



Annual plant functional traits explain shrub facilitation in a desert community

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Keywords

Abiotic stress; Arid environment; Competition; Dryland; Facilitation; Monte Desert; Nurse plant; Plant strategies; Plant–plant interaction; Specific root volume; Stress-gradient hypothesis

Nomenclature

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Abstract

Question: For a desert where winter is the driest, harshest season we asked: does the effect of dominant shrubs (*Bulnesia retama*) on annual species depend on (1) the functional traits of the latter, (2) the season of the year, or (3) the activity of livestock?

Location: A low-density goat farm in central-northern Monte Desert, Argentina.

Methods: We estimated the effect of shrubs using a log response ratio based on annual species population sizes underneath shrub canopies and in open spaces. We collected density data of annual species in 18 visits between Aug 2010 and Apr 2013 in permanent 50-cm square areas laid out according to a split-plot design, in which the activity of livestock (fenced and unfenced; plots were 10-m squares) was the main factor, and microsite type (shrub and open) was the subordinate factor, with 20 replicates for each combination. We also gathered data on eight functional traits (characterizing whole plants, leaves, roots and seeds) from annual plants collected in the study site following standardized protocols.

Results: Annual species with acquisitive attributes (high specific leaf area, intermediate-to-low leaf dry matter content, large leaves and high specific root volume) were more benefited by shrubs compared to species with the opposite, relatively conservative attributes. Facilitative influences of shrubs were pervasive during winter, while competitive influences increased in frequency during summer, when total plant density was higher. This pattern was not affected by livestock.

Conclusions: The outcome of species interactions depended on the interplay between plant strategies and abiotic stress: facilitated species were mostly acquisitive, and shrub facilitation was more important during the harshest season (winter). Specific root volume, along with widely used functional traits (specific leaf area, leaf dry matter content, leaf size) delineated such strategies. This underlines the importance of considering below-ground traits when studying plant–plant interactions. Single traits achieved superior explanatory power of shrub effects than composite ones (i.e. principal component axes based on single traits), reinforcing the idea that single functional traits are themselves meaningful indicators of complex physiological trade-offs that ultimately affect community structure and dynamics.

Introduction

Trait-based approaches constitute valuable tools in ecology since they contribute to explain and predict the organization of ecological communities (Lavorel & Garnier 2002; McGill et al. 2006; Laughlin & Laughlin 2013). These approaches are specifically based on ‘functional traits’,

which are morpho-physio-phenological traits that affect individual fitness components: growth, reproduction and survival (Violle et al. 2007). Historically, trait-based approaches have been largely devoted to understand community structure in terms of composition and abundance of species along environmental gradients (Keddy 1992; Lavorel & Garnier 2002; McGill et al. 2006; Cingolani

et al. 2007; Laughlin & Laughlin 2013). However, whether functional traits determine the abundance of species within a given community remains an unresolved question (Cornwell & Ackerly 2010; see also Bernard-Verdier et al. 2012; Laliberté et al. 2012), and particularly how nurse plants in deserts mediate trait–abundance relationships is not an exception (Soliveres et al. 2015).

Deserts are characterized by water and/or thermal stress, and vegetation usually consists of patches immersed in a matrix of bare soil (Aguilar & Sala 1999). Mechanisms behind this spatial association between plants involve positive effects of previously established plants (usually called nurse plants) on seed dispersal and/or plant establishment of beneficiary species (Aguilar & Sala 1999; Flores & Jurado 2003; Brooker et al. 2008). Seed arrival facilitation in deserts is usually mediated by water and wind, whereas mechanisms of plant–plant facilitation include increased soil resources, decreased thermal stress and protection against herbivores (Aguilar & Sala 1999; Flores & Jurado 2003; Brooker et al. 2008). Further, the stress-gradient hypothesis poses that positive plant–plant interactions become less frequent when factors that limit plant growth (abiotic stress, disturbances, consumers) are lessened or removed, and competition can thus prevail (Bertness & Callaway 1994).

