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Positive effects of shrubs on plant species diversity do not change along a gradient in grazing pressure in an arid shrubland

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Abstract

Facilitative or positive interactions among species are driven mainly by the environmental amelioration or protection from grazing provided by nurse plants. Some studies have suggested that protection from grazing is inconsequential in water-limited environments because of low herbivore densities and their grazing effects. Others, however, argue that herbivores have a major effect on semi-arid plant communities, and that protection from grazing is a significant factor driving positive plant–plant interactions in such environments. We identified a gradient in grazing pressure in a semi-arid shrubland in south-eastern Australia along which we compared soil condition, incident radiation and plant composition beneath two nurse shrub species with open (shrub-free) interspaces. Our aim was to assess the degree of microclimatic amelioration provided by both shrubs, and changes in the interactions (intensity, importance and frequency) between both nurse shrubs and their understorey species, and their effects on species richness at the community level. Both the relative interaction intensity (RII) and interaction importance (I_{imp}) indices of plant–plant interactions were generally positive and independent of grazing pressure. Soil beneath both nurse plants had significantly greater indices of nutrient cycling and infiltration, and contained more C and N than soil in the open. Almost twice as many species occurred under the canopies of both shrubs (44 species) than in the open (23 species), and the composition of species differed significantly among microsites. Fifty-four percent of all perennial plant species occurred exclusively under shrubs. Our results suggest that environmental amelioration is a stronger driver of the facilitatory effect of shrubs on their understorey species than protection from grazing. Our conclusions are based on the fact that the substantial effect of plant–plant interactions on plant species richness was largely independent of grazing pressure. Irrespective of the underlying mechanism for this effect, our study illustrates the ecological role of shrubs as refugia for understorey plants in semi-arid environments and cautions against management practices aimed at reducing shrub populations.

Zusammenfassung

Positive oder fördernde Interaktionen zwischen Arten beruhen hauptsächlich auf einer Verbesserung der Umwelt oder auf dem Schutz vor Beweidung, der durch Ammenpflanzen zur Verfügung gestellt wird. Einige Untersuchungen ließen vermuten, dass der Schutz vor Beweidung in Umwelten mit einer begrenzten Verfügbarkeit von Wasser ohne Konsequenzen bleibt, weil die Herbivorendichten und ihr Beweidungseffekt gering sind. Andere argumentieren jedoch damit, dass die Herbivoren einen ausschlaggebenden Effekt auf semiaride Pflanzengemeinschaften haben und dass der Schutz vor Beweidung ein signifikanter Faktor

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ist, der positive Pflanzen-Pflanzen-Interaktionen in diesen Umwelten vorantreibt. Wir untersuchten einen Gradienten im Beweidungsdruck in einem semiariden Buschland im süd-östlichen Australien und verglichen die Bodenbeschaffenheit, die einfallende Strahlung und die Pflanzenzusammensetzung unter zwei Ammenstraucharten mit offenen (buschfreien) Zwischenräumen. Unser Ziel war es, den Grad der mikroklimatischen Verbesserung, der durch die beiden Straucharten zur Verfügung gestellt wurde, und die Veränderungen in den Interaktionen (Intensität, Bedeutung und Häufigkeit) zwischen den beiden Straucharten und ihren Unterwuchsarten sowie ihre Effekte auf den Artenreichtum auf der Gemeinschaftsebene abzuschätzen. Sowohl die Indizes der relativen Interaktionsintensität (RII) als auch der Bedeutung der Interaktionen (Iimp) waren im Allgemeinen positiv und unabhängig vom Beweidungsdruck. Der Boden unter beiden Ammenpflanzen besaß signifikant höhere Indizes in Bezug auf den Nährstoffkreislauf und die Durchlässigkeit und enthielt mehr C und N als der Boden in offenen Bereichen. Unter dem Dach der beiden Straucharten kamen fast doppelt so viele Arten vor (44 Arten) wie in den offenen Bereichen (23 Arten) und die Zusammensetzung der Arten unterschied sich signifikant zwischen den Mikrostandorten. 54% der perennierenden Arten kamen ausschließlich unter Büschen vor. Unsere Ergebnisse lassen vermuten, dass die Verbesserung der Umwelt ein Faktor ist, der für die fördernden Effekte von Büschen auf ihre Unterwuchspflanzen eine größere Bedeutung hat als der Schutz vor Beweidung. Unsere Schlussfolgerungen basieren auf der Tatsache, dass der substantielle Effekt der Pflanzen-Pflanzen-Interaktionen auf den Pflanzenartenreichtum im Großen und Ganzen vom Beweidungsdruck unabhängig war. Unabhängig von den zugrundeliegenden Mechanismen für diesen Effekt, zeigt unsere Untersuchung anschaulich die ökologische Rolle der Büsche als Refugien für Unterwuchspflanzen in semiariden Umwelten, und sie warnt vor Managementpraktiken, die darauf abzielen die Strauchpopulationen zu verringern.

