

Do species' strategies and type of stress predict net positive effects in an arid ecosystem?

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Abstract. A proposed refinement to the stress-gradient hypothesis requires consideration of the strategies of the interacting species and the characteristics of the stress factors. While the strength and direction of these interactions can be predicted for different ecosystems, this idea remains largely untested in the field. We performed a manipulative field experiment complemented with a descriptive study to test the predictions in a natural setting that represents the extreme end of a precipitation gradient. There, wind driven desiccation and water availability are the main stressors (non-resource and resource-based stresses, respectively). We evaluated the interaction between the shrub and grasses that are dominant in the Patagonian steppe. The species had differences in morpho-functional traits and drought tolerance that fit into the C–S axis of Grime's strategies. We experimentally separated root zones to limit direct competition for soil moisture and reduce the resource-based stress on grasses. We also manipulated the distance to shrubs to evaluate non-resource stress amelioration by canopies (e.g., sun and wind) on grasses. Finally, we evaluated the distribution of naturally established C and S grasses in the neighborhood of C and S shrubs to infer process-pattern relationships. Our growth data coincide to a large degree to the predictions. We found positive effects on the growth of beneficiaries when stress was non-resource based and when strategies differed (i.e., $C_{\text{shrub}}-S_{\text{grass}}$ and $S_{\text{shrub}}-C_{\text{grass}}$). We also found strong negative effects when the abiotic stress was driven by water, particularly on C grasses. Additionally, shrubs only increased the survival of grasses when strategies differed (i.e., $C_{\text{shrub}}-S_{\text{grass}}$ and $S_{\text{shrub}}-C_{\text{grass}}$). Our manipulative and descriptive study supported previous results that showed that stress-tolerant species are important for the persistence of competitive species at high stress. While the applicability and generality of these predictions remains to be tested with more field experiments, some ecological factors, such as stress types and species traits, can explain much of the variation in how dominant shrubs and grasses interact in this extreme arid environment. Moreover, this framework could be extended to specifically test the importance of facilitation under different levels of stress.

Key words: arid environments; facilitation; plant-plant interactions; species traits; stress gradient hypothesis.

INTRODUCTION

In their seminal paper, Bertness and Callaway (1994) proposed that facilitation among plants should predominate over competition in high stress environments. This prediction, in the context of what is currently known as the stress gradient hypothesis (SGH), has been thoroughly questioned in arid and semiarid ecosystems (Maestre et al. 2005, Lortie and Callaway 2006, Michalet 2006, Soliveres et al. 2014). This is mainly due to the fact that several field studies have found no support for the positive relationship between water limitation and facilitation in dry systems (Tielbörger and Kadmon 2000, Maestre and Cortina 2004, Armas and Pugnaire 2005, Maestre et al. 2005, Graff et al. 2007, Weedon and Facelli 2008). Variability in the results obtained in field studies seemed to depend on several factors not considered by

the SGH (Michalet 2006, 2007, Maestre et al. 2009). For example, the life-history strategies of both the benefactor and beneficiary species in the interaction can explain the absence of facilitation (Liancourt et al. 2005). As environmental severity increases, life-history strategies of plant species change. Stress-tolerant species (S) become dominant over stress-intolerant competitive species (C) (sensu Grime 1977), and at the extremes of the gradient, only S species persist (Michalet et al. 2006). Positive effects are then expected only when both strategies coexist within a system, and C species are the most likely to be facilitated by S neighbors at high stress (Michalet et al. 2006). Another crucial issue, not considered in the SGH, is how resource vs. non-resource stress factors can lead to different sets of interactions. Whereas facilitation is expected to increase in highly stressed conditions, driven by non-resource factors (such as wind, heat, cold, or salinity), competition is also expected to increase if those highly stressed conditions are driven by a resource factor (such as the lack of soil water or nutrients; Michalet 2007, Maestre et al. 2009). Therefore, depending on the

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combination of all these factors, both facilitation and competition can be found across broad ranges of water availability.

Recent refinements of the SGH have explicitly considered the species strategies (C and S, *sensu* Grime 1977) and the type of stress (i.e., resource vs. non-resource), and have established clear predictions about the outcome of species interactions at different levels of environmental stress (Michalet 2006, 2007, Maestre et al. 2009). Maestre et al. (2009) predicted that in highly stressed conditions, the outcome of the pair-wise interactions between potential benefactor (e.g., shrubs) and beneficiary plants (e.g., grasses) will be the following: (1) If abiotic stress is driven by a non-resource stress factor (e.g., wind, temperature, high irradiance, etc), architecture-mediated amelioration of harsh environmental conditions by the benefactor is expected to be higher than competition. Therefore, positive outcomes for beneficiaries are expected. The positive effect will be stronger if both interacting species differ in their life-history strategies (Fig. 1a). Positive effects of a stress tolerant benefactor on a competitive beneficiary should increase until a

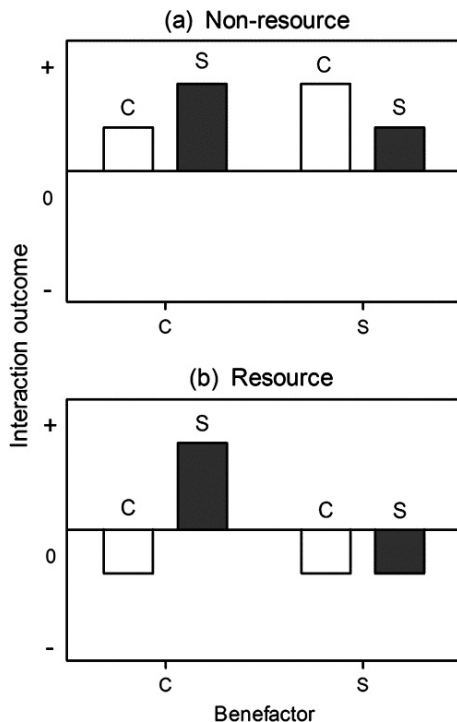


FIG. 1. Maestre et al.'s (2009) predicted relationship between the nature of the abiotic stress (non-resource or resource driven) and the outcome of the benefactor/beneficiary interaction in a high stress environment. The interacting species fitted into competitive (C) and stress-tolerant (S) categories. + = net facilitation; - = net competition; 0 = neutral interaction. Bars represent the effect of benefactors on beneficiary. White bars represent competitive beneficiary species (C) and grey bars represent stress-tolerant beneficiaries (S). Differences in the magnitude of facilitative interactions within a given interaction and stress level are noted by the size of the bar in the Y axes. (predictions obtained from Maestre et al. 2009: Table 1).

plateau is reached, defined by the stress levels at which “beneficiaries” growing without neighbors die (Maestre et al. 2009). On the other hand, competitive benefactors should continue benefiting stress-tolerant beneficiaries by architecture-mediated protection after they die but remain standing (Maestre et al. 2009). (2) If abiotic stress is driven by a resource (e.g., soil water availability), negative effects are expected due to an increase of competition. Beneficiary species are more likely to be negatively affected when both interacting species have similar “competitive” or “stress-tolerant” life histories (Fig. 1b), since they are likely to compete for resources all along the abiotic stress gradient (Maestre et al. 2009). Resource based stress, however, could also determine positive outcomes for beneficiaries according to Maestre et al. (2009). Under high levels of stress, competitive benefactors could die due to the shortage of resources, and tolerant beneficiaries would be favored from the benefactor’s legacy on soil properties, even after the death of the competitive species (Fig. 1b).

Despite of the potential strength of Maestre et al.’s (2009) framework to understand and predict species interactions in several environments, it has been rarely applied when studying the outcome of pair-wise interactions existing within local communities (He and Bertness 2014, Soliveres et al. 2014). This is partly because the predictions cannot be robustly tested through a purely observational study. A more mechanistic understanding needs to experimentally separate the responses related to the type of stress (i.e., resource vs. non-resource) and include benefactor and beneficiary species with different competitive-stress tolerance capacities (Maestre et al. 2009, He and Bertness 2014). To the best of our knowledge, there are no studies that have already tested those predictions within a system.