The relative importance of facilitation may also depend on plant functional traits (see recent reviews of Maestre et al. 2009; He et al. 2013). In particular, it has been shown that conservative (stress-tolerant) species are often facilitators, while acquisitive (stress-intolerant) species are more likely to be the beneficiary (e.g. Liancourt et al. 2005). In addition, acquisitive species invest fewer resources in physical or chemical defences against herbivores and are therefore more consumed (for a recent review, see Carmona et al. 2011). Moreover, large herbivores can severely damage plants without necessarily consuming them, mostly through trampling and other activities (e.g. Rolhauser et al. 2011), and sclerophyllous leaves of conservative species are usually more resistant to such non-trophic physical hazards (see e.g. Pérez-Harguindeguy et al. 2013). Non-trophic effects of large herbivores may also be positive; for instance, trampling can enhance seed burial and promote seedling emergence of desert herbaceous plants (Rotundo & Aguilar 2004).

Here we explore patterns of facilitation and competition among plant species in a summer rainfall desert in relation to their functional traits. The study site is an open shrubland dominated by *Bulnesia retama* (Zygophyllaceae), where annual plants grow underneath shrub canopies and, eventually, in the open spaces among them. *B. retama* is a slow growing, aphyllous shrub (up to 3 m high in our study area) regarded as being highly tolerant to water stress (Jobbágy et al. 2011). Water balance, judged on the

basis of rainfall, temperature and solar irradiance data, appears to be more favourable in summer than in winter (Appendix S1). In this system, we addressed three questions: does the effect of *Bulnesia* shrubs on annual species depend on (1) the functional traits of the latter, (2) the season of the year, or (3) the activity of livestock?

We estimated the effect of *Bulnesia* shrubs using a log response ratio (Hedges et al. 1999) based on annual species population sizes underneath shrub canopies and in open spaces. If shrubs benefit acquisitive species and limit conservative ones, the effect of shrubs should be positively related to functional traits that reflect plant growth rate and competitive ability (such as specific leaf area or plant height), whereas it should be negatively related to those reflecting resource-use efficiency (such as foliar dry matter content; see Pérez-Harguindeguy et al. 2013). Further, if water balance determines the strength of facilitation exerted by shrubs, their overall effect should be more positive in winter than in summer. Alternatively, if thermal stress is more important, the effect of shrubs may depend on the sensitivity of winter and summer species to cold and heat stress, respectively. Additionally, if shrubs protect annual plants against livestock, their estimated effect should be more positive in the presence than in the absence of livestock. We also evaluated the interacting effects of shrubs, season of the year and livestock on two community-level properties (total annual plant density and annual species richness), with the expectation that shrubs might enhance both variables particularly in winter. The effect of livestock on total plant density and species richness might depend on the overall response of annual species to both trophic and non-trophic effects.

Methods

Study site

Our study was conducted within the region of Médanos Grandes dune field, San Juan, Argentina (31°43'18" S, 68°08'17" W; 576 m a.s.l.), which is one of the driest areas of the Monte Desert (Rolhauser 2015). The site occupies about 20 ha and is located on private land mostly used for extensive goat farming. The local farmers have a small herd of goats (about 25–30 mothers) and a few horses, which determines a low effective stock density in our study site. Mean temperature is 27.0 °C in Jan and 7.9 °C in Jul, and mean annual precipitation is 92 mm, peaking in summer (data from San Juan Airport, 32 km NW of site, period 1979–2012; see details in Appendix S1). Atmospheric demand, measured in terms of reference evapotranspiration, is highest in Dec and lowest in Jun, although the difference between such demand and local rainfall offer is larger in winter than in summer (Appendix S1). Data collected using digital thermometers (iButton temperature

logger DS1920) indicate that *Bulnesia* shrubs ameliorate air temperature extremes, both in winter and in summer (Appendix S2).

The site is located on a flat area among dunes, with a gentle south–west slope (<1%) from Pie de Palo hills; the soil in this area is mostly sandy. The vegetation is an open shrubland (cover ~15%), where *Bulnesia* shrubs are accompanied by other shrub species such as *Larrea divaricata*, *Capparis atamisquea*, *Lycium ciliatum* and *Atriplex lampa*. The herbaceous vegetation is mostly composed of annual species, although some perennial herbs (mostly *Heliotropium mendocinum*) can also be abundant. Annual species can be roughly classified as cold season, ‘winter’ species (e.g. *Schismus barbatus* and *Chenopodium papulosum*) or as warm season, ‘summer’ species (e.g. *Gomphrena martiana* and *Tribulus terrestris*) according to their vegetative period. We consider here as annual both obligate and facultative species, the latter being those that can perennate in other (wetter) environments, but can only achieve annual life spans in our study site (e.g. *Senecio leucostachys* and *S. pinnatus*). In addition to livestock, there are native herbivores in the study area (*Microcavia australis* and *Dolichotis patagonum*, both rodent species) although we have no information on their abundance or activity.