Introduction

Positive or facilitative interactions among plant species are strongly dependent on environmental conditions and play a major role in structuring communities in most biomes (Callaway 2007; Brooker et al. 2008). Most studies of the relationships between plant–plant interactions and environmental conditions have been inspired by the seminal 'stress–gradient hypothesis' (SGH; Bertness & Callaway 1994), which suggests that the frequency of facilitative species interactions increases monotonically with increases in abiotic or consumer stress. Although facilitative interactions between plants are common under harsh conditions such as water limitation (e.g. Holzapfel, Tielbörger, Parag, Kigel, & Sternberg 2006), their monotonic increase with increasing abiotic stress has recently been questioned (e.g. Maestre, Valladares, & Reynolds 2005). The outcome of plant–plant interactions depends largely on the nature and level of the stressors involved (Maestre, Callaway, Valladares, & Lortie 2009; Smit, Rietkerk, & Wassen 2009), the ecological strategy of the interacting species, the performance measure or the interaction indicator used (Brooker et al. 2005; Maestre et al. 2005) and the interaction among different stressors (Baumeister & Callaway 2006; Soliveres, García-Palacios, et al. 2011). Disentangling the relative importance of these multiple factors as drivers of plant–plant interactions is an important part of understanding how these interactions will behave along environmental gradients or under changing climatic conditions, and how they might influence plant community dynamics (Brooker et al. 2008).

Abiotic constraints and consumer pressure often co-occur in arid and semi-arid ecosystems, and are particularly important in defining the dynamics of vegetation communities (McNaughton 1985; Hendricks, Bond, Midgley, & Novellie 2005). However, the relative importance of these stressors in structuring arid and semi-arid plant communities, and more specifically, their joint effects on plant–plant interactions, remains poorly understood (Gómez-Aparicio, Zamora, Castro, & Hódar 2008). Recent theory predicts a relatively low importance of grazing protection by nurse plants in water-limited environments (Smit et al. 2009). The logic underpinning this prediction is that herbivores in such environments are sparsely distributed, and abiotic constraints such as limited water or nutrients are more important for vegetation and therefore for plant–plant interactions than herbivory (Ellis & Swift 1988). Moreover, plant species adaptations to drought such as hairy and thick leaves, are also related to grazing resistance (Smit et al. 2009). Drought-adapted and therefore herbivory-resistant plant species are expected to be a major component of plant communities under arid and semi-arid conditions (e.g. Grime 1973; McNaughton 1985). Under harsh environmental conditions therefore, we would expect a relatively lower importance of grazing protection for most species at the community level (Smit et al. 2009). Conversely, other studies have demonstrated contrasting results and have shown how herbivores exert substantial pressure on vegetation and soils in water-limited environments (e.g. McNaughton 1985; Lunt, Eldridge, Morgan, & Witt 2007). Accordingly, grazing protection has been shown to be a crucial mechanism underlying plant–plant interactions in arid and semi-arid environments, with shifts from negative to positive interactions under high grazing pressure (Graff, Aguiar, & Chaneton 2007; Soliveres, García-Palacios, et al. 2011). Furthermore, the ability of plants to recover after herbivore damage is directly influenced by the availability of resources (Wise & Abrahamson

2005). Micro-environmental amelioration provided by nurse plants can play, therefore, a crucial role in the recovery of their neighbors after grazing (Acuña-Rodríguez, Cavieres, & Gianoli 2006; Soliveres, García-Palacios, et al. 2011). These contradictory theories and results present in the literature create considerable controversy and make predictions at the community level extremely difficult. More community-level studies are needed to help clarify the relative importance of grazing protection under extreme climatic conditions (Smit et al. 2009).

Understanding the relative importance of grazing protection vs. microclimatic amelioration as drivers of plant–plant interactions under arid and semi-arid conditions is especially relevant in situations where shrubs are a predominant component of the landscape. Shrub encroachment is a global phenomenon affecting the vast majority of semi-arid environments and is thought to result from overgrazing, among other factors (van Auken 2009). Increases in shrub density have been shown to alter soil functioning and plant composition at landscape scales (van Auken 2009, but see Eldridge et al. 2011) and therefore shrub removal is promoted in many areas to enhance ecosystem diversity and pastoral value (Eldridge et al. 2011). However, studies at the patch scale contradict these landscape patterns, as arid and semi-arid shrubs are known to act as nurse plants, improving microclimatic conditions and increasing the diversity, biomass and stability of neighboring species (Holzapfel & Mahall 1999; Maestre & Cortina 2005; Holzapfel et al. 2006; Soliveres, Eldridge, et al. 2011). Moreover, these woody species, which are often unpalatable to livestock might be expected to protect palatable species from herbivory through mechanisms of shared defences or "associational resistance" (Callaway 2007). However, grazing protection provided by these nurse shrubs wanes under extremely high grazing levels (Smit, Vandenberghe, den Ouden, & Muller-Scharer 2007). It is unclear, therefore, whether the observed reductions in diversity of plant species in encroached shrublands result from competition for resources by the shrubs themselves or from the effects of extensive grazing pressure in shrublands (Eldridge et al. 2011). There is a need to reconcile this uncertainty and to separate the effects of grazing from the effects of the shrubs themselves in order to develop ecologically sustainable management strategies for environments subject to shrub encroachment.

The aim of this study was to examine whether the relative importance, intensity and frequency of interactions between shrubs and their understorey neighbors changed, at the community level, along a grazing pressure gradient in a semi-arid shrubland. The generality of our results was assessed by testing the effect of two different shrub species, with contrasting ecological features, on their neighbors along such a gradient. Specifically, we addressed the following questions: (1) Are shrubs important for plant species richness at the community level? (2) Do shrub-neighbor interactions depend on grazing pressure? (3) Does the response of these interactions depend on the indicator used (intensity, importance or frequency)?