We performed a transplanting field experiment to test Maestre et al.’s (2009) predictions (Fig. 1a, b) in a species-poor/high abiotic stress Patagonian steppe community. In the western Patagonian steppe, non-resource and resource-driven stresses converge (Soriano 1956). Wind driven desiccation and low water availability are the main non-resource and resource stressors, respectively, contributing to stress severity for plants during the growing season (Fernández and Paruelo 1988). Shrubs coexist with grasses in dense stands, whereas the areas between shrubs have scattered tussocks, interspersed with bare soil (Soriano et al. 1994). This patch structure creates well-differentiated microenvironments. Within this layer, grasses close to shrubs experience less non-resource stress than in the scattered-tussock patches, since canopy amelioration decreases wind velocity and potential evaporation rates. However, grasses also experience higher resource stress near shrubs than in the scattered-tussock patches, where soil water potential is lower because of an intense root competition (Aguiar et al. 1992, Aguiar and Sala 1994). We experimentally separated shrub and grass root zones to limit direct competition for soil moisture and reduce the resource-based

stress on grasses. We also manipulated the distance to shrubs to evaluate the effect on grasses of non-resource stress amelioration provided by shrub canopies. The site where we performed the experiment represented the driest end of a precipitation gradient where species with competitive and stress-tolerant strategies might coexist (Bertiller et al. 1995).

The general features of the “stress-tolerant” (S) strategy (sensu Grime 1977: table 2) comprise a slow growth rate, extended leaf production, xerophytic leaf traits, conservative leaf economic trait values, such as low specific leaf area (SLA) and leaf N content, and low palatability to herbivores. On the contrary, the “competitive” (C) syndrome involves a high, dense canopy of wide-spreading leaves, rapid growth in leaf area, rapid potential relative growth rate (RGR), high morphological plasticity to stress, high rates of uptake of water and nutrients when available, short longevity of leaves and clear peaks of leaf production, high production of litter and high palatability. For the experiment we selected two out of the three dominant native shrubs and two out of the four dominant native perennial grasses that represent contrasting strategies in the C–S Grime’s axis. We carefully collected information of plant traits in order to determine the strategies. Therefore, shrubs and grasses were represented by a competitive or water demanding species (C) and a drought stress tolerant (S) species, respectively (C_{shrub} , S_{shrub} and C_{grass} , S_{grass}). We extended the predictions to patterns of species distribution. Since both types of stress for grasses converge in arid ecosystems (Maestre et al. 2009), we expected that, as the net result of the interactions, beneficiaries would be more closely associated to benefactors if their strategies differed (C–S or S–C).

MATERIALS AND METHODS

Abiotic conditions

Field studies were conducted in the Patagonian steppe in south-western Chubut, Argentina (lat 45°41 S, long 70°16 W, 500 m a.s.l.). The study site was located within a 150-km² area at the Río Mayo Experimental Field Station (Instituto Nacional de Tecnología Agropecuaria). This community is co-dominated by few long-lived shrubs and perennial grasses, which contribute more than 96% of the total plant cover and plant biomass (Fernandez et al. 1991). Forbs contribute <1% to plant cover. The vegetation pattern is a two-phase mosaic: Shrubs and grasses forming high cover patches, within a matrix of sparse tussock grasses. The dominant shrub species are the two cushion-like shrubs *Mulinum spinosum* Cav. Pers., *Senecio filaginoides* De Candolle, and the legume *Adesmia volkmannii* Philippi. The dominant grass species are: *Pappostipa speciosa* Trin. et Rupr., *Pappostipa humilis* Cav., *Poa ligularis* Nees ap. Steud and *Bromus pictus* Hook. *Poa ligularis* and *Bromus pictus* are the two palatable species that sustain sheep production in the steppe (Bonvissuto et al. 1983).

The climate is arid, with an intense summer drought (Paruelo et al. 1988). Mean annual precipitation in the last 30 yr (1984–2013) was 134 mm with a winter and early spring (May to September) rainy season. Average monthly temperatures range from 3°C in winter to 16°C in summer (1984–2013; Field meteorological station data: <http://anterior.inta.gov.ar/region/pas/sipas2/cmp/agromet/index.html>). Strong, dry winds blow predominantly from west to east with high intensities throughout the year (Paruelo et al. 1988), averaging more than 20 km/h during the growing season (Beltrán 1997). The scarce precipitation and its distribution during winter lead to a high summer water deficit (Paruelo et al. 1988). Therefore, stress during the growing season is mainly based on belowground resources (water and nutrients) and aboveground non-resources (wind, temperature, etc.).

Benefactor species

Study species were two out of the three dominant shrubs in the steppe: *Mulinum spinosum* (Cav.) Pers and *Senecio filaginoides*, De Candolle; hereafter *Mulinum* and *Senecio*, respectively. They account for more than the 85% of the shrub production and the 76% of the shrub cover in the Patagonian steppe (Fernandez et al. 1991). Both shrubs are hemispherical, cushion-like shrubs with closed and tall canopies, in contrast to *Adesmia volkmannii*, which has a cone-inverted scattered canopy (Soriano et al. 1994, Oñatibia et al. 2010). Soil thermal amplitude is only significantly reduced by *Mulinum* and *Senecio* canopies (Flombaum and Sala 2012). *Mulinum* and *Senecio* strongly differ in phenology, leaf traits, hydraulic architecture and water relations traits and physical and chemical defenses against herbivory (Table 1). *Mulinum* (Apiaceae) is a deciduous species with marked differences in the leaf time span and *Senecio* (Asteraceae) is an evergreen species. Studies on Patagonian shrub species have indicated that *Mulinum* has traits that allow it to grow fast when soil water availability is high (e.g., high xylem-specific and leaf hydraulic conductivity, high effective water potential and water use efficiency (WUE), light wood density and high SLA; Golluscio and Oesterheld 2007, Bucci et al. 2009). *Senecio*, in turn, has higher longevity of leaves, more xerophytic leaf traits, denser wood, lower hydraulic conductivity, lower SLA and slower growth than *Mulinum* (Table 1). *Mulinum* is also highly palatable despite its spiny leaves, whereas *Senecio* is not browsed due to its small, thick and pubescent leaves with high concentration of secondary metabolites (Fernández et al. 1992, Cavagnaro et al. 2003). Within the Patagonian Phytogeographic Province, *Mulinum* extends into the wetter Subandean District (León et al. 1998). In relative terms, *Mulinum* fits into a more competitive (or less stress tolerant) strategy than *Senecio* (Table 1).

Both shrub species have a shallow tap root (<1 m) with long lateral roots that grow close to the soil surface in *Senecio*, and 15 cm below the soil surface in *Mulinum*

TABLE 1. Trait comparison between two Patagonian shrubs used to infer benefactor C–S strategy (Grime 1977).

Trait	Shrub species		Source
	<i>Mulinum spinosum</i>	<i>Senecio filaginoides</i>	
Palatability	High	Very low	Bonvissuto et al. (1983), Cavagnaro et al. (2003)
Carbon based secondary metabolites: oil, phenols and hydrocarbon compounds (%)	17.24 ± 0.5 (mean ± SE)	21.22 ± 0.8 (mean ± SE)	Cavagnaro et al. (2003: fig. 2)
Plant phenology (number of months in which plants of the studied species had green leaves during 1 yr).	7	12	Golluscio et al. (2005), Flombaum and Sala (2012: fig. 1)
Specific leaf area (cm ² /g)	57 ± 2.16 (mean ± SE)	45 ± 2.16 (mean ± SE)	Bucci et al. (2009: fig. 8)
Wood density (g/cm ³)	0.36 ± 0.01 (mean ± SE)	0.47 ± 0.01 (mean ± SE)	Bucci et al. (2009: fig. 8)
Relative growth rate	1.3 ± 0.13 (mean ± SE)	1.2 ± 0.16 (mean ± SE)	Flombaum and Sala (2012: fig. 1)
Specific hydraulic conductivity (Ks: kg·m ⁻¹ ·s ⁻¹ ·MPa ⁻¹)	0.43 ± 0.03 (mean ± SE)	0.33 ± 0.04 (mean ± SE)	Bucci et al. (2009: fig. 6)
Leaf specific hydraulic conductivity (Kl: × 10 ⁻⁴ kg·m ⁻¹ ·s ⁻¹ ·MPa ⁻¹)	0.51 ± 0.03 (mean ± SE)	0.38 ± 0.05 (mean ± SE)	Bucci et al. (2009: fig. 6)
Water use efficiency/effective water potential	21.15 ± 2.3 (mean ± SE)/–0.22	10.57 ± 0.5 (mean ± SE)/–0.82	Golluscio and Oesterheld (2007: fig. 3)
Relative strategy	C	S	Grime (1977)

(Fernández and Paruelo 1988, Bucci et al. 2009). Woody and herbaceous growth forms compete for resources in the upper soil layers (Bucci et al. 2009). Aboveground and belowground effects of shrubs on abiotic conditions were described before (Soriano and Sala 1986, Aguiar and Sala 1994, Flombaum and Sala 2012). Potential soil nitrification and ammonification have been reported to be significantly higher below both shrub species than in open spaces, whereas water content is significantly lower (González Polo 2010; see Appendix S1: Table S1). Wind speed below the shrub canopy is reduced by 75–85% (Soriano and Sala 1986) and daily evaporation is reduced by 70% (Aguiar and Sala 1994).