Plant density

In autumn 2009 we fenced 20 plots of 10 × 10 m to exclude domestic livestock (goats and horses). The plots were scattered across the study area, and minimum distance between them was about 5 m. Fenced plots were constructed with wooden poles and five strands of wire 25 cm apart. Field observations (direct observation of livestock behaviour, damage to plants and trampling signs) indicated that these fences excluded livestock effectively (although they may not have been effective for smaller herbivores). Each fenced plot included an adult of *Bulnesia* and a surrounding area without shrubs was considered as a microsite, hereafter called ‘shrub’ and ‘open’, respectively. Next to each fenced plot, we selected an equivalent 10 × 10 m area containing a shrub and an open microsite, i.e. subjected to trophic and non-trophic effects of livestock. The experimental layout resulted in a split-plot design, in which livestock activity (fenced and unfenced) was the main (or plot) factor, and microsite type (shrub and open) was the subordinate (or subplot) factor, with 20 replicates for each combination of factors. In each selected microsite, we laid out a 50 × 50 cm permanent frame where we counted the number of plants per annual species. Frames within plots were at least 3 m apart, and those corresponding to shrub microsites were placed beneath the southern side of *Bulnesia* shrubs. We visited the frames 18 times between Aug 2010 and Apr 2013, i.e. covering three

complete growing seasons (see Appendix S5). Visits were conducted after rain events to follow emerged cohorts as closely and often as possible.

Functional traits

We followed standardized protocols for both sample collection and processing (Pérez-Harguindeguy et al. 2013). For foliar and root traits, we collected ten healthy individuals per annual species within the study site. All individuals of each species were approximately the same size and were collected on the same day. Collection timing (between Nov 2010 and Mar 2014) and place (in open areas or underneath shrub canopies) depended on the temporal and spatial distribution of species. Individuals were collected with most of their root systems and were processed within 24 h after adequate rehydration. All intact leaves from each individual were weighed fresh and immediately scanned using a flatbed scanner under 300-dpi resolution. All roots with diameters between ~0.01 and 0.1 mm were collected from each individual and scanned; thinner and thicker roots were cut and discarded. After scanning, roots and leaves were oven-dried at 60 °C for at least 72 h and then weighed. We took morphometric measurements of roots and leaves (length, width, perimeter, area) using ImageJ (rsbweb.nih.gov/ij). For each individual, we obtained average values of leaf size (LS, area), leaf dissection (LD, perimeter/ $\sqrt{\text{area}}$), specific leaf area (SLA, area/dry weight), leaf dry matter content (LDMC, fresh weight/dry weight), specific root length (SRL, length/dry weight) and specific root volume (SRV, volume/dry weight). We estimated leaf dissection as the ratio between leaf perimeter and the square root of its area; this index has a lower limit that matches the shape of a circle, i.e. $2\sqrt{\pi} \approx 3.54$ (cf. Kincaid & Schneider 1983).

We estimated seed mass (SM, dry mass) for each annual species from field-collected material. Seeds were harvested from at least three individuals (although at least eight individuals were used for most species) between Nov 2010 and Mar 2014; collection timing and place depended on the temporal and spatial distribution of species. Harvested seeds were oven-dried at 60 °C for at least 96 h and then weighed. We also obtained data on the maximum height of plants from field measurements for each annual species. Overall, we compiled information on eight quantitative functional traits (LS, LD, SLA, LDMC, SRL, SRV, SM and plant height) that characterized 16 winter and 17 summer annual species (out of the 19 and 24 species found, respectively, in the density survey). For the analyses below, trait values of collected individuals were averaged to obtain a single value per species; a finer, intraspecific level of variation was not considered. Finally, we collected information on the photosynthetic pathway of all 24 summer species

(which are supposed to vary in this trait; while winter species are all C_3) from published material (Appendix S3).