(4) Do the two shrub species exert different effects on abiotic conditions and understorey species diversity? (5) Does the effect of both shrubs on their understorey species change along the grazing pressure gradient?

Methods

The study area

The field work was undertaken in an arid area undergoing shrub encroachment, about 150 km south of Broken Hill, NSW, Australia (33°43′S, 143°02′E). The climate is characterized by low and variable rainfall (250 mm; mean annual rainfall), high evapotranspiration ($\sim$1500 mm yr^{-1}), hot dry summers (daily mean temperature: 30 °C, daily maximum: 47.8 °C, daily minimum: >15 °C) and cool winters (daily mean: ≤17 °C, daily maximum: 32.2 °C, daily minimum: ≤6 °C). All of the sites were situated on extensive plains of Quaternary aeolian material. The vegetation community comprised an open woodland with various stages of encroachment from open to dense shrubland. The upperstorey was dominated by the trees *Casuarina pauper*, *Alectryon oleifolius*, *Eucalyptus socialis*, *Eucalyptus dumosa* and *Myoporum platycarpum*. The shrubland was dominated by the shrubs *Eremophila sturtii*, *Senna artemesioides*, *Dodonea viscosa* and *Acacia rigens*, and the understorey comprised a mixture of grasses and herbs.

Plot selection and sampling strategy

The study was conducted along a grazing–induced degradation gradient representing four levels of degradation (Table 1). These levels resulted from major differences in contemporary and historical grazing by feral, domestic and native (reintroduced) herbivores. The gradient ranged from a lightly grazed exclosure, close to pre-European grazing levels (Sanctuary Ungrazed), to extensive pastoral paddocks supporting a high density of sheep, cattle and goats (Pastoral Grazed). A detailed description of the gradient is given in the Appendix A. Each of the four points along the gradient was replicated three times for a total of 12 study plots. Study plots covered an area of about 0.5 km^2 and were at least 5 km apart and therefore statistically independent at the scale at which shrubs are likely to affect their understorey plant species and the surrounding abiotic components of the landscape.

Within each plot we measured biotic and abiotic attributes from within 90 0.25 m^2 quadrats; 30 each from under the canopies of *E. sturtii* and *S. artemesioides* and 30 in the open. The nearest shrub of each species was selected every 10 m along three 100 m long transects. Open quadrats were at least 2 m from the edge of any shrub. This resulted in a total of 1080 quadrats (4 degradation classes × 3 replicate sites × 3 microsites × 30 quadrats). Both *E. sturtii* and *S. artemesioides* have canopy areas greater than 0.25 m^2.

Table 1. Description of the main attributes of the four points along the degradation gradient in the West-Darling area of Eastern Australia. Data for different animal densities have been converted to a common unit (dry sheep equivalents – DSE) using published and unpublished literature (see Appendix A).

Name	Degradation state	Grazing pressure	Stocking rate (DSE)	Herbivore types and densities (km^{-2})	Area (km^2)
Sanctuary Ungrazed	Pre-European	Very low	0.10	Bilbies, bettongs (5.6), kangaroos (<0.1)	37
Sanctuary Grazed	Slightly altered	Low	0.87	Kangaroos (0.2), rabbits (1500)	32
Pastoral Recovering	Recovering	Moderate	1.97	Kangaroos (0.3), rabbits (1500), goats (30)	40
Pastoral Grazed	Degraded	High	3.85	Kangaroos (0.3), rabbits (1500), goats (40), sheep and cattle (100)	75

E. sturtii is a relatively large (to 3 m high), inverted cone-shaped, often multi-stemmed unpalatable shrub, which could physically restrict grazing by herbivores. *S. artemesioides* is smaller (~1.5 m high), globular-shaped, and of low palatability. These morphological differences would be expected to result in different effects on understorey species.

Data collection

We recorded the cover and abundance, by species, of all perennial plants growing within each of the 1080 quadrats. We restricted the study to perennial species, thereby avoiding potential problems arising from isolated germination events on parts of the gradient.

To identify environmental factors associated with the presence of shrub and open microsites, we made detailed measurements of the morphology of the soil surface from within 15 of the 90 quadrats within each plot (five from each patch type). Thirteen soil surface condition attributes were used to (1) explore possible links between soil surface condition and grazing intensity or shrub presence; and (2) validate the existence and extent of the degradation gradient selected and the degree of soil amelioration provided by the shrubs studied, and (3) derive three biogeochemical indices of soil function that describe the extent to which the soil cycles nutrients, conducts water, and resists erosion. The 13 attributes (described in Appendix A: Table 1) were surface roughness, crust resistance, crust brokenness, crust stability, cryptogamic crust cover, cover of erosion, cover of deposited materials, plant foliage cover, plant basal cover, soil texture, litter cover, litter origin and degree of litter incorporation. The infiltration index was derived from the sum of scores for roughness, crust resistance, crust stability, plant basal cover, soil texture and the product of litter cover, origin and incorporation. The stability index was derived from the sum of scores crust resistance, brokenness and stability, cryptogam cover, erosion cover, cover of deposited materials, plant foliage cover, and litter cover. The nutrient index was derived from the sum of scores for surface roughness, cryptogam cover,

plant basal cover and the product of litter cover, origin and incorporation (Appendix A: Table 1).

