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Research article

Nurse plant effects on plant species richness in drylands: The role of grazing, rainfall and species specificity

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ABSTRACT

The outcome of plant–plant interactions depends on environmental (e.g. grazing and climatic conditions) and species-specific attributes (e.g. life strategy and dispersal mode of the species involved). However, the joint effects of such factors on pairwise plant–plant interactions, and how they modulate the role of these interactions at the community level, have not been addressed before. We assessed how these species-specific (life strategy and dispersal) and environmental (grazing and rainfall) factors affected the co-occurrence of 681 plant species pairs on open woodlands in south-eastern Australia. Species-specific attributes affected the co-occurrence of most species pairs, with higher co-occurrence levels dominating for drought-intolerant species. The dispersal mechanism only affected drought-tolerant beneficiaries, with more positive co-occurrences for vertebrate-dispersed species. Conversely, the percentage of facilitated species at the community scale declined under higher rainfall availabilities. A significant grazing \times rainfall interaction on the percentage of facilitated species suggests that grazing-mediated protection was important under low to moderate, but not high, rainfall availabilities. This study improves our ability to predict changes in plant–plant interactions along environmental gradients, and their effect on community species richness, by highlighting that: (1) species-specific factors were more important than environmental conditions as drivers of a large amount ($\sim 37\%$) of the pairwise co-occurrences evaluated; (2) grazing and rainfall interaction drive the co-occurrence among different species in the studied communities, and (3) the effect of nurse plants on plant species richness will depend on the relative dominance of particular dispersal mechanisms or life strategies prone to be facilitated.

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Introduction

Positive interactions among plants are crucial for maintaining species richness in plant communities, particularly in harsh environments (Hacker and Bertness, 1999; Callaway, 2007; Soliveres et al., 2011a). These positive (facilitatory) plant–plant interactions co-occur with negative (competitive) ones, and their relative importance and net effect on diversity depend strongly on the environmental conditions (Bertness and Callaway, 1994; Hacker and Bertness, 1999; Holmgren and Scheffer, 2010). An increasing

body of research suggests that the effects of positive interactions on species richness at the community level are prevalent at moderate levels of stress (Hacker and Gaines, 1997; Michalet et al., 2006). However, such effects also depend upon the nature of, and interrelationships among, the different stressors present within the environmental gradients studied (Maestre et al., 2009; Smit et al., 2009).

The joint effects of herbivory and abiotic stress on plant–plant interactions have seldom been addressed, even though these two stressors commonly co-occur in nature and strongly shape plant communities (Ibáñez and Schupp, 2001; Gómez-Aparicio et al., 2008; Sasaki et al., 2008; Suzuki et al., 2008). The effects of grazing on plant communities and plant–plant interactions are known to vary with water and nutrient status (e.g. Illius and O'Connor, 1999; Veblen, 2008). Some research suggests that the impact of grazing on plant performance can be extremely important in water-limited environments due to low vegetation productivity, which may cause a higher grazing pressure in the remaining palatable tissues (Illius and O'Connor, 1999). Protection against herbivory by nurse plants can, therefore, be crucial for the maintenance of diversity in

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water-limited environments (e.g. Rebollo et al., 2002; Graff et al., 2007; Smit et al., 2007; Soliveres et al., 2011b). However, other lines of inquiry suggest that the role of herbivory-mediated facilitation at the community level is important at moderate to high, but not at low, levels of water availability (Smit et al., 2009; Holmgren and Scheffer, 2010; but see Gómez-Aparicio et al., 2008). This is explained by the relatively low abundance of herbivores under such conditions that, together with the lower palatability and productivity of drought-adapted plants, would explain the relatively weak impact of herbivory on arid and semiarid plant communities regarding the prevalent harsh abiotic conditions (reviewed in Smit et al., 2009; see also Howard et al., 2012). The contrasting results and theories found in the literature, together with the elevated number of factors affecting plant–plant interactions, require that more empirical studies be undertaken to advance our understanding about the role of plant–plant interactions on community diversity along environmental gradients involving both biotic and abiotic stressors (Bertness and Shumway, 1993; Smit et al., 2009; Bulleri et al., 2011).