Data analysis

We analysed three response variables: a log response ratio (calculated for each species), maximum total density and species richness (the latter two calculated for the whole community). Log response ratios are useful measures of interaction strength and have desirable statistical properties, namely response linearization and normality (Hedges et al. 1999). We calculated log response ratios based on species' maximum annual density, which is somewhat independent of within-year population dynamics that may affect alternative measures, such as the average density across months. For each species and visit, we first calculated the average density across frames for each of the combinations of microsite type (shrub and open) and livestock activity level (fenced and unfenced), and then calculated the maximum (average) density among visits within each year on record (for all four factor combinations separately). Further, for each species we calculated the logarithm of the ratio of maximum annual density (plus one) in shrub and open microsities (for livestock activity levels separately). This log response ratio quantifies the spatial association between annual species and *Bulnesia* shrubs, and is interpreted here as an indicator of the strength of shrub facilitation (values >0) or competition (values <0). For simplicity, the log response ratio is hereafter referred to as 'shrub effect'.

Preliminary analyses of our data indicated that relationships between shrub effect and functional traits (the latter used as predictors) were consistent across years (Appendix S4). Therefore, shrub effect in the analyses below was calculated using species maximum annual densities averaged across years. First, shrub effect was compared between livestock activity levels using paired *t*-tests for winter and summer species separately (see classification of species in Table 1). This test assessed whether *Bulnesia*'s effect was affected by livestock. Second, we compared shrub effects between winter and summer species (i.e. two completely different assemblages) within each livestock activity level using *t*-tests for unequal variances. This test assessed whether *Bulnesia*'s effect varied with season. Third, for the subset of species with quantitative functional data, we analysed the relationship between shrub effect (i.e. the response variable) and functional traits (i.e. the predictors) using second-order polynomial (quadratic) regression models for winter and summer species separately. These tests assessed whether functional responses were either rectilinear or curvilinear (with a maximum or a minimum). Functional traits were log-transformed before the

Table 1. Average maximum annual density (per m²) of winter and summer annual species recorded in two microsite types (shrub and open) and in two levels of livestock activity (fenced and unfenced) across 18 visits between 2010 and 2013 in a site within central-northern Monte Desert, Argentina. The values shown result from calculating the average density across samples (50-cm square frames) for each visit, then finding the maximum (average) density among visits within each year, and finally averaging across years.

Species	Fenced		Unfenced	
	Shrub	Open	Shrub	Open
Winter annuals				
<i>Bowlesia incana</i>	14.27	0.07	3.80	–
<i>Chenopodium papulosum</i>	20.20	0.73	21.13	1.93
<i>Cryptantha diffusa</i>	1.07	0.27	1.60	0.20
<i>Descurainia erodiifolia</i>	29.13	0.80	19.00	0.53
<i>Gamochaeta filaginea*</i>	0.07	–	0.20	–
<i>Pseudognaphalium aff. lacteum*</i>	–	–	0.07	0.13
<i>Lappula redowskii</i>	2.33	0.07	5.87	–
<i>Laennecia sophiifolia</i>	0.20	–	–	0.07
<i>Lecanophora ecristata</i>	0.07	0.13	0.13	–
<i>Lepidium myrianthum</i>	24.33	1.47	20.73	1.53
<i>Nama undulatum</i>	0.73	0.80	1.27	0.73
<u><i>Parietaria debilis</i></u>	0.60	0.07	0.47	–
<i>Phacelia artemisioides</i>	12.20	1.73	12.87	2.13
<i>Plantago patagonica</i>	0.13	–	0.13	0.33
<u><i>Schismus barbatus</i></u>	24.13	1.87	51.33	2.47
<i>Senecio leucostachys*</i>	0.07	0.13	0.07	0.07
<i>Senecio pinnatus*</i>	0.07	–	–	–
<u><i>Sisymbrium irio</i></u>	0.67	0.13	0.60	0.20
<i>Sphaeralcea miniata*</i>	2.60	7.13	4.33	5.33
Summer annuals				
<i>Allionia incarnata*</i>	21.33	13.73	11.07	10.87
<i>Amaranthus persimilis</i>	0.07	–	–	–
<i>Amaranthus standleyanus</i>	89.20	1.93	50.47	5.07
<i>Bouteloua aristidoides</i>	0.67	17.53	4.07	31.93
<i>Bouteloua barbata</i>	–	0.07	0.27	0.13
<u><i>Boerhavia diffusa*</i></u>	37.47	19.60	22.00	23.13
<i>Euphorbia catamarcensis</i>	3.27	0.93	5.60	1.93
<i>Flaveria bidentis</i>	0.93	0.47	3.07	2.27
<i>Gomphrena martiana</i>	22.07	35.87	47.67	26.47
<i>Gomphrena mendocina</i>	0.13	0.13	0.27	–
<i>Ibicella parodii</i>	–	–	0.07	–
<i>Kallstroemia tribuloides</i>	0.60	–	–	0.07
<i>Mirabilis ovata*</i>	0.07	–	–	–
<i>Munroa mendocina</i>	12.07	51.60	12.87	23.13
<i>Oenothera mendocinensis*</i>	–	–	–	0.07
<i>Parthenium hysterophorus</i>	29.27	1.00	47.53	1.40
<i>Portulaca echinosperma</i>	–	0.07	0.07	–
<i>Portulaca grandiflora</i>	0.13	0.13	0.93	–
<u><i>Portulaca oleracea</i></u>	2.33	2.13	3.13	3.67
<i>Sclerophylax amottii</i>	61.07	30.80	60.00	34.13
<i>Solanum euacanthum</i>	0.60	0.13	1.20	0.13
<i>Sphaeralcea sp.*</i>	–	–	0.13	–
<u><i>Tribulus terrestris</i></u>	120.13	290.33	113.53	383.27
<i>Verbesina encelioides</i>	1.00	–	–	–