At the same sites used to assess soil surface condition we sampled the top 10 cm of the surface to assess total C and total N using a high combustion LECO CNS-200 Analyser. Instantaneous photosynthetically active radiation (PAR) measurements were also taken from beneath the canopies of *Eremophila* and *Senna*, and in the open, using a LI-COR LI-250A light meter.

Measurement of plant–plant interactions

We therefore used three complementary indices to assess the (1) importance, (2) intensity and (3) frequency of facilitative interactions. Both species cover and species diversity were used to determine both importance and intensity of plant–plant species interactions. The intensity of plant–plant interactions, i.e. the effect that the nurse plants have on species richness and cover, ignoring the influence of other environmental factors (Brooker et al. 2005), was measured using the Relative Interaction Index (RII; Armas, Ordiales, & Pugnaire 2004). The RII was calculated as $(P_{nurse} - P_{open})/(P_{nurse} + P_{open})$, where P_{nurse} is either mean cover or mean species richness under the canopy of a nurse plant (*Eremophila* or *Senna*) and P_{open} is either mean cover or mean species richness in the open. RII has values range from -1 to 1, is symmetrical around zero and is negative for competitive species interactions and positive for facilitative species interactions (Armas et al. 2004).

The importance of the species interactions, i.e. the relative effect that shrub nurses have on the richness and cover of the target species when compared to other environmental factors (Brooker et al. 2005), was measured using the Interaction Importance Index (I_{imp}; Seifan, Seifan, Ariza, & Tielbörger 2010) calculated as $I_{imp} = N_{imp}/|N_{imp}| + |E_{imp}|$, where N_{imp} and E_{imp} are the nurse plant and environmental contributions to species richness or total cover, respectively. N_{imp} was calculated as $N_{imp} = P_{nurse} - P_{open}$, and E_{imp} was calculated using $E_{imp} = P_{open} - MP_{open/nurse}$, where $MP_{open/nurse}$ is the maximum value of species richness or mean cover found in

the entire gradient, irrespective of the microsite sampled. I_{imp} has similar statistical properties to the RII, its values range from -1 to 1, it is symmetrical around zero and is negative for competitive species interactions and positive for facilitative species interactions. Due to the similarity in the properties the RII and I_{imp} the indices are easily comparable across the grazing gradient. The frequency of positive plant–plant species interactions was assessed using the percentage of facilitation obligates (those plant species only present under one or both nurse plants). Increasing number of facilitation obligates indicates more favorable environmental conditions under nurse species due to facilitative interactions between nurses and their understorey beneficiary species. We also assessed the effect of nurse plants on vegetation community by measuring microsite effects on plant species composition. This allowed us to assess the effect of the different environmental conditions provided by the nurse shrubs on both presence and relative abundances within each microsite. Differences in neighbor plant composition among microsites is a useful surrogate for the effect of plant–plant interactions on plant communities (Tewksbury & Lloyd 2001).

Statistical analysis

We used a mixed-models, permutational, multi-variate analysis of variance (PERMANOVA, Anderson 2001) to assess differences among the three microsites (*Eremophila*, *Senna*, Open) and four positions along the gradient, in relation to the matrix of 13 soil surface condition attributes. The first stratum considered gradient effects, and the second stratum microsite effects and its interaction with gradient position. Data were standardized by maximum value, and a Multi-Dimensional Scaling (MDS) analysis undertaken using the Euclidean distance resemblance measure with 9999 permutations. A second PERMANOVA analysis, using the Bray–Curtis distance measure and 9999 permutations, was used to examine potential differences in species composition across the gradient and among microsites using the same mixed-models structure. The relative positions of the four points along the gradient and the three microsites were displayed using a Canonical Analysis of Principal Coordinates (CAP) biplot.

We used the same mixed-models model structure as above, but using a univariate ANOVA approach, to analyze differences in soil C and N, the three surface condition indices, incident radiation, and both RII and I_{imp} for diversity and cover across the gradient and among microsites. The same analysis structure was used to assess differences in species richness, plant abundance and the frequency of positive plant–plant interactions. Abundance data were $\log_{10}$ transformed prior to analyses. The degree of association of plant species with respect to microsite or position within a gradient was measured with Indicator Species Analysis (Dufrene & Legendre 1997) using PC–ORD (McCune & Mefford 2011). Indicator values combine information on relative abundance
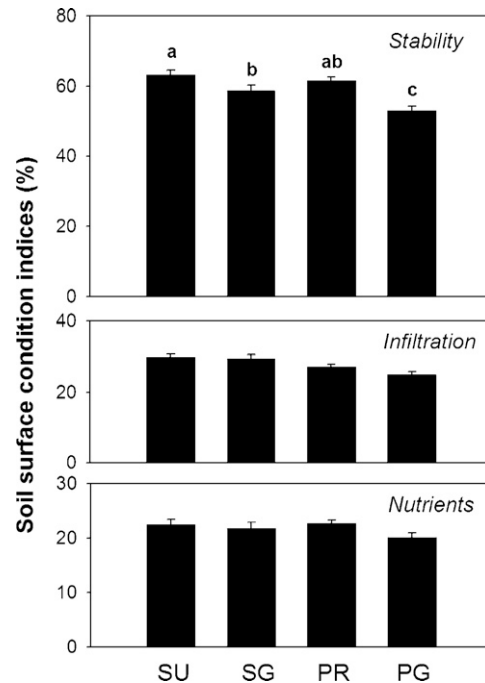

Fig. 1. Mean ($\pm$ SE) indices of soil surface condition for the four positions within the gradient. Different letters indicate a difference in the index at $P < 0.05$. SU, Sanctuary Ungrazed; SG, Sanctuary Grazed; PR, Pastoral Recovering; PG, Pastoral Grazed.

and frequency of species, and the indicator value is maximal (IV = 100%) when all individuals of a given species are restricted to a particular microsite (e.g. *Senna*), and all samples from the particular microsite contain an occurrence of that species.