Irrespective of the environmental conditions, it is well known that species-specific features of particular species, such as their ecological traits, dispersal mechanisms or evolutionary relationships, determine, to a large degree, the magnitude and direction of the interactions among them (e.g. Liancourt et al., 2005; Gómez-Aparicio, 2008; Pueyo et al., 2008; Soliveres et al., 2012). The response of plant–plant interactions to herbivory is also known to be highly dependent on the plant species involved (Callaway et al., 2000; Skelinen, 2008). The outcome of these interactions will depend largely on the tolerance to herbivory of the facilitated species, and on the ability of the nurse to moderate the effects of herbivores (Baraza et al., 2006; Vanderberghe et al., 2009). Alternatively, nurse plants not only protect neighbors against herbivory, but also enhance their recovery after grazing by providing higher levels of resources (Rand, 2004; Acuña-Rodríguez et al., 2006). This may also lead to species-specific responses depending on the identity of the limiting resource for each beneficiary species, and on how its availability is affected by both herbivory and nurse plants (Wise and Abrahamson, 2005; Soliveres et al., 2011b). To understand the role of plant–plant interactions on the maintenance of plant diversity, therefore, we need to know how these multiple environmental and species-specific attributes affect pairwise interactions and how this influences overall trends at the community level. Undoubtedly, this will “help in the development of general theory and in explaining apparently contradictory results found in the literature” (Brooker et al., 2008).

The main aim of our study was to determine how different levels of both rainfall availability and grazing pressure, and their interaction, affected plant–plant interactions. Specifically, we endeavored to answer the following questions: (1) what is the relative importance of environmental factors (grazing, rainfall) and species-specific attributes as drivers of pairwise plant–plant interactions? (2) Do grazing and rainfall modulate the effects of these interactions on plant species richness at the community level?

Methods

Study area and establishment of the rainfall and grazing gradients

The study was conducted within 27 open eucalypt woodland plots (50 m × 50 m) located in south-eastern Australia. The plots were positioned along a 1200 km west–east transect with average annual rainfall decreasing from western Sydney (33°33′43″S, 150°43′51″E), in the east, to Wentworth (34°06′40″S, 142°11′27″E),

in the west. Rainfall is the most important abiotic stressor for these plant communities (e.g. Eldridge et al., 1991). Consequently, it was the predominant abiotic factor forming the environmental gradient studied, as it varied from 220 mm in Wentworth (mean minimum to mean maximum annual temperature: 10.3–23.7 °C) to 900 mm in western Sydney (mean minimum to mean maximum annual temperature: 11.3–24.4 °C). The plots had similar soil types (clay-loam soils with gradational profiles), and were located on landscapes of similar aspect and slope to minimize the influence of factors other than climate in our conclusions. Vegetation was characterized by the presence of large eucalypt trees (*Eucalyptus populnea* F. Muell., *Eucalyptus intertexta* R.T. Baker, *Eucalyptus microtheca* F., *Eucalyptus tereticornis* S., *Eucalyptus moluccana* Roxb. and *Eucalyptus crebra* F. Muell.) and shrubs (*Eremophila mitchellii* Benth., *Dodonaea viscosa* (L.) Jacq., and *Bursaria spinosa* Cav.).

We established a fully factorial design with three levels of rainfall (western Sydney: 800–900 mm, Cobar: 350–450 mm, and Wentworth: 220–280 mm) and grazing (high, moderate and low), each replicated three times ($n=27$ plots). We selected plots with a similar cover of both trees and shrubs to minimize any potential effects of such cover on plant species richness at the community level. The average cover of woody plants, determined from a 200 m transect in all the plots, was $30 \pm 3\%$ for trees and $11 \pm 2\%$ for shrubs (mean \pm SE, $n=27$). The three contrasted levels of grazing pressure were selected based on four attributes: (1) the standardized stocking rates, (2) land use, (3) distance to water points, and (4) vegetation composition. We converted the different animal densities to a common unit: DSE ha⁻¹ (dry sheep equivalents), which rates was calculated using unpublished, long-term average sheep stocking rate figures from western NSW (Office of Environment and Heritage – OEH, Rangeland Assessment Program) and density data for different herbivores obtained from OEH and Department of Lands data (see Moles et al., 2012; Howard et al., 2012) and unpublished reports (Table 1). These variables have been repeatedly shown as good surrogates of herbivore activity in Australia and elsewhere (Andrew, 1988; Landsberg et al., 1999; Barnes, 2001). Plots in the low grazing regime were located in either National Parks or Nature Reserves at distances of more than 5 km from water, i.e. outside the grazing range of sheep and goats (Pringle and Landsberg, 2004). These sites were characterized by a plant community of high cover, abundance and biomass of native plant species. Among these species, palatable grasses were abundant, suggesting low grazing levels (Illius and O'Connor, 1999). Sites in the moderate grazing category were either on individual grazing properties or on areas adjacent to major roads along which livestock are moved periodically (traveling stock reserves). We combined these different land management types because both are characterized by intermittent grazing. The traveling stock reserves are grazed intermittently because strict regulations require that livestock must move a minimum distance each day, thereby preventing overgrazing. On individual grazing properties, grazing by feral herbivores is restricted by the use of herbivore-proof fencing, and domestic herbivores are moved regularly between paddocks to avoid overgrazing and soil disturbance (time-controlled grazing; Johnston et al., 1996), which also promotes intermittent grazing. Plots under the high grazing regime were all pastoral properties that practice a set-stocking strategy, with livestock being grazed continuously in the same paddock. Sites were generally close to livestock watering points (<2 km), a reasonable piosphere (i.e. area of high grazing impact around water points) for this region (Andrew, 1988; Pringle and Landsberg, 2004). Therefore, these sites are heavily grazed by sheep, cattle, and sometimes horses, and also have variable, but often large, populations of feral grazers (goats, rabbits). The stocking rates and management of the sampled plots has been consistent over the past 50 years. Our approach, therefore,