Beneficiary species

The selected species were two out of the four dominant native perennial grasses from Patagonian rangelands: *Bromus pictus* Hook and *Poa ligularis* Nees ap. Steud., hereafter *Bromus* and *Poa*. *Bromus* is the most different species in functional traits related to forage quality, being the most palatable species, whereas *Poa* shares similar morphological and chemical traits with the other two dominant species in the steppe (*Pappostipa speciosa* and *Pappostipa humilis*) (Adler et al. 2004). However, it is considered a palatable species that decreases with grazing intensity as *Bromus* (Perelman et al. 1997). *Bromus* and *Poa* differ also in several traits related to their tolerance to stress (sensu Grime 1977). *Bromus* has more mesophytic leaf traits, with a higher nitrogen content in green tissues, higher leaf production, and lower lignin concentration in leaves than *Poa* (Table 1 in Couso and Fernández 2012). *Bromus* has the highest potential growth rate in the system

and showed also the greatest plasticity in performance traits in response to drought, which is linked to a lower performance under stress (Cenzano et al. 2013). It is also the most sensitive grass to water stress within the steppe (Golluscio and Oesterheld 2007), and after a simulated drought, the number of dead plants was more than two fold higher in *Bromus* than in *Poa* (see Couso and Fernández 2012 for experimental test). *Poa*, on the other side, displays mechanisms to maintain photosynthetic activity under drought conditions through the increase of photosynthetic pigments (Cenzano et al. 2013). In relative terms, *Bromus* exhibits an acquisitive resource-use strategy compatible with Grime's "competitive" syndrome, whereas *Poa* fits into a stress tolerant strategy (Table 2; Couso and Fernández 2012).

Pair-wise interactions field experiment

We followed Graff et al. (2007) field experiment design to allow the comparison of resource vs. non-resource stress factors on the interaction of two shrubs and two grass species that in relative terms fitted into C or S Grime's strategies (Bucci et al. 2009, Couso and Fernández 2012, Flombaum and Sala 2012). Shrubs could improve microclimate for grasses in their surroundings, but did not necessarily increase their water availability. Indeed, they decreased through direct water uptake, rainfall interception and evaporation (Sala et al. 1989, Maestre et al. 2003, Valladares et al. 2008). Therefore, grasses close to shrubs could experience higher resource-based stress from root competition and, at the same time, experience less non-resource stress through canopy amelioration than in open areas. In the opposite way, non-resource stress is

TABLE 2. Trait comparison between two Patagonian grasses used to infer benefactor C–S strategy (Grime 1977).

Trait	Grass species		Source
	<i>Bromus pictus</i>	<i>Poa ligularis</i>	
Palatability	High	Intermediate	Bonvissuto et al. (1983), Couso and Fernández (2012: table 1)
N (%)	1.15	0.73	Adler et al. (2004: table 3)
C/N leaf	33–9	61–9	Adler et al. (2004: table 3)
Relative growth rate _{max}	0.078 ± 0.010	0.009 ± 0.020	Leva et al. (2013)
Specific leaf area (cm ² /g)	175	125	Leva et al. (2013)
Water use efficiency/effective water potential	12.22 ± 3 (mean ± SE)/–1.45	13.03 ± 2 (mean ± SE)/–1.31	Golluscio and Oesterheld (2007: fig. 3)
Proportion of dead plants with drought (%)	55	25	Couso and Fernández (2012: fig. 8)
Plasticity index to drought	0.51	0.4	Couso and Fernández (2012: fig. 7)
Relative strategy	C	S	Grime (1977)

higher for plants growing far from shrubs, but resource-based stress is lower, since competition decreases as distance from shrubs increases. In addition, water infiltration rates are higher in open areas than in high cover patches. Therefore, resource and non-resource stress experienced by grasses have different spatial pattern of intensity (Fig. 2a, c). In May 2010 (beginning of winter season), we

randomly collected *Bromus* (C_{grass}) and *Poa* (S_{grass}) plants from grazing exclosures. Plants were divided to obtain 5-tiller individual transplants. Since *Bromus* and *Poa* plants are perennial, we selected stem bases with green tillers coming from the tussock periphery to form the transplants. Within each of 6 grazing exclosures (blocks $n = 6$), we selected naturally established *Mulinum* (C_{shrub})

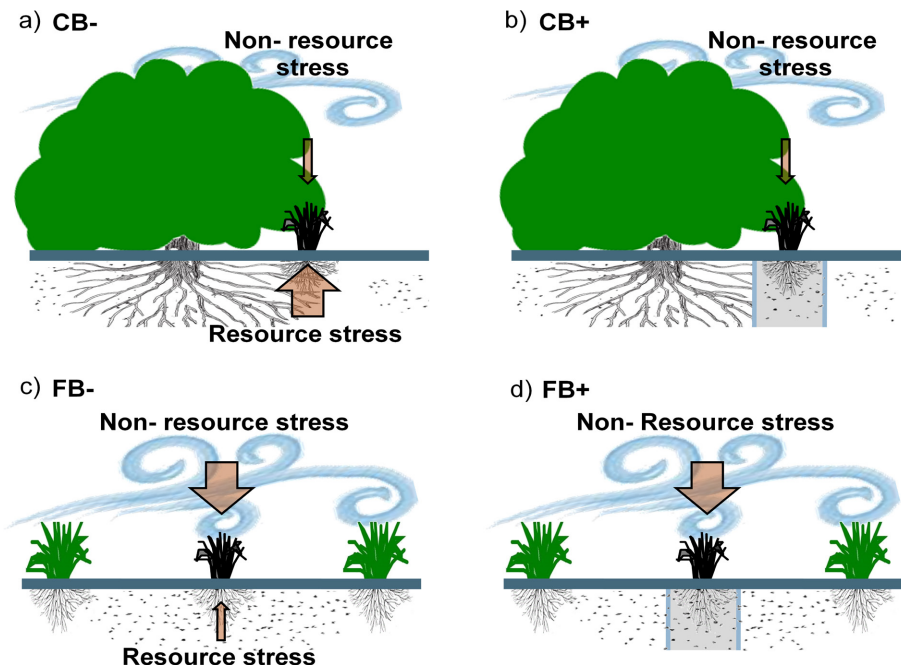


FIG. 2. Experimental design to test for the effects of non-resource stress and resource stress on the interaction among shrubs and grasses. The same design was used for each C and S shrub species and C and S grass species. The smaller black plant represents a grass transplant, *Bromus pictus* (C_{grass}) or *Poa ligularis* (S_{grass}). Upper panels represent the treatments where transplants were growing at the edge of shrub canopies (*Mulinum spinosum* (C_{shrub}) or *Senecio filaginoides* (S_{shrub})), whereas lower panels represent the treatments where transplants were growing in adjacent open areas, far from shrubs. Right panels show the treatment where transplants were growing within the barrier to prevent root competition and reduce resource based stress. C and F indicate distance from shrub neighbor: close and far, respectively. (B–) indicates no belowground barrier or root competition at the natural level, whereas (B+) indicates that a barrier was added. Calculations of the effects are explained in full detail in the *Materials and Methods*. [Color figure can be viewed at wileyonlinelibrary.com]

and *Senecio* (S_{shrub}) shrubs of similar height, basal diameter and far from other shrubs (>3 m), to form shrub-grass species pairs. Treatments were applied in a factorial of benefactor species (*Mulinum* (C_{shrub}) and *Senecio* (S_{shrub})), beneficiary species (*Bromus* (C_{grass}) and *Poa* (S_{grass})), distance to shrub canopy (close and far) and barrier to belowground competition (root barrier present or absent). There were 2 sub-replicates per block of each treatment combination for *Bromus*, and 4 sub-replicates (2 females and 2 males) per block of each treatment combination for *Poa*.