Results

Differences in environmental variables and plant composition along the grazing gradient

The index of stability was least under the Pastoral Grazed treatment ($53.0 \pm 2.1\%$, mean $\pm$ SE) and greatest under the Sanctuary Ungrazed treatment ($63.2 \pm 1.9\%$, $F_{3,16} = 8.90$, $P = 0.006$). Neither the index of infiltration ($29.9 \pm 1.4\%$ to $24.9 \pm 0.9\%$) nor nutrient cycling ($22.5 \pm 1.4\%$ to $20.1 \pm 2.5\%$) changed with increasing grazing level ($P > 0.42$; Fig. 1). We detected no differences in soil C, soil N or radiation across the gradient. However, the Pastoral Grazed sites differed in their makeup of the 13 soil surface condition variables (PERMANOVA: Pseudo $F_{3,16} = 2.49$, P (perm) = 0.004). The second dimension of the MDS biplot separated Pastoral Grazed sites (sparse plant cover, $r = 0.67$; extensive erosion and deposition, $r = 0.60$) from the other sites.

We recorded 50 perennial groundstorey species across the grazing gradient. Composition and abundance, but not richness, partially reflected the results found for environmental
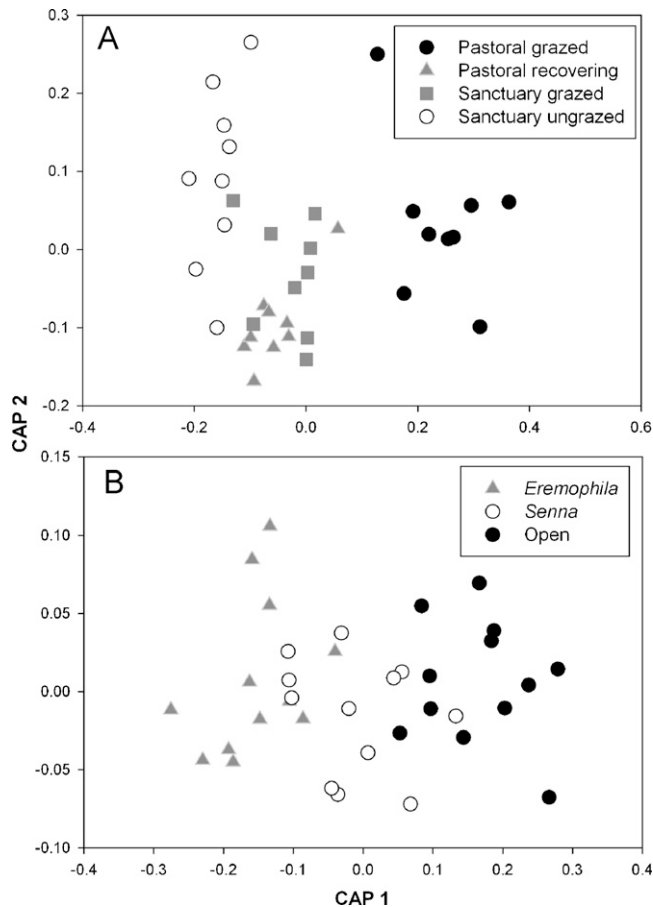
Fig. 2. Canonical Analysis of Principal Coordinates (CAP) biplot based on species composition among the four positions along the grazing gradient (A) and the three microsites (B).

Table 2. Mean ($\pm$ SE) of the three soil functional indices for each of the three microsites across the gradient.

Indices	Eremophila		Senna		Open	
	Mean	SE	Mean	SE	Mean	SE
Stability index						
Sanctuary Ungrazed	63.3	1.85	63.2	1.80	63.2	1.90
Sanctuary Grazed	55.5	1.83	58.0	2.01	60.2	1.93
Pastoral Recovering	60.2	1.59	61.0	1.68	63.5	1.68
Pastoral Grazed	56.2	2.15	51.3	1.89	51.5	2.25
Average	58.8	1.21	58.4	1.79	59.6	1.78
Infiltration index						
Sanctuary Ungrazed	31.9	2.19	30.7	0.95	27.2	1.11
Sanctuary Grazed	31.4	1.33	30.7	1.39	25.7	1.18
Pastoral Recovering	27.4	0.92	29.6	1.02	24.6	0.77
Pastoral Grazed	25.3	0.78	27.5	1.03	22.0	0.80
Average	29.0	1.06	29.7	0.83	24.9	0.74
Nutrient cycling index						
Sanctuary Ungrazed	23.3	1.45	23.7	1.41	20.5	1.40
Sanctuary Grazed	21.9	1.08	22.3	1.32	18.9	0.89
Pastoral Recovering	22.7	1.18	24.7	1.30	20.5	1.03
Pastoral Grazed	22.0	1.38	20.8	4.84	17.4	1.39
Average	22.5	0.76	22.8	0.92	19.3	0.66