Table 1
 Characteristics of the 27 study sites in relation to species richness, rainfall and grazing levels, the composition and density of grazers. Grazers: H = horses, C = cattle, S = sheep, G = goats, K = kangaroos, and R = rabbits. Different animal densities have been converted to a common unit (dry sheep equivalents – DSE ha⁻¹) using published and unpublished literature (see maintext).

Site	Species richness	Rainfall level	Grazing level	Grazers composition	DSE ha ⁻¹
Caravans	37	High	High	H, C, R, K	20.6
Hoxton Canal	29	High	High	H, C, R, K	17.3
Swan's nest	39	High	High	H, C, R, K	19.0
Cowra reserve	23	High	Medium	K, R	2.5
Quandialla	19	High	Medium	K, C	6.9
Rickaby's	36	High	Medium	K, R	3.8
Cowra Hwy	32	High	Low	K, R	0.2
Hoxton woodland	34	High	Low	K	0.1
Millenium	36	High	Low	K	0.1
Etiwanda	22	Medium	High	S, K, R, G	3.8
Florida	29	Medium	High	S, K, R, G	4.3
Truganini	18	Medium	High	S, K, R, G	4.2
Cobar Common	25	Medium	Medium	K, G, R	2.9
Minesite	28	Medium	Medium	K, G, R	3.2
The Wire	31	Medium	Medium	K, G, R	2.9
Gilgunnia	40	Medium	Low	K	0.9
Wagga Tank	38	Medium	Low	K, G, R	2.4
Yathong	34	Medium	Low	K, G, R	2.4
LG1	12	Low	High	S, C, G, K, R	5.2
WG1	12	Low	High	S, C, G, K, R	4.2
WR1	11	Low	High	G, K, R	4.0
PG1	14	Low	Medium	S, K, G, R	3.5
WG3	16	Low	Medium	K, C, S, R	3.4
WR2	19	Low	Medium	K, R, G	1.2
KP1	16	Low	Low	K	1.0
KP2	19	Low	Low	K	1.0
LP1	13	Low	Low	K	1.0

does not underestimate the well-known mid- and long-term effects of herbivory on soil properties, seed banks or the existing plant composition prior to sampling (Milchunas and Lauenroth, 1993; Tongway et al., 2003).

Any study reporting differences in herbivore intensities across environmental gradients will invariably encounter differences in the composition of herbivores across the gradient. Similar changes on the composition of plants and the identity of nurse plant species are expected across the gradient. However, in most natural systems and ecological models, a different herbivory intensity is often (implicitly or not) related to a different composition of herbivores and plant species across environmental gradients (Milchunas et al., 1988; Cingolani et al., 2005). Changes in plant-herbivore composition, some including livestock and some others not, could surely affect our results. However, grazing by livestock and wild herbivores is a major driver of plant community dynamics in drylands, and their relative densities/compositions – together with their effect on plants – changes depending on the environmental conditions and land management (Holechek, 1988; Osem et al., 2002; Chamaillé-Jammes et al., 2007). Thus, we believe that the differential composition of both plants and herbivores across the studied gradients is a more realistic test of our hypotheses, rather than a limitation of our study.

Vegetation survey

We sampled three markedly different microsites (Open, Shrub, and Tree) at each site. Open microsites were located more than 1 m away from the canopy edge of any shrub or tree. Shrub species (hereafter Shrub microsite) differed across the gradient, but all were inverse cone-shaped (e.g. *E. mitchellii*, *D. viscosa*, *Senna artemisioides* [Gaudic. ex DC.] Randell, or *B. spinosa*). The tree species sampled (hereafter Tree microsite) also changed across the gradient, but were always large trees from the genus *Eucalyptus* with the same general form and morphology, and were characterized by a deep litter layer beneath their canopies (see Appendix A).

The two types of nurses studied here (trees and shrubs) ameliorate their abiotic environment by altering shade, temperature and soil fertility compared with Open microsites (Weltzin and Coughenour, 1990; Warnock et al., 2007). However, we studied the effects of trees and shrubs separately to broaden the generality of our conclusions, as these species differ in a number of ways (Appendix A), and their interactions with neighbors would therefore be expected to change along the grazing and rainfall gradients studied. The shrubs at our study sites were generally multi-stemmed, and their stem arrangement created a structure that restricts access to large grazers. Tree microsites were single-stemmed *Eucalyptus* spp. trees; their growth form