*Facultative annual; exotic species are underlined.

analyses, which were carried out for each functional trait separately. We also analysed the relationship between shrub effect and two composite traits (the latter used as predictors) calculated for winter and summer species separately. These were the first two axes of principal components analysis based on the eight simple quantitative traits ln-transformed (see Appendix S5). Residuals of such regression models did not depart significantly from normality.

Further, we evaluated the interacting effects of shrubs, season and livestock on two community-level properties: maximum total density and species richness. For each frame, we calculated the cumulated density across all annual species for each visit, and then the maximum (among visits) within two seasons (winter and summer) for each year on record, i.e. the maximum total density. The cold season or 'winter' was defined here to occur between May and Nov, whereas the warm season or 'summer' was between Dec and Apr. Maximum total density (plus one, log-transformed) and species richness (plus one, log-transformed) per frame were compared between microsite types, livestock activity levels and seasons of the year using mixed linear effects models (see e.g. Jiang 2007) implemented with the routine `lme` of the package `nlme` in R (R Foundation for Statistical Computing, Vienna, AT). Microsite type, livestock, and season (and their interactions) were modelled as fixed effect factors. Data structure was specified in the random effects component of the model with the following hierarchy: Year/Plot/Sub-plot/Frame. In these models, variance was allowed to vary among grouping factors using the function `varIdent`. Residuals of the two response variables did not depart significantly from normality.

Results

Overall, we counted 54 439 plants that were classified into 19 winter and 24 summer annual species (Table 1; see also Appendix S5). Shrub effect on annual species density was significantly higher (more positive) in winter than in summer, and was not significantly affected by livestock (Fig. 1). Variation of shrub effect across species was at least partly explained by some functional traits (Fig. 2). For winter species, the effect of shrubs was positively related to specific leaf area (SLA; Fig. 2); the remaining single and composite traits showed no significant effects (results not shown, but see correlation coefficients in Appendix S5). For summer species, the effect of shrubs showed a curvilinear relationship with a maximum with respect to leaf dry matter content, which explained 43% of total variation (Fig. 2). Further, shrub effect on summer species was positively related to leaf size (LS) and specific root volume (SRV), which explained 24% and 25% of total variation,

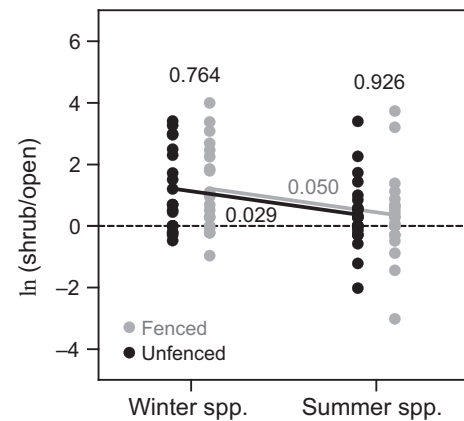


Fig. 1. Effect of *Bulnesia* shrubs on plant density measured as logarithm of the ratio of average maximum annual density (plus one) beneath shrub canopies and in open spaces ($\ln[\text{shrub}/\text{open}]$) for 19 winter and 24 summer annual species in a site within central-northern Monte Desert, Argentina. *P*-values for *t*-test comparisons between levels of livestock activity (fenced and unfenced) and between winter and summer species within each level of livestock activity are shown. Solid lines connecting group averages are shown to facilitate visual comparison.