Differences in environmental variables and plant composition among microsites

Soil condition (based on the 13 soil surface attributes) in the Open microsites was significantly different from that in the two shrub microsites (PERMANOVA: Pseudo $F_{2,16} = 10.80$, P (perm) < 0.001). The first dimension of the MDS biplot, which was positively correlated with cryptogam cover (Pearson's $r = 0.89$) and negatively with litter cover ($r = 0.74$), separated open from shrub microsites. Soil from *Eremophila* and *Senna* microsites had higher indices of infiltration (29.3%, $F_{2,16} = 25.0$, $P < 0.001$) and nutrient cycling (22.6%, $F_{2,16} = 7.42$, $P = 0.005$) than that from the Open microsites (Infiltration: 24.9%. Nutrients: 19.3%; Table 2). Open microsites contained significantly less C (0.66%, $F_{2,16} = 15.37$, $P < 0.001$) and N (0.047%, $F_{2,16} = 23.80$, $P < 0.001$) than either *Senna* (C: 0.97%, N: 0.064%) or *Eremophila* (C: 0.96%, N: 0.071%) microsites (Appendix A: Table 2). Shrub microsites were exposed to more than five-times less radiation (*Senna*: 179.2 μmol m^{-2} s^{-1}; *Eremophila*: 175.2 μmol m^{-2} s^{-1}) than Open microsites (1043.5 μmol m^{-2} s^{-1}, $F_{2,16} = 12.02$, $P = 0.001$).

Significantly more individuals were found under the canopies of *Eremophila* ($n = 1487$) and *Senna* ($n = 1448$) than in the open ($n = 953$, $F_{2,16} = 13.20$, $P < 0.001$), suggesting a lower limitation in plant recruitment in the two former microsites. Similarly, significantly more species were found under the canopies of both *Eremophila* ($n = 48$ species) and *Senna* ($n = 40$) than in the open ($n = 23$; $F_{2,16} = 41.77$, $P < 0.001$). Species composition also differed significantly between shrub and open microsites

variables, with a greater abundance, and different composition of species, at the less degraded sites. Species richness, which ranged between 30 and 34 species per plot, did not differ across the gradient ($P = 0.16$), though there was a general decline in abundance (total number of plant individuals sampled) with increasing degradation ($F_{3,16} = 5.11$, $P = 0.029$). The Sanctuary Ungrazed sites supported almost three–times greater abundance ($n = 1539$ individuals) than the Pastoral Grazed sites ($n = 538$). There was a marginally significant difference in species composition across the gradient (PER-MANOVA: Pseudo $F_{3,16} = 1.45$, P (perm) $= 0.067$; Fig. 2A). Indicator Species Analyses supported this result, showing that six of the species observed were significant indicators of the different degradation states. *Austrostipa scabra* (Indicator Value [IV] $= 38.5\%$, $P < 0.001$), *Chenopodium ulicinum* (IV $= 33.3\%$, $P = 0.042$), *Maireana triptera* (IV $= 34.3\%$, $P = 0.044$), and *Sida* sp. (IV $= 33.3\%$, $P = 0.049$) were significant indicators of the Sanctuary Ungrazed sites, while *Oxalis* sp. (IV $= 47.4\%$, $P = 0.008$) and *Sclerolaena diacantha* (IV $= 32.5\%$, $P = 0.017$) were significant indicators of Pastoral Recovering sites.

Table 3. The number facilitation obligates found beneath *Eremophila*, *Senna* and the total under both shrub species.

Treatment	No. of species	Obligates to		Obligates to either
		Eremophila	*Senna*	
Sanctuary Ungrazed[a]	34	8	2	20
Sanctuary Grazed[a]	34	10	3	21
Pastoral Recovering[a]	32	10	2	21
Pastoral Grazed[a]	30	4	4	20
Total[b]	50	10	1	27

Note that the values in columns 3 and 4 refer to species found only under either *Eremophila* or *Senna*, respectively. However, column 5 reports the sum of species found only under *Eremophila*, or under *Senna*, plus any species found under *Eremophila* or *Senna*, but not in the Open.

[a] Includes replicates combined.

[b] Includes all sites and replicates together.

(PERMANOVA: pseudo $F_{2,16} = 3.59$, $P < 0.001$; Fig. 2B). Indicator Species Analyses demonstrated that three of the 50 perennial species, *Einadia nutans* (IV = 41.2, $P = 0.013$), *Enchylaena tomentosa* (IV = 48.1, $P = 0.031$) and *Olearia pimeleoides* (IV = 34.5, $P = 0.052$), were significant indicators of *Eremophila* microsites. Nurse plant size had a marginal effect on the richness of understorey plants ($F_{1,58} = 1.30$, $P = 0.07$).

Changes in plant–plant interactions across the grazing gradient

Both *Eremophila* and *Senna* had facilitative effects on the cover and diversity of their understorey beneficiary species at every position along the gradient. Almost all of the Relative Interaction Intensity (RII) and Interaction Importance (I_{imp}) indices were positive, irrespective of the level of degradation and the different environmental conditions within a site (Fig. 3). However, there were no overall trends in RII or I_{imp} for cover or diversity across the gradient. We detected consistent differences between the two nurse plants. *Eremophila* (RII cover = 0.46) had a significantly greater positive effect on the cover of its understorey beneficiary species than *Senna* (RII cover = 0.20; $F_{1,8} = 5.80$, $P = 0.043$). Similarly, the Importance Index (I_{imp}) for diversity was greater for *Eremophila* (I_{imp} diversity = 0.36) than *Senna* (I_{imp} diversity = 0.20; $F_{1,8} = 17.02$, $P = 0.003$), and the mean I_{imp} for cover was significantly greater for *Eremophila* (I_{imp} cover = 0.24) than *Senna* (I_{imp} cover = 0.13; $F_{1,8} = 8.61$, $P = 0.019$; Fig. 3).