We experimentally separated shrub and grass root zones to reduce the resource-based stress on grasses by limiting direct competition for soil moisture instead of manipulating water. Water in arid systems stimulates nutrient mineralization, N losses and nitrate leaching (Austin et al. 2004, Yahdjian and Sala 2010). Those changes could increase the competitive advantage for deep-rooted species like shrubs in the steppe (Yahdjian and Sala 2010), and the desired effect of a resource based stress reduction on grasses would not be reached due to an increase in competition. Other studies have also reported an increase in competition for growth with water manipulations (Kadmon 1995, Corcket et al. 2003, Liancourt et al. 2005). We transplanted grasses at the edge of the shrub, where root density is higher (Soriano et al. 1994) and a reduced resource based stress treatment that was achieved by digging a hole of 0.30 m in diameter by 0.30 m deep, fitting a fine mesh cloth in the pits, which functioned as a barrier to prevent the growth of roots of neighbor plants under beneficiary target plants (Aguiar et al. 1992, Graff et al. 2007, 2013, Fig. 2b). The holes were filled with the extracted soil after removing roots and stones by sieving it. Transplants with no mesh around the sieved soil core were those that did not receive a reduced resource stress treatment (Fig. 2a). Large shrub patches are frequently encircled with a dense ring of grasses that could obscure shrub effects on target species (Aguiar and Sala 1994), so before applying the treatments, we removed the surrounding grasses to isolate the effect of the shrub on *Bromus* and *Poa* beneficiary species.

Non-resource stress on beneficiaries was isolated by transplanting *Bromus pictus* (C_{grass}) and *Poa ligularis* (S_{grass}) at two distances from each shrub canopy. Transplant were placed close (0 cm) and far (within the matrix, more than 1 m away) from shrubs. All transplants in these treatments also had root barriers to protect the grasses from the root growth of shrubs (Graff et al. 2007, 2013), to isolate the effect of non-resource stress from belowground resource stress (Fig. 2b, d). All transplants were located northeast of shrubs, where wind speed is five times slower and evaporative demands are two times lower than those of exposed windward areas (Soriano and Sala 1986, Aguiar and Sala 1994). Therefore, non-resource stress amelioration by shrub canopies is more likely to occur in eastern edges.

Net shrub/grass interaction effects were evidenced by comparing the performance of transplants growing with

full influence of shrub neighbors (i.e., growing at the edge of shrub canopies and without the barrier to prevent root competition) vs. completely isolated from neighbors (i.e., growing far from shrubs within a mesh; Fig. 2a, d). We also compared the net shrub/grass effects as in a typical experiments, where the performances of target species beneath nurses and in adjacent open areas are compared, without manipulating root competition (Fig. 2a, c). These kind of experiments assume that in open areas target plants do not have any influence of other plants.

Transplants were harvested in January 2012, after two growing seasons, by digging pits 0.20 m in diameter by 0.3 m deep where the transplants were located. Vegetative (shoot and root) and reproductive (panicles) material was separated, oven dried at 70°C for 48 h, and weighed. Species were easily distinguished by their root morphology (Leva et al. 2009), so roots were separated by species from sandy soils by flotation and sieving (0.2 mm mesh sieve).

The predicted relationships between the nature of the abiotic stress and the outcome of the shrub-grass interactions in the Patagonian steppe were analyzed by calculating the intensity of interactions on beneficiaries using the Relative Interaction Index “RII” (Armas et al. 2004) per block. Response variables were total vegetative biomass (roots and shoots) and survival. Panicle biomass was not included since some seeds were dispersed before harvesting the plants. We averaged the sub-replicates per block for calculations.

We calculated *resource-based interactions* as follows:

$$\text{RII:}(\text{CB}^- - \text{CB}^+)/(\text{CB}^- + \text{CB}^+),$$

Non-resource based interactions were estimated as follows:

$$\text{RII:}(\text{CB}^+ - \text{FB}^+)/(\text{CB}^+ + \text{FB}^+),$$

Net interaction effects as follows:

$$\text{RII:}(\text{CB}^- - \text{FB}^+)/(\text{CB}^- + \text{FB}^+),$$

and “typical” *Net effects* as follows:

$$\text{RII:}(\text{CB}^- - \text{FB}^-)/(\text{CB}^- + \text{FB}^-),$$

where C is close to shrub, F is far from shrubs, and B is the barrier to prevent root overlapping treatment (+ and - superscripts mean with or without the mesh cloth, respectively). RII is symmetrical around 0 and ranges from +1 to -1. We constructed the 95% confidence intervals from the RII values obtained per block. Positive values indicate facilitation, negative values indicate competition, and values not significantly different from zero indicate neutral/no effects (Armas et al. 2004). We tested whether RII values different from zero using a *t*-test for single means. To analyze changes of interaction indices with shrub and grass species, we used linear mixed effects models (procedure lme, package nlme, R software) with benefactor species (*Mulinum* (C_{shrub}) and *Senecio* (S_{shrub})) and beneficiaries (*Bromus* (C_{grass}) and *Poa* (S_{grass})) as fixed factors and block as random factor.

Neighborhood distributions

To complement the field experiment, we included an assessment of the cumulative frequency distribution of *Bromus* (C_{grass}) and *Poa* (S_{grass}) plants in relation to the distance from shrub canopies measured during the flowering season. We used four long-term exclosures from sheep grazing and other large herbivores (settled in 1956, 1972, 1983 and 1994, respectively) to minimize the influence of large herbivores on the spatial distribution of plants. In each of the four exclosures, we selected 10 pairs of *Mulinum-Mulinum* and 10 *Senecio-Senecio* shrubs of modal size. Selections were based on the edge of each shrub in the pair being, separated 2 m (which is approximately the maximum distance between shrub pairs found in exclosures; Cipriotti and Aguiar 2010). Transects were placed from the edge of one shrub to the half distance of the other shrub edge in order to avoid the influence area of the second shrub in the distribution of *Bromus* (C_{grass}) and *Poa* (S_{grass}) plants. At each transect, *Poa* and *Bromus* distance to focal shrub was recorded. We merged the data points from the ten transects per shrub per exclosure and then performed cumulative frequency distributions of the number of *Bromus* and *Poa* plants at distances from shrubs. The distributions of cumulative frequencies of grass species occurrence at varying distances from *Mulinum* (C_{shrub}) or *Senecio* (S_{shrub}) edges were compared using Kolmogorov–Smirnov tests.

RESULTS

At the end of the two growing seasons, only 54% of *Bromus* (the less stress tolerant species) plants survived, whereas for *Poa*, the survival was 77% (Fig. 3). Transplants also demonstrated differential survival depending on the type of stress and the benefactor species involved (Fig. 3a, c). Both beneficiary species experienced shrub amelioration of non-resource stress (Fig. 3a, b). A strong positive and significant effect on survival and biomass was detected when both interacting species differed in their strategy (i.e., $S_{shrub}-C_{grass}$ and $C_{shrub}-S_{grass}$), but neutral effects resulted from the interaction between species with similar traits (i.e., $C_{shrub}-C_{grass}$ and $S_{shrub}-S_{grass}$; Fig. 3a, b; see Appendix S2: Table S1 for analysis). The shrub \times grass interaction was more evident on the RII of growth than on survival ($P = 0.04$ and $P = 0.09$, respectively; see Appendix S3: Table S1 for analysis).