respectively (Fig. 2). The effect of shrubs on summer species was also significantly related to a composite trait (i.e. the first principal component), which was in turn correlated with LS and SRV (among other traits) and explained 28% of total variation (Fig. 2; see also Appendix S5). Within summer species, the effect of shrubs was not significantly different between C_3 and C_4 species (Appendix S3).

Maximum total density depended significantly on the interaction between microsite type and season, although it was not significantly affected by livestock (see statistical summary in Appendix S5). Maximum total density was significantly higher in shrub than in open microsites only in winter, while there was no significant difference between microsites in summer, when density was higher (Fig. 3a). Similarly, species richness depended significantly on the interaction between microsite type and season, and was not significantly affected by livestock (see statistical summary in Appendix S5). Species richness was significantly higher in shrub than in open microsites only in winter, while there was no significant difference between microsites in summer, when richness was higher (Fig. 3b).

Discussion

Facilitative effects of *Bulnesia* shrubs on annual species were larger in winter (compared to summer), when both total plant density and richness were relatively low. Winter in our study site is characterized by a combination of extremely low rainfall (only 38 mm on average from May to Nov) and low temperatures (e.g. 35 days on average from

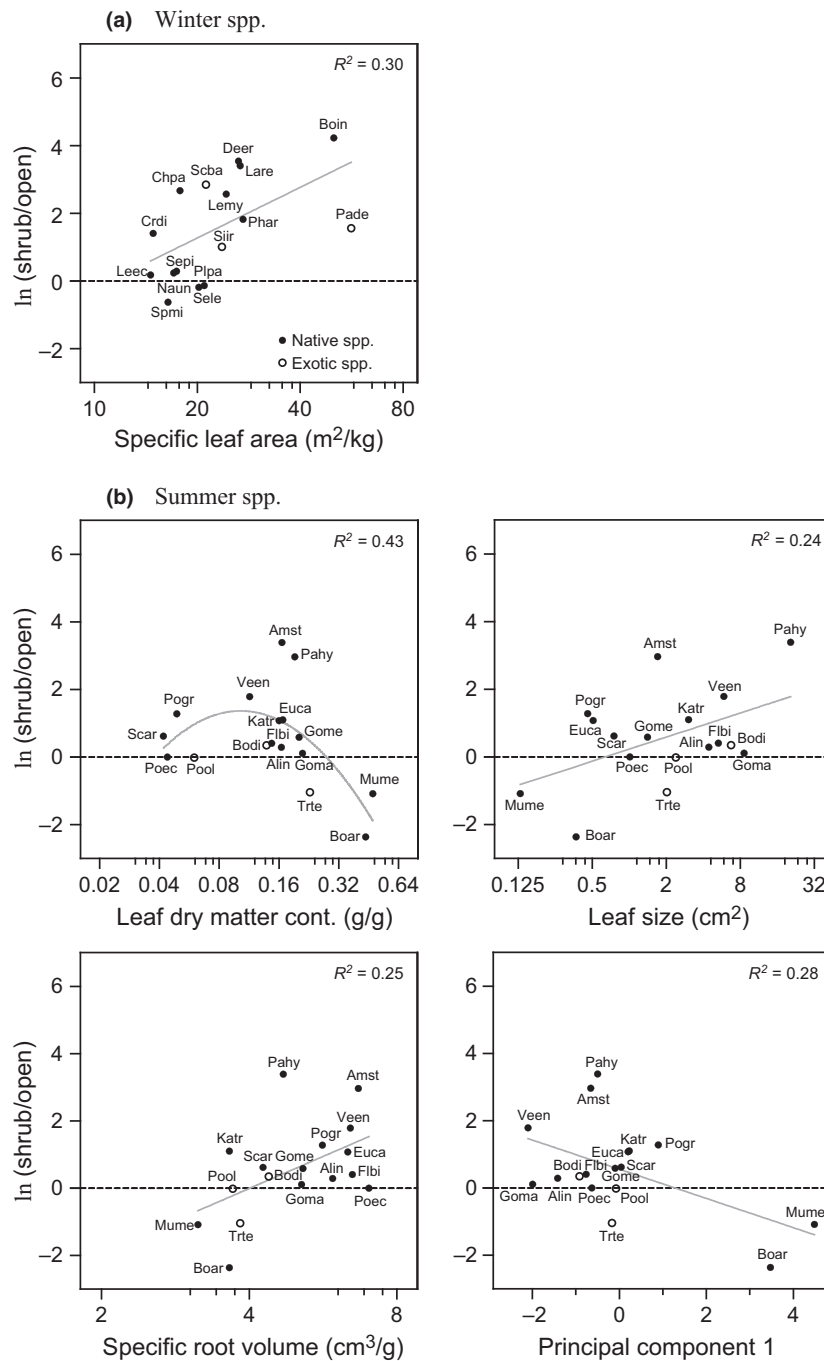


Fig. 2. Significant relationships ($P < 0.05$) between functional traits and the effect of *Bulnesia* shrubs on plant density, measured as $\ln(\text{shrub/open})$, for 16 winter (a) and 17 summer (b) annual species in a site within central-northern Monte Desert, Argentina. R^2 and the line (in grey) predicted by the best-fitting model are shown; quadratic terms were conserved in the models only when they had a significant effect ($P < 0.05$). Species codes are the first two letters of genus and specific epithet (see Table 1).