The number of facilitation obligates did not change with increasing degradation ($P > 0.28$; Table 3). Twenty-seven of the 50 perennial species (54%) were facilitation obligates for either one or both nurse plants indicating that about half of the perennial understorey species would be absent with the loss of these two shrub species. These results indicate the substantial role played by nurse plants in relation to abundance of understorey species.

Discussion

In contrast to previous research (Bertness & Callaway 1994; Graff et al. 2007; Smit et al. 2007), we failed to detect changes in the direction of plant–plant interactions at the community level along our grazing pressure gradient. Rather, the frequency of positive plant–plant interactions, and thus their intensity and importance, remained almost constant across the gradient. This lack of a relationship between plant–plant interactions and grazing pressure cannot be explained by a uniformity in plant and soil attributes, as we measured unambiguous changes in soil attributes and plant composition along the gradient. Our results accord with the recent theoretical framework proposed by Smit et al. (2009), which predicted a low importance of grazing protection as a facilitatory mechanism under low productivity conditions, such as those found in this study (see also Gómez-Aparicio et al. 2008). However, this scenario contrasts with empirical observations in other arid and semi-arid environments, where grazing protection is an important driver of plant interactions at both pairwise and community levels (Graff et al. 2007; Soliveres, García-Palacios, et al. 2011). These contrasting results could be caused by differences in the grazing gradients, a differential degree of grazing protection provided by each of the nurses used in each study, or differences in the grazing-sensitivity of the species pool. Notwithstanding these results, our study is one of very few that incorporates entire communities, rather than just a few species, which could explain the differences we encountered.

We would expect to record substantial changes in species richness and composition with increasing grazing pressure (e.g. Hendricks et al. 2005; O'Connor et al. 2011). However, despite the differences in soil and plant composition across the gradient, we found no effect on plant species richness. Two possible explanations might explain these contrasting results. First, we measured only perennial species, so the lack of a gradient effect on plant richness might be due to the absence of any effects on ephemeral species, which are known to dominate overgrazed areas. Second, although we did not find a significant grazing pressure effect on plant species richness, we did find a marginal effect on composition. Thus, although the number of species did not change, our results may reflect a shift in plant composition, from a higher abundance of grazing-sensitive species under low grazing pressure (Sanctuary Ungrazed) to the virtual disappearance of grazing-sensitive species and the dominance of grazing-resistant species under higher grazing pressures (Grime 1973; McNaughton 1985; Lunt et al. 2007).

The strong nurse plant effect found in our study reinforces the notion that facilitative interactions are a dominant process in these semi-arid shrublands, as facilitative interactions consistently exceeded competitive ones across the
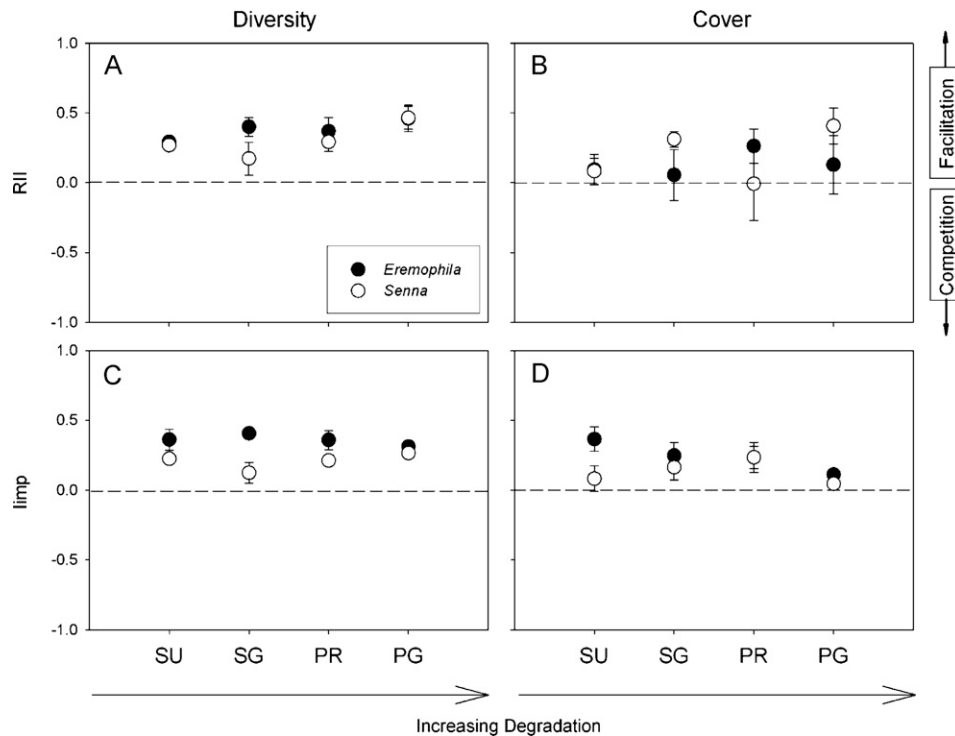
Fig. 3. Mean ($\pm$ SE; $n = 3$) for the indicators of plant–plant interaction intensity (RII) and importance (I_{imp}) along the grazing gradient for both *Eremophila* (filled circles) and *Senna* (open circles). SU, Sanctuary Ungrazed; SG, Sanctuary Grazed; PR, Pastoral Recovering; PG, Pastoral Grazed.

