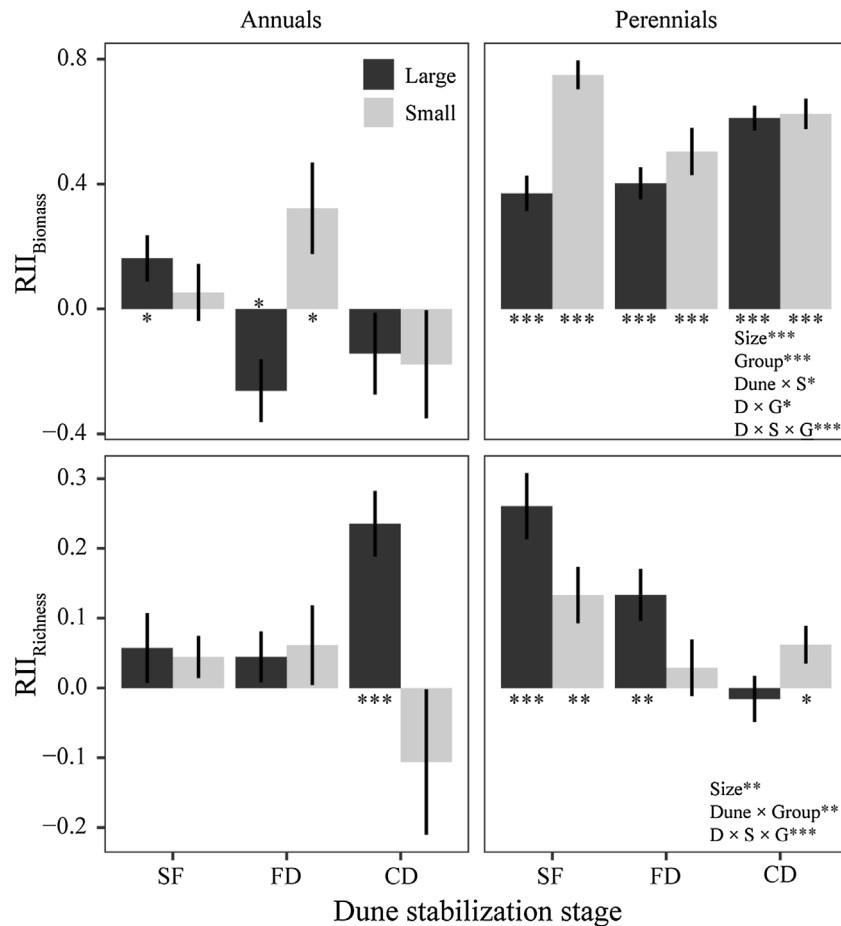


**Fig. 3.** Mean  $\pm$  SE ( $N = 15$ ) of aboveground biomass, richness, and abundance of annuals (light grey) and perennials (dark grey) in the open plots of different shrub sizes across the dune stabilization gradient. Significant results of the Three-way ANOVA for the effects of dune stabilization (D), shrub size (S), life-history groups (G), and their interactions are shown in the upper right part of each panel: \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ . SF; semi-fixed dunes; FD, fixed dunes; and CD, crusted dunes.

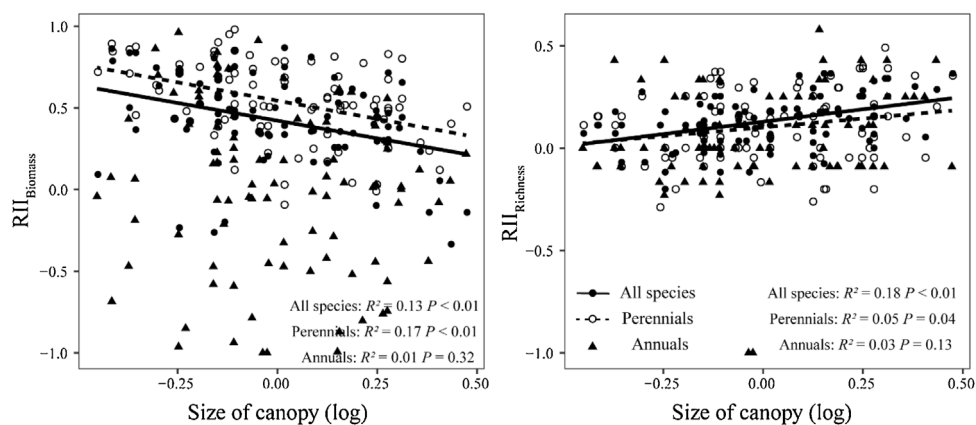
occurs across ontogenic stages and with respect to shrub size (but see Forey et al. 2009). However, contrasting results have been documented depending on the mechanism involved in the interaction. Pugnaire, Haase, and Puigdefabregas (1996) and Allegranza et al. (2016) obtained stronger positive effects for large shrubs than for small shrubs in arid systems on stabilized soils. In comparison, Le Bagousse-Pinguet et al. (2013) found that shrub size and effects increased in coastal sand dunes with increasing nutrient availability, but that these effects were either positive or negative depending on water stress. In our system, large shrubs probably had stronger negative effects on the biomass of perennial species than small shrubs, particularly in fixed dunes, due to increased competition for soil moisture.