Resource stress amelioration by shrubs was not detected in the beneficiaries. On the contrary, negative effects were intense (Fig. 3c, d), particularly on beneficiaries growth (biomass) and in the expected shrub/grass combinations ($C_{shrub}-C_{grass}$, $S_{shrub}-C_{grass}$ and $S_{shrub}-S_{grass}$; Fig. 3d). Even though RII single means did not differ from zero (see Appendix S2: Table S1 for analysis), RII values were more negative for the survival of the competitive grass species than for the survival of stress tolerant grasses

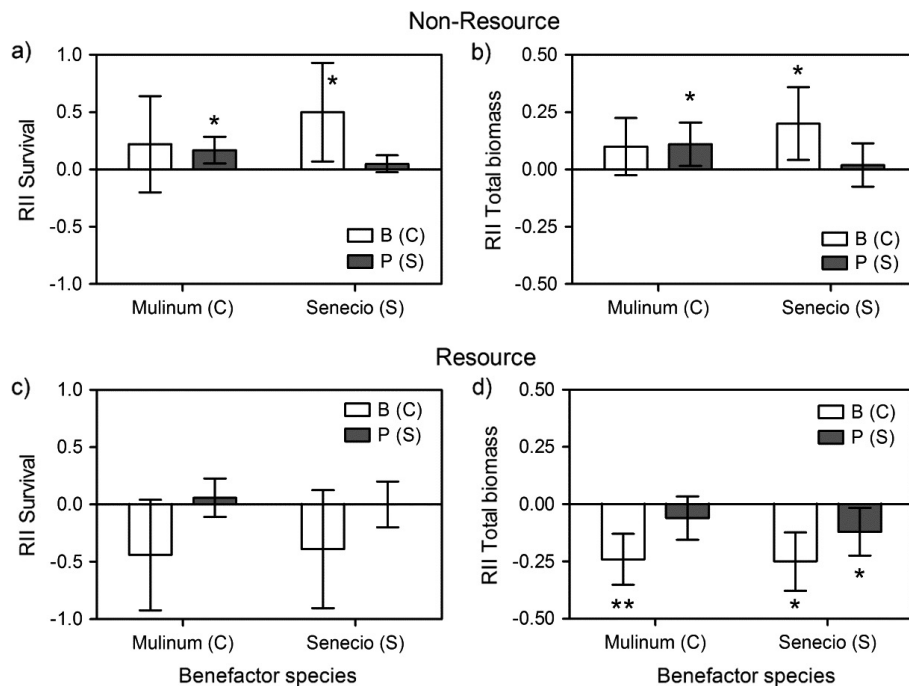


FIG. 3. The observed relationship between the nature of the abiotic stress (resource and non-resource based) and the outcome of the shrub-grass interaction in the dry Patagonian steppe. Bars represent the Relative Interaction Index (RII, Armas et al. 2004) of *Mulinum spinosum* and *Senecio filaginoides* benefactor shrubs on beneficiary *Bromus pictus* (B, white bars), and *Poa ligularis* (P, grey bars) species. Both shrubs and grasses fitted into two broad categories of species (C = “competitive” and S = “stress-tolerant”). Values are RII means and 95% confidence intervals. Stars above or below bars indicate significant deviation from zero value (one-sample t -tests) * $P < 0.05$, ** $P < 0.01$ (analysis in Appendix S2: Table S1). Calculations of the effects are explained in full detail in the *Materials and Methods*.

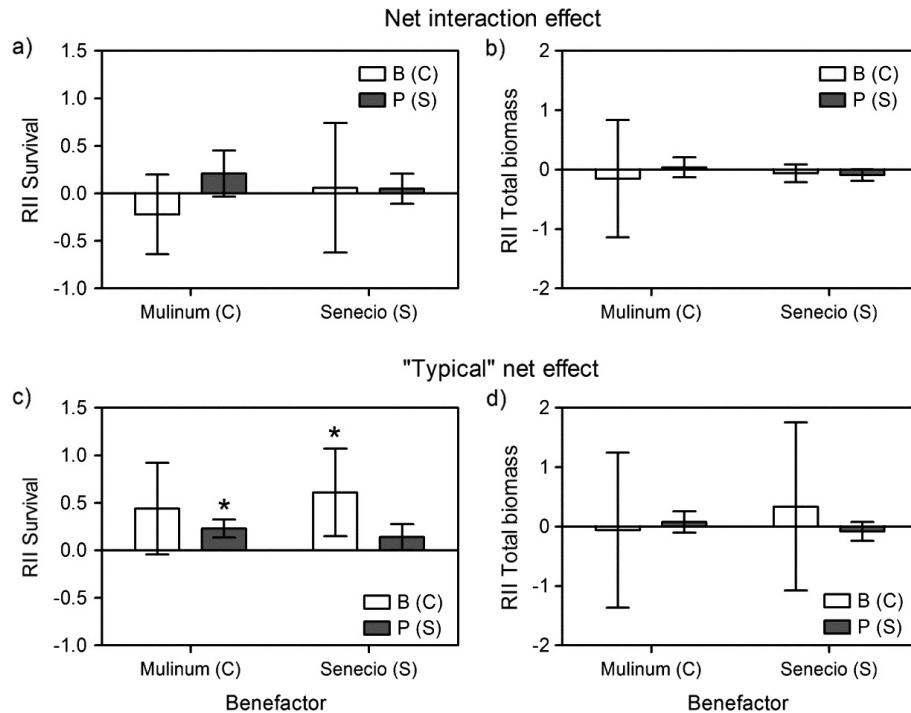


FIG. 4. Net outcomes among shrubs and grass species of the Patagonian steppe. Bars represent the Relative Interaction Index (RII, Armas et al. 2004) of *Mulinum spinosum* and *Senecio filaginoides* benefactor shrubs on beneficiary *Bromus pictus* (B, white bars), and *Poa ligularis* (P, grey bars) species. Both shrubs and grasses fitted into two broad categories of species (C = “competitive” and S = “stress-tolerant”). Values are RII means and 95% confidence intervals. Stars above bars indicate significant deviation from zero value (one-sample *t*-tests) * $P < 0.05$, ** $P < 0.01$ (analysis in Appendix S2: Table S1). Calculations of the effects are explained in full detail in the *Materials and Methods*.

(Fig. 3c; $P = 0.0080$; see Appendix S3: Table S1 for analysis).

Net interaction effects of shrub grass interactions were neutral for all the species pairs (Fig. 4a, b). Net effects obtained as in a typical interaction experiment/study were positive for survival when shrubs and beneficiary grasses differed in their traits (Fig. 4c, d; see Appendix S2: Table S1 for analysis).

The relative distribution of *Poa* and *Bromus* plants in relation to shrub distances was different depending on the shrub species considered. *Poa* and *Bromus* did not differ in their cumulative frequency in relation to *Mulinum* edges (the C shrub species; $K-S$, D : 0.1604, $P = 0.33$; Fig. 5a). On the contrary, *Bromus* and *Poa* curves strongly differed ($K-S$, D : 0.2873, $P = 0.009$) when looking at the frequency of plants related to *Senecio* (the S shrub species) edges. *Bromus* were found to be more closely associated with *Senecio* than *Poa* (Fig. 5b).

DISCUSSION

It has been postulated that the existing controversies regarding the response of plant–plant interactions along stress gradients can be reconciled by integrating species strategy (C or S sensu Grime 1977) with the nature of the stress factor (resource and non-resource stress factor;

Liancourt et al. 2005, Maestre et al. 2009, Soliveres et al. 2014). This is the first time that the predicted pair-wise relationships were explored through a manipulative field experiment at the dry end of an aridity gradient. It is precisely in this kind of ecosystems where most of the debate about the relative impact of positive and negative interactions has centered. Our results provide partial support for the predictions; the growth data coincide to a large degree, while our results for survival do not (Fig. 3). Growth responses likely take place over such shorter time-scales than survival responses and may be affected by a different range of resource levels (Maestre et al. 2009). Additionally, survival is often insensitive to the effect of neighbors on target plants (Maestre et al. 2005). Therefore, there is little reason to expect similar patterns of response in these two performance measures to interactions. However, a significant net effect of shrubs on grass survival when species differed in their strategy highlights the importance of the conditions for the occurrence of facilitation in this arid ecosystem, and the potential link with the spatial patterns observed (Figs. 4, 5). Our manipulative and descriptive study supported previous results that showed that stress-tolerant shrubs are often the main benefactors of competitive species at high stress (Liancourt et al. 2005, He et al. 2012, 2013, Rolhauser and Pucheta 2016), potentially, enlarging their realized niche (Bruno et al. 2003).