May to Nov, with minimum temperatures below zero; see climatic data in Appendix S1). The higher importance of positive shrub effects during winter may have resulted from such harsh abiotic conditions. During summer, a more favourable water balance coupled with higher

temperatures may have enabled more plants to establish, intensifying competition. This would be consistent with the original version of the stress-gradient hypothesis, which suggests that the importance of facilitation increases with physical stress (Bertness & Callaway 1994).

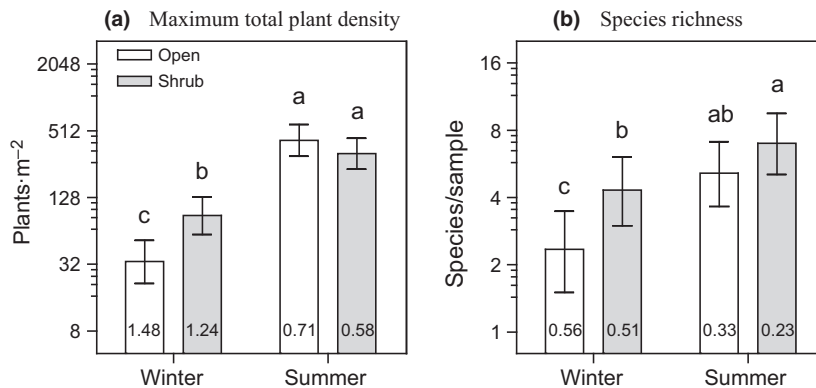


Fig. 3. Maximum total plant density (a) and richness (b) of annual species per sample (50-cm square frame) in two microsite types (shrub and open) and in two seasons (winter and summer) between Aug 2010 and Apr 2013 (18 visits) in a site within central-northern Monte Desert, Argentina. Total density is the sum across 43 annual species, from which maxima among visits were calculated for each season within each year on record. Dispersion bars are 95% confidence intervals and letters above bars indicate significant differences ($P < 0.05$) among the four combinations of factors. Numbers inside bars are SD estimated for each combination. Statistical summaries of these analyses can be found in Appendix S5.

Shrub effects varied among annual species, and some of this variation was explained by their functional traits. In particular, single traits achieved superior explanatory power compared to composite traits. This result agrees with recent studies that show more robust responses when using functional traits separately as explanatory variables than when using composite axes (Spasojevic & Suding 2012; Butterfield & Suding 2013; Herben & Goldberg 2014). At least in part, this may be due to the fact that functional traits are themselves indicators of complex trade-offs in resource allocation and have mechanistic relationships with ecophysiological processes that determine individual performance (McGill et al. 2006; Violle et al. 2007). Consequently, composite traits could mask the effects of single functional traits, especially if the latter are related to opposing ecological processes (Spasojevic & Suding 2012).