gradient. We believe that the facilitative mechanism operates through amelioration of the abiotic environment because facilitative interactions did not change with increasing grazing pressure. It must be recognized, however, that the design of the study did not allow us to distinguish between positive effects caused by abiotic amelioration or those effects related to associational resistance to herbivory (i.e. protection from grazers; Smit et al. 2007). Further manipulative experiments would be needed to disentangle the mechanisms driving these plant–plant species interactions, and to determine their importance for community structure. However, if grazing-mediated indirect effects were the primary stressor contributing to the net outcome of plant–plant interactions, then we would have expected the strength of facilitation to have declined with decreased grazing pressure (*sensu* Graff et al. 2007; Smit et al. 2007; Soliveres, García-Palacios, et al. 2011). This, however, was not the case, confirming that facilitation by abiotic amelioration is the principal mechanism accounting for the net outcome of species interactions in this shrubland. However, it must be noted that positive co-occurrences between species pairs (our facilitation obligate species) could also be caused by the dispersal mechanism of the species involved. In order words, an additional mechanism related to the elevated number of facilitated species could be related to seed dispersal by both wind and animals and its accumulation under shrub microsites (e.g. Dean, Milton, & Jeltsch 1999; Gómez-Aparicio 2008). Unfortunately, we cannot differentiate with our observational

approach among those positive co-occurrences related to dispersal, those occurring solely through facilitative processes or those caused by facilitative interactions and dispersal acting together.

Nurse plant effects on community dynamics

Abiotic stress amelioration observed under both shrub species included increased values of the infiltration and nutrient cycling indices, greater soil C and N concentrations, and significantly reduced levels of solar radiation. The higher nutrient content beneath the canopies of both *Eremophila* and *Senna* likely resulted from a combination of lower radiation, increased soil moisture and infiltration rates, greater throughfall nutrient content, and animal defecation on and beneath the shrubs (Callaway 2007). *S. artemesioides* has been shown to shed considerable litter in our study area ($\sim$160 g m^{-2} yr^{-1}; Samantha Travers, unpublished data). Shrub cover ranged from 38 to 48% across the gradient, providing the dominant structural component in this landscape, and therefore potentially engineering the landscape into a mosaic of fertile and infertile patches. The significant impact of both shrub species was overwhelming, with 54% of the perennial understorey species were only observed under the shrub species, suggesting that many of these species would be disadvantaged by the loss of the nurse plants (e.g. Holzapfel & Mahall 1999; Maestre et al. 2005).

The results of our study support the hypothesis that community stability is often determined by one or a few dominant species that have strong effects on interspecific interactions within a community (Deruiter, Neutel, & Moore 1995). The community of shrubs and their understories maintained diversity across a landscape that would otherwise consist of a depauperate vegetation community of only a few stress-tolerant species (Pugnaire & Luque 2001), as suggested by the high number of facilitation obligates species and the change in species composition between the nurse plant and open microsites.

It is unclear why the two nurse plants differed in their ability to facilitate groundstorey species, as there were no significant differences in their microhabitats. However, species-specific variation in plant–plant interactions can be caused by numerous subtle factors (Callaway 2007). In our case, there are two plausible explanations for the higher positive effect of *Eremophila* in comparison to *Senna*. Firstly, the average canopy area of *Eremophila* ($5.7 \pm 0.14\,\mathrm{m}^2$; mean $\pm$ SE) was twice that of *Senna* ($2.7 \pm 0.08\,\mathrm{m}^2$), and secondly, *Eremophila* had a slightly higher, though only marginally significant ($P = 0.07$), percentage of soil N beneath its canopy than *Senna*. The larger canopy area and the more fertile conditions are likely to provide a greater range of surface microsites and a greater capacity to ameliorate harsh environmental conditions, therefore, increasing the number of species able to colonize the shrub patch (Pugnaire & Luque 2001; Maestre et al. 2005).

Conclusions

Our study showed that abiotic amelioration was a more important driver of plant–plant interactions than grazing protection in our water-limited, semi-arid woodland. This was supported by the lack of a strong relationship between such interactions and the well-defined grazing gradient studied. The two shrub species differed in their ability to facilitate their beneficiary species, probably due to the larger size of *Eremophila*. In spite of this difference, however, both shrubs played a crucial role in the maintenance of plant species richness in the studied ecosystem. This study questions the common misconception that shrub encroachment leads to desertification and that shrublands are ecologically depauperate (Baez & Collins 2008). Our results indicate that woody nurse plants are critically important for maintaining a high diversity of groundstorey plants (Holzapfel & Mahall 1999; Maestre et al. 2005; Soliveres, Eldridge, et al. 2011). Shrublands are also known to provide habitat for a wide variety of animal taxa (e.g. Eldridge et al. 2011). The ecological role of woody species as refugia from grazing and harsh abiotic conditions of arid environments should be considered, therefore, when contemplating management practices aimed at shrub removal.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2012.02.008.

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