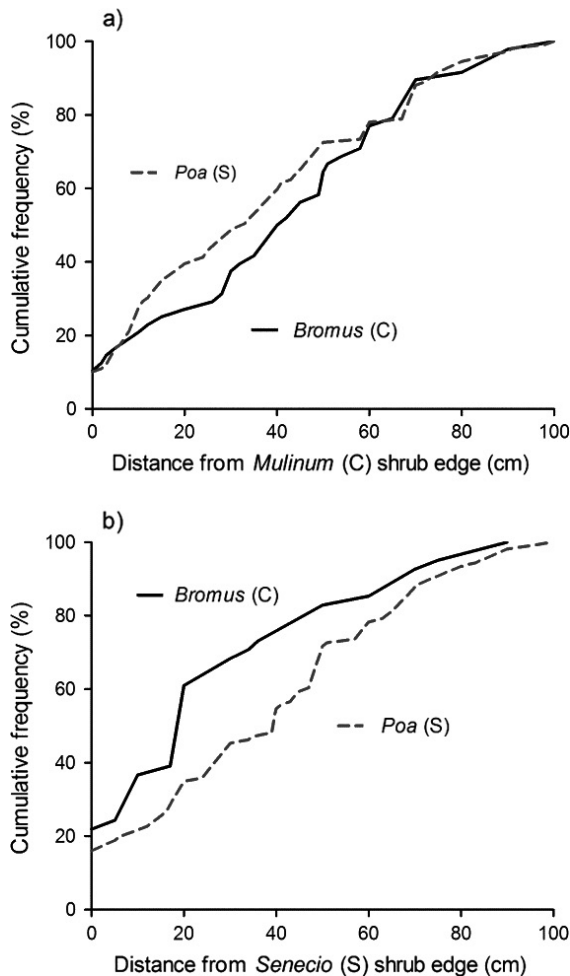


FIG. 5. Cumulative frequency distribution of *Bromus pictus* (competitive, C) and *Poa ligularis* (stress-tolerant, S) grass species from the edge of (a) *Mulinum spinosum* (competitive, C) and (b) *Senecio filaginoides* (stress-tolerant, S) benefactor species.

When abiotic stress was driven by non-resource factors (e.g., wind, temperature, high irradiance), architecture-mediated amelioration of harsh environmental conditions by benefactors on beneficiaries was expected to be higher than competition, particularly if species differ in their life-history strategies (Maestre et al. 2009). We found strong positive effects on the growth and survival of beneficiaries when benefactors differed from beneficiaries in their strategy (i.e., C–S or S–C; Fig. 3a, b). The fact that both growth and survival were positively affected is an indicator of the importance of facilitation. Survival rate integrates plant responses over time and has a clear impact on plant demography and community organization (Maestre et al. 2005). Less intense positive effects were predicted for C–C and S–S pairs (Maestre et al. 2009), but we found no significant effects ($\alpha = 0.05$) despite a positive trend. The lack of a significant positive influence of *Mulinum* (C) on *Bromus* (C) and *Senecio* (S) on *Poa* (S) could also be explained by the variation

among species in ameliorating/tolerating high irradiance rather than water atmospheric demand only. Drought and high irradiance can cause oxidative damage in plant tissue, and that effect could be more pronounced on species with mesophytic traits (like *Bromus*; Fitter and Hay 2002). Therefore, a competitive species (C) is more likely to show higher growth under a canopy which efficiently intercepts light than a stress tolerant (S) species (Michalet 2007, Holmgren et al. 2012). Even though the microclimate below shrub canopies did not differ among species during the period of maximum stress (i.e., summer), *Senecio* intercepted more radiation than *Mulinum* since it is an evergreen species. The dense canopy of *Senecio* could exert a stronger positive effect on *Bromus* than on *Poa*, by decreasing the harmful effect caused by high irradiance. Strong positive effects of *Senecio* shrubs on *Bromus* were also supported by the observational approach, where naturally established *Bromus* plants tended to grow more closely to shrub edges than *Poa*. On the contrary, the lack of a positive influence of a canopy is more likely to occur in species that are relatively tolerant to high light and dry conditions (Holmgren et al. 2012). *Poa*, the more xerophytic species, has been shown to increase chlorophyll content and photoprotective carotenoids concentration under drought (Cenzano et al. 2013). Therefore, *Poa* could be more protected than *Bromus* against high irradiance stress and could even be photoinhibited in shade. Similar results were recorded for Mediterranean shrub seedlings, which showed increased photoinhibition beneath adult shrub canopies, due to lower photosynthetic efficiency with the onset of drought (Valladares 2004, Valladares et al. 2008).

We found strong negative effects of shrubs on grass growth as predicted (Fig. 3d), since the main resource-based stress factor coincided for both the benefactor and the beneficiary species (Maestre and Cortina 2004, Michalet 2007). Competition for soil water is the main limiting factor for plant growth of both life forms in the steppe (Sala et al. 1989), whereas grasses and shrubs seem to reduce competition for nitrogen by having different nutrient use strategies. Grasses preferentially absorb ammonium, whereas shrubs absorb nitrate (Gherardi et al. 2013). The negative effect of *Senecio* on both grass species was expected to be intense as predicted from its traits (it is a stress tolerant shrub species) and also because it has most of its roots in the same soil layer as grasses (0–0.25 m; Fernández and Paruelo 1988). We also found strong negative belowground effects of *Mulinum* on *Bromus* as expected, because they share similar traits (both are competitive species). The competitive grass was more affected by the shortage of the limiting resource than the stress tolerant grass (Michalet 2007, Maestre et al. 2009). This was evident in the magnitude of the RII effect on both survival and growth performance measurements.

Despite the predicted positive effect on the $C_{\text{shrub}}-S_{\text{grass}}$ interaction proposed by Maestre et al. (2009) when stress

was resource-based, we did not detect facilitation in our stress tolerant beneficiaries (Fig. 3d). The prediction was based on the idea that shrubs improve soil conditions and increase water availability (Holmgren et al. 1997). Therefore, under high stress conditions, the competitive shrubs could die and tolerant beneficiaries will be favored by the benefactor's legacy on soil conditions (Facelli and Brock 2000, Maestre et al. 2009). Although nutrients are higher below shrubs, understories are drier than open areas (see Appendix S1: Table S1; Aguiar and Sala 1994). Canopy interception of these desert shrubs reduces the amount of water reaching the soil (Sala et al. 1989) and no hydraulic lift driven by Patagonian shrubs has been described (Bucci et al. 2009). Therefore, it is unlikely that positive effects will emerge from the interaction of shrubs and grasses when stress is water-based.

It has been claimed that the environmental conditions representing "high or extreme stress" have rarely been analyzed. Therefore, when evaluating responses to stress, the latter should be quantitatively defined (Lortie 2010). It has been suggested that low, medium, and high stresses occur when 20%, 30–50%, and 50–80% of target species performance, when growing alone, is limited within a specific time span (e.g., a growing season or life stage; Lortie 2010, He and Bertness 2014). The severity of the abiotic stress experienced was high, and medium for the C and S species, respectively. Out of all the individuals planted far from shrubs and other grasses, only 44% (21 of 48 plants) of *Bromus* (C_{grass}) survived. Whereas, out of those planted close to shrubs, 46% survived when growing without the barrier to root competition, and almost all (84%) survived when competition was reduced. Therefore, non-resource stress limited the performance of *Bromus* by 56% and resource stress limited it by 54%. For *Poa*, the more stress tolerant species (S_{grass}), non-resource stress limited the survival of plants growing far from shrubs by 31% (66 out of 96 plants survived) and resource stress by 12% (42 out of 48 plants survived when growing close but without the barrier against root competition). It is interesting to note that the site where we performed the experiment could be considered as the driest end of a precipitation gradient where the selected beneficiary and benefactor species could coexist (Bertiller et al. 1995). However, the years in which the experiment was conducted (2010 to 2012) were 12% wetter than the mean annual precipitation (i.e., 2010 = 152.2 mm and 2011 = 149 mm), with an extraordinarily wet summer (61% more precipitation than the average, <http://anterior.inta.gov.ar/region/pas/sipas2/cmp/agromet/index.html>). That means that from the point of view of the beneficiary plants, "wet" years are still highly stressful, and we can expect an intensification of positive interactions via stress amelioration as well as negative effects due to resource competition in average years with intense summer droughts. Thus, positive as well as negative interaction outcomes can be detected within the same set of species depending on the intensity and length of the drought events.

The experimental approach taken here allowed us to compare the influence of the factors (resource vs. non-resource) involved in the interaction, which are those that control plant growth and survival. In arid systems, amelioration of radiation, temperature, evaporation and wind desiccation could be counterbalanced by an increase in water stress due to competition for belowground resources (Aguiar et al. 1992, Holmgren et al. 1997, Maestre et al. 2003). In fact, we detected neutral effects when the net interaction outcome was calculated. Surprisingly, net effects calculated as in typical experiments, where the performances of target species beneath nurses and in adjacent open areas were compared, determined positive effects on survival. In arid and semiarid systems, below-ground distribution of biomass does not mirror the highly clumped above-ground pattern, and lateral roots may largely extend beyond the crowns of individuals into the "open" areas (Schenk and Jackson 2002). That is why root competition, although less intense, could still act far from shrubs and for other grass species (Casper and Jackson 1997).