In the case of winter species, the effect of shrubs was positively correlated with specific leaf area (SLA). This trait is an inverse indicator of leaf internal density and leaf production costs (i.e. the higher the SLA, the lower the costs), and as such would reflect a trade-off between resource conservation and growth rate (Vile et al. 2005; Poorter et al. 2009). During winter, shrubs appeared to benefit acquisitive species (with high SLA), while exerting a neutral or slightly negative effect on more conservative species (with lower SLA). Such low SLA species may be better adapted to open spaces (more exposed to wind, solar irradiation and colder nocturnal temperatures), whereas high SLA species may have leaves with higher light interception efficiency under shaded conditions (see Poorter et al. 2009).

When considering summer species, the effect of shrubs showed a maximum, curvilinear relationship with respect

to leaf dry matter content (LDMC), while it was positively related to leaf size (LS) and specific root volume (SRV). Leaf dry matter content reflects leaf hardness or 'sclerophylly', as opposed to leaf 'succulence' (e.g. Vendramini et al. 2002), and is inversely proportional to specific leaf area (SLA), leaf thickness and leaf internal density (Vile et al. 2005). The structures that allow water conservation in sclerophyllous leaves (e.g. thick cell walls and thick parenchyma tissues) are expensive and may also limit leaf photosynthetic capacity (Gibson 1996), implying a trade-off between water conservation and growth (cf. Vendramini et al. 2002). Leaf size responds at least partially to a trade-off between light interception efficiency (maximized by large leaves) and gas exchange and heat dissipation efficiencies (maximized by small leaves) Givnish 1987; Falster & Westoby 2003). Further, SRV is an inverse indicator of root tissue density and root production costs (i.e. the higher the SRV, the lower the costs), reflecting a trade-off between growth rate and durability, herbivore resistance and embolism resistance of root tissues (Eisenstat 1997; Wahl & Ryser 2000). The finding of SRV as a useful predictor of plant facilitation stresses the importance of considering below-ground traits when studying plant-plant interactions in particular, and vegetation dynamics in general (see also Kattge et al. 2011). Together, these functional traits (LDMC, LS and SRV) delineate a functional gradient within summer species that opposes two strategies with respect to their sensitivity to the presence of *Bulnesia*.

At one end of the summer species functional gradient, there would be drought- and/or heat-tolerant species, equipped with relatively tough, small leaves and dense root tissues. Examples are the exotic *Tribulus terrestris*, which dominates open spaces among shrubs during

summer, and two summer annual grasses, *Bouteloua aris-tidooides* and *Munroa mendocina*. At the other end, there would be more acquisitive species, with large, intermediately succulent leaves and fleshy roots (i.e. with high SRV), like *Amaranthus standleyanus* and *Verbesina encelioides*. Interestingly, more succulent species (i.e. with high LDMC) were not benefited by *Bulnesia* as much as those with intermediate LDMC. This suggests a third strategy within summer species, characterized by relatively tender but succulent leaves, apparently capable of tolerating to some extent summer stress (i.e. *Sclerophylax arnottii* and *Portulaca* spp.). This third strategy can be seen as a fleshy variant within the acquisitive strategy. Our results further indicate that the overall effect of shrubs on C₃ summer species was not significantly higher compared to C₄ species. Therefore, the main ecological strategies found within summer species were not clearly related to their photosynthetic pathway. Although the C₄ pathway makes more efficient use of CO₂, water and nutrients (Sage 2004), it may not be enough to colonize open spaces in our study site; such an endeavour may need to be accompanied by investment in tougher leaves and roots.

Overall, our results suggest that facilitative effects of *Bulnesia* were larger on putative acquisitive species than on relatively conservative ones, both in winter and in summer. However, different traits were involved to differentiate such responses in winter (SLA) and in summer (LDMC, LS, and SRV). In winter, plant facilitation may be mediated by a trade-off between water and cold stress tolerance vs shade tolerance at leaf tissue level, which may be captured by SLA. In summer, an equivalent trade-off between leaf heat dissipation combined with root water conductance vs light interception efficiency combined with root growth rate may underpin the strength of facilitation.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Climatic data of study site.

Appendix S2. Average hourly temperatures for January and July.

Appendix S3. Photosynthetic pathway of summer species.

Appendix S4. Evaluation of inter-annual variability of functional responses.

Appendix S5. Complementary results.