### Facilitative effects of *A. ordosica* on understory species richness

The increase in facilitation for species richness of perennials in the most disturbed dunes was probably due to disturbed habitat being located at the lower margin of the recruitment niche of these species along disturbance gradients (Liancourt et al. 2005, 2017). Perennials are less tolerant to disturbance than annuals (Grime 1974). Thus, the recruitment and survival of perennials might be enhanced beneath shrubs compared to perennials in the open patch in highly disturbed semi-fixed dunes, and was more equal in the two microhabitats of the fixed dunes. In comparison, annuals are never facilitated by shrubs at any point along



**Fig. 4.** Mean  $\pm$  SE (N = 15)  $RII_{Biomass}$  and  $RII_{Richness}$  of understorey plant species of the two life-history groups (perennials and annuals) of large and small shrubs along the dune stabilization gradient. Significant results of the Three-way ANOVA for the effects of dune stabilization (D), shrub size (S), life-history groups (G), and their interactions are shown in the lower left part of each panel: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ . Asterisks below or above bars represent significant deviations of mean RII values from zero (one-sample t-tests: \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ). SF; semi-fixed dunes; FD, fixed dunes; and CD, crusted dunes.



**Fig. 5.** Relationship between the canopy size of *A. ordosica* and  $RII_{Biomass}$  and  $RII_{Richness}$  for all plots (stabilization stages of dunes are pooled). Regression lines fitted to the data are shown. More details are presented in the Appendix A: Table S4.

the gradient because of their higher tolerance to disturbance and lower shade-tolerance. Gross et al. (2010) proposed that species responses to neighbors are more dependent on species strain than on stress quantified at the community

level. Species strain is the physiological stress perceived by a species depending on the location of the site in its ecological niche space. In comparison, stress is defined as a limiting factor for the productivity of plant communities inde-



pendent of specific physiological performance (Grime 1974). In this dune system, perennials benefited more from shrubs in semi-fixed dunes than in fixed dunes, probably because they suffered higher strains in the open patches of semi-fixed dunes than in that of the open patches of two fixed dunes.

The highest facilitation found for the species richness of perennials in the most disturbed dune was consistent with that obtained by Bertness and Callaway (1994) and Brooker and Callaghan (1998), who proposed that facilitation should increase with increasing disturbance. In contrast, this result does not support the model of collapse of facilitation of Michalet et al. (2006), who argued that facilitation should peak at the mid position along environmental severity gradient and collapse in extreme environmental conditions because nurse species are too weak to ameliorate physical stress. The collapse of facilitation has been supported by several experiments conducted under extreme environmental conditions of either stress or disturbance (Saccone et al. 2009; Forey et al. 2010; Koyama & Tsuyuzaki 2013; Le Bagousse-Pinguet, Maalouf, Touzard, & Michalet 2014a; Michalet, Brooker, Lortie, Maalouf, & Pugnaire 2015a; Noumi, Chaieb, Le Bagousse-Pinguet, & Michalet 2016, but see Callaway 2013; Pugnaire, Zhang, Li, & Luo 2015, and debates in He & Bertness 2014; Michalet et al. 2014). Forey et al. (2010) found that facilitation for both richness and biomass of understorey species in the coastal dunes of south west France was the highest in the most stabilized dunes dominated by stress-tolerant shrubs and collapsed in the most disturbed dunes dominated by ruderal grasses, which was associated with a collapse in species richness and community biomass. The opposite results obtained by the current study might be explained by a lower disturbance occurring in our semi-fixed dunes as opposed to the highly disturbed foredunes of Forey et al. (2010), as suggested by the different patterns of species richness and biomass observed along the dune stabilization gradients between the two systems. In addition, facilitation for species richness was weaker when shrubs were smaller (thus likely younger), probably due to cyclic replacements after natural dieback, which was triggered by local disturbances and species accumulation over a longer time span, which supports the collapse model along a shrub size gradient (Michalet et al. 2006). Larger canopies might also capture more wind-dispersed seeds than smaller ones (Pugnaire & Lázaro 2000).

### Shrub–herb interactions and implication for ecological restoration

Our study showed that *A. ordosica* had positive effects on understorey species in this dune system. Thus, the shrub *A. ordosica* could act as a nurse to help ecological restoration in this highly disturbed and dry ecosystem. Perennials were more sensitive than annuals to the facilitative effects of

shrubs, leading to a turnover in the distribution of annuals vs. perennials with dune stabilization. These changes in species composition enhanced the stability of the herb community, because perennials have higher competitive ability and stability than annuals (Bai, Han, Wu, Chen, & Li 2004; Liancourt et al. 2005; Michalet et al. 2006).

However, there are still two issues that cannot be overlooked. First, we found that the ability of shrubs to promote the growth of understorey herbs decreased with increasing shrub size. In other words, with increasing shrub age, the effect of shrubs in enhancing the growth of understorey herbs gradually vanished, or even became negative. Shrub seedlings might also face pressure from competition with herbaceous plants (Brown, Scanlan, & McIvor 1998). Thus, the whole community would incur the problem of “aging” during the restoration process, leading to a community only consisting of old shrub individuals and relatively few herb species. Second, we found that the ability of shrubs to improve the richness of understorey herbs decreased with dune stabilization. Thus, along the ecological restoration process, the community might be subject to a decrease in diversity and, eventually, of ecosystem key functions. Thus, even though *A. ordosica* could be a useful nurse plant for short-term restoration in this dry system subject to high disturbance, the community might be subject to a long-term decline in diversity and ecological functions. Further studies are needed to test this hypothesis in full, with longer observations and targeted manipulation experiments being required in the future.

### Author contributions

Bai, Y. and Zhang, Y. designed the research. Bai, Y. and She, W. conducted the experiments. Bai, Y. analyzed the data. Bai, Y., Zhang, Y. and Richard, M. wrote the manuscript; all authors contributed to the interpretation of the results and the revision of all stages.

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### Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.baae.2019.06.001>.

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