Spatial patterns at any given time integrate dynamic processes playing out over long periods. The study of local spatial patterns is a complementary approach to analyze the role of plant interactions (e.g., competition, facilitation) in structuring communities (Kikvidze et al. 2005). Under the assumption that the spatial association between species at a neighborhood scale correlate with the direction and strength of plant interactions, researchers often interpret aggregated patterns as evidence of facilitation and segregated patterns as evidence of interference (Kikvidze et al. 2005). We found a higher frequency of *Bromus* than *Poa* adult plants close to *Senecio* shrubs ($S_{\text{shrub}}-C_{\text{grass}}$; Fig. 5b). These results are in line with our manipulative experiment and other studies and meta-analyses (Liancourt et al. 2005, He et al. 2012, 2013, Rolhauser and Pucheta 2016). They could indicate a greater relative importance of positive S shrub effects than that of negative ones on the distribution and persistence of less drought tolerant grasses in harsh environments. Although we did not detect a higher frequency of S grasses (*Poa*) close to C shrubs (*Mulinum*) as expected (Fig. 5a), previous spatial analysis of shrub-grass interactions in the Patagonian steppe (Wiegand et al. 2006; M. R. Aguiar, P.A. Cipriotti and T. Wiegand, *unpublished data*) provide additional support for the prediction of a positive association of $C_{\text{shrub}}-S_{\text{grass}}$. *Pappostipa humilis*, considered a highly stress tolerant grass species (Soriano et al. 1994), showed strong positive association with *Mulinum* and *Adesmia volkmanii* up to spatial scales of 1 m (Wiegand et al. 2006; M. R. Aguiar, P.A. Cipriotti and T. Wiegand, *unpublished data*). These two shrubs, out of the three Patagonian dominants shrub species, are considered to be very similar in their response to water availability and with a contrasting behavior with respect to the S shrub *Senecio filaginoides*. In other words, *Mulinum* and *Adesmia* avoid drought by having deeper roots and showing the highest effective soil water

potential and WUE values (Golluscio and Oesterheld 2007). Moreover, the perennial grass *Pappostipa humilis* was negatively associated with *Senecio* ($S_{\text{shrub}} - S_{\text{grass}}$; Soriano et al. 1994, Wiegand et al. 2006; M. R. Aguiar et al., unpublished data). Previous studies also showed that a complete grass ring were clearly detected around *Mulinum* shrubs, whereas around *Senecio*, grasses showed only a weak tendency for aggregation (Soriano et al. 1994). The three stress tolerant grasses (*Poa ligularis*, *Pappostipa speciosa* and *Pappostipa humilis*) were more frequently associated to *Mulinum* than to *Senecio* rings (Soriano et al. 1994). Most dominant grasses in the steppe (tolerant species) tended to aggregate with the competitive shrubs, whereas the persistence and growth of the most competitive grass seemed to be enhanced below stress tolerant shrubs. In line with the general predictions, these patterns suggest that shrubs facilitate grasses in their immediate neighborhood, and that effect seemed to be stronger when species differed in their strategies. However, these predictions remain to be tested with the other components of the community.

Our results reinforce the idea that competition as well as facilitation act simultaneously in this arid ecosystem, and the strength of this balance on the growth of grass species could be reasonably predicted by considering the strategies of the shrubs and grasses involved in the interaction. Additionally, our descriptive study supported the idea that stress-tolerant species could be the main benefactors of competitive species at high stress (Liancourt et al. 2005, He et al. 2012), potentially, enlarging their realized niche (Bruno et al. 2003). This study is limited to the response of four species, and generalizations to other systems should accordingly be interpreted with caution. The applicability and generality of Maestre et al. (2009) predictions remain to be tested by more field experiments and spatial analysis. However, it seems that some ecological factors, such as the nature of the abiotic stress and species traits can yield valuable information to understand the processes shaping communities in severe environments. Ecologists are still in the process of generating the primary data to test the underlying model. We are confident that further generality will come in the form of future similar experiments in comparable systems, and eventually broad-scale meta-analyses.

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LITERATURE CITED

- Adler, P. B., D. G. Milchunas, W. K. Lauenroth, O. E. Sala, and I. C. Burke. 2004. Functional traits of graminoids in semi-arid steppes: a test of grazing histories. *Journal of Applied Ecology* 41:653–663.
- Aguiar, M. R., and O. E. Sala. 1994. Competition, facilitation, seed distribution and the origin of patches in a Patagonian steppe. *Oikos* 70:26–34.
- Aguiar, M. R., A. Soriano, and O. E. Sala. 1992. Competition and facilitation in the recruitment of grass seedlings in Patagonia. *Functional Ecology* 6:66–70.
- Armas, C., and F. I. Pugnaire. 2005. Plant interactions govern population dynamics in a semi-arid plant community. *Journal of Ecology* 93:978–989.
- Armas, C., R. Ordiales, and F. I. Pugnaire. 2004. Measuring plant interactions: a new comparative index. *Ecology* 85:2682–2686.
- Austin, A. T., L. Yahdjian, J. M. Stark, J. Belnap, A. Porporato, U. Norton, D. A. Ravetta, and S. M. Schaeffer. 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* 141:221–235.
- Beltrán, A. 1997. Caracterización microclimática del distrito occidental de la estepa Patagónica. University of Buenos Aires, Buenos Aires, Argentina.
- Bertiller, M. B., N. O. Elissalde, C. M. Rostagno, and G. E. Defossé. 1995. Environmental patterns and plant distribution along precipitation gradient in western Patagonia. *Journal of Arid Environments* 29:85–97.
- Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. *Trends in Ecology & Evolution* 9:191–193.
- Bonvissuto, G., E. Moricz de Tecso, O. Astibia, and J. Anchoarena. 1983. Resultados preliminares sobre los hábitos dietarios de ovinos en un pastizal semidesértico de Patagonia. *Informativo de Investigaciones Agrícolas (IDIA)* 36: 243–253.
- Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18:119–125.
- Bucci, S. J., F. G. Scholz, G. Goldstein, F. C. Meinzer, and M. E. Arce. 2009. Soil water availability and rooting depth as determinants of hydraulic architecture of Patagonian woody species. *Oecologia* 160:631–641.
- Casper, B. B., and R. B. Jackson. 1997. Plant competition underground. *Annual Review of Ecology and Systematics* 28: 545–570.
- Cavagnaro, F. P., R. A. Golluscio, D. F. Wassner, and D. A. Ravetta. 2003. Caracterización química de arbustos patagónicos con diferente preferencia por parte de los herbívoros. *Ecologia Austral* 13:215–222.
- Cenzano, A. M., M. C. Varela, M. B. Bertiller, and M. V. Luna. 2013. Effect of drought on morphological and functional traits of *Poa ligularis* and *Pappostipa speciosa*, native perennial grasses with wide distribution in Patagonian rangelands, Argentina. *Australian Journal of Botany* 61:383–393.
- Cipriotti, P. A., and M. R. Aguiar. 2010. Resource partitioning and interactions enable coexistence in a grass-shrub steppe. *Journal of Arid Environments* 74:1111–1120.
- Corcket, E., P. Liancourt, R. Callaway, and R. Michalet. 2003. The relative importance of competition for two dominant grass species as affected by environmental manipulations in the field. *Écoscience* 10:186–194.
- Couso, L. L., and R. J. Fernández. 2012. Phenotypic plasticity as an index of drought tolerance in three Patagonian steppe grasses. *Annals of Botany* 110:849–857.

- Facelli, J. M., and D. J. Brock. 2000. Patch dynamics in arid lands: localized effects of *Acacia papyrocarpa* on soils and vegetation of open woodlands of south Australia. *Ecography* 23:479–491.
- Fernández, R. J., and J. M. Paruelo. 1988. Root systems of two Patagonian shrubs: a quantitative description using a geometrical method. *Journal of Range Management* 41:220–223.
- Fernandez, R. J., O. E. Sala, and R. A. Golluscio. 1991. Woody and herbaceous aboveground production of a Patagonian steppe. *Journal of Range Management* 44:434–437.
- Fernández, R. J., A. H. Nuñez, and A. Soriano. 1992. Contrasting demography of two Patagonian shrubs under different conditions of sheep grazing and resource supply. *Oecologia* 91:39–46.
- Fitter, A., and R. Hay. 2002. *Environmental physiology of plants*. Third edition. Academic Press, London, UK.
- Flombaum, P., and O. E. Sala. 2012. Effects of plant species traits on ecosystem processes: experiments in the Patagonian steppe. *Ecology* 93:227–234.
- Gherardi, L. A., O. E. Sala, and L. Yahdjian. 2013. Preference for different inorganic nitrogen forms among plant functional types and species of the Patagonian steppe. *Oecologia* 173:1075–1081.
- Golluscio, R. A., and M. Oesterheld. 2007. Water use efficiency of twenty-five co-existing Patagonian species growing under different soil water availability. *Oecologia* 154:207–217.
- Golluscio, R. A., M. Oesterheld, and M. R. Aguiar. 2005. Relationship between phenology and life form: a test with 25 Patagonian species. *Ecography* 28:273–282.
- González Polo, M. 2010. Efectos de la heterogeneidad espacial sobre las comunidades microbianas del suelo de ecosistemas naturales de Patagonia. University of Buenos Aires, Buenos Aires, Argentina, 153 pp.
- Graff, P., M. R. Aguiar, and E. J. E. J. Chaneton. 2007. Shifts in positive and negative plant interactions along a grazing intensity gradient. *Ecology* 88:188–199.
- Graff, P., F. Rositano, and M. R. Aguiar. 2013. Changes in sex ratios of a dioecious grass with grazing intensity: the interplay between gender traits, neighbour interactions and spatial patterns. *Journal of Ecology* 101:1146–1157.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169–1194.
- He, Q., and M. D. Bertness. 2014. Extreme stresses, niches, and positive species interactions along stress gradients. *Ecology* 95:1437–1443.
- He, Q., B. Cui, M. D. Bertness, and Y. An. 2012. Testing the importance of plant strategies on facilitation using congeners in a coastal community. *Ecology* 93:2023–2029.
- He, Q., M. D. Bertness, and A. H. Altieri. 2013. Global shifts towards positive species interactions with increasing environmental stress. *Ecology Letters* 16:695–706.
- Holmgren, M., M. Scheffer, and M. A. Huston. 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78:1966–1975.
- Holmgren, M., L. Gómez-Aparicio, J. L. Quero, and F. Valladares. 2012. Non-linear effects of drought under shade: reconciling physiological and ecological models in plant communities. *Oecologia* 169:293–305.
- Kadmon, R. 1995. Plant competition along soil moisture gradients: a field experiment with the desert annual *Stipa capensis*. *Journal of Ecology* 83:253–262.
- Kikvidze, Z., F. I. Pugnaire, R. W. Brooker, P. Choler, C. J. Lortie, R. Michalet, and R. M. Callaway. 2005. Linking patterns and processes in alpine plant communities: a global study. *Ecology* 86:1395–1400.
- León, R. J. C., D. Bran, M. B. Collantes, J. M. Paruelo, and A. Soriano. 1998. Grandes unidades de vegetación de la Patagonia extra andina. *Ecología Austral* 8:126–141.
- Leva, P. E., M. R. Aguiar, and M. Oesterheld. 2009. Underground ecology in a Patagonian steppe: root traits permit identification of graminoid species and classification into functional types. *Journal of Arid Environments* 73:428–434.
- Leva, P. E., M. R. Aguiar, and A. C. Premoli. 2013. Latitudinal variation of geneecological traits in native grasses of Patagonian rangelands. *Australian Journal of Botany* 61:475.
- Liancourt, P., R. M. Callaway, and R. Michalet. 2005. Stress tolerance and competitive response ability determine the outcome of biotic interactions. *Ecology* 86:1611–1618.
- Lortie, C. J. 2010. Synthetic analysis of the stress-gradient hypothesis. Pages 125–147 in F. I. Pugnaire, editor. *Positive plant interactions and community dynamics*. CRC, Boca Raton, Florida, USA.
- Lortie, C. J., and R. M. Callaway. 2006. Re-analysis of meta-analysis: support for the stress-gradient hypothesis. *Journal of Ecology* 94:7–16.
- Maestre, F. T., and J. Cortina. 2004. Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. *Proceedings of the Royal Society B: Biological Sciences* 271:S331–S333.
- Maestre, F. T., S. Bautista, and J. Cortina. 2003. Positive, negative, and net effects in grass-shrub interactions in mediterranean semiarid grasslands. *Ecology* 84:3186–3197.
- Maestre, F. T., F. Valladares, and J. F. Reynolds. 2005. Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology* 93:748–757.
- Maestre, F. T., R. M. Callaway, F. Valladares, and C. J. Lortie. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology* 97:199–205.
- Michalet, R. 2006. Is facilitation in arid environments the result of direct or complex interactions? *New Phytologist* 169:3–6.
- Michalet, R. 2007. Highlighting the multiple drivers of change in interactions along stress gradients. *New Phytologist* 173:3–6.
- Michalet, R., R. W. Brooker, L. A. Cavieres, Z. Kikvidze, C. J. Lortie, F. I. Pugnaire, A. Valiente-Banuet, and R. M. Callaway. 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters* 9:767–773.
- Oñatibia, G. R., M. R. Aguiar, P. A. Cipriotti, and F. Troiano. 2010. Biomasa individual y poblacional de arbustos dominantes en estepas patagónicas pastoreadas. *Ecología Austral* 20:269–279.
- Paruelo, J. M., M. R. Aguiar, and R. A. Golluscio. 1988. Soil water availability in the Patagonian Arid Steppe: gravel content effect. *Arid Soil Research and Rehabilitation* 2:67–74.
- Perelman, S. B., R. J. C. Leon, and J. P. Bussacca. 1997. Floristic changes related to grazing intensity in a Patagonian shrub steppe. *Ecography* 20:400–406.
- Rolhauser, A. G., and E. Pucheta. 2016. Annual plant functional traits explain shrub facilitation in a desert community. *Journal of Vegetation Science* 27:60–68.
- Sala, O. E., R. A. Golluscio, W. K. Lauenroth, and A. Soriano. 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia* 81:501–505.
- Schenk, H. J., and R. B. Jackson. 2002. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology* 90:480–494.
- Soliveres, S., C. Smit, and F. T. Maestre. 2014. Moving forward on facilitation research: response to changing environments

- and effects on the diversity, functioning and evolution of plant communities. *Biological Reviews* 90:297–313.
- Soriano, A. 1956. Los distritos florísticos de la provincia Patagónica. *Revista de Investigaciones Agropecuarias* 3: 323–347.
- Soriano, A., and O. E. Sala. 1986. Emergence and survival of *Bromus setifolius* seedlings in different microsites of a Patagonian arid steppe. *Israel Journal of Botany* 35: 91–100.
- Soriano, A., O. E. Sala, and S. B. Perelman. 1994. Patch structure and dynamics in a Patagonian arid steppe. *Vegetatio* 111:127–135.
- Tielbörger, K., and R. Kadmon. 2000. Indirect effects in a desert plant community: is competition among annuals more intense under shrub canopies? *Plant Ecology* 150:53–63.
- Valladares, F. 2004. Photoinhibition and drought in Mediterranean woody saplings: scaling effects and interactions in sun and shade phenotypes. *Journal of Experimental Botany* 56:483–494.
- Valladares, F., J. Zaragoza-Castells, D. Sánchez-Gómez, S. Matesanz, B. Alonso, A. Portsmouth, A. Delgado, and O. K. Atkin. 2008. Is shade beneficial for mediterranean shrubs experiencing periods of extreme drought and late-winter frosts? *Annals of Botany* 102:923–933.
- Weedon, J. T., and J. M. Facelli. 2008. Desert shrubs have negative or neutral effects on annuals at two levels of water availability in arid lands of South Australia. *Journal of Ecology* 96:1230–1237.
- Wiegand, T., W. D. Kissling, P. A. Cipriotti, and M. R. Aguiar. 2006. Extending point pattern analysis for objects of finite size and irregular shape. *Journal of Ecology* 94:825–837.
- Yahdjian, L., and O. E. Sala. 2010. Size of precipitation pulses controls nitrogen transformation and losses in an arid patagonian ecosystem. *Ecosystems* 13:575–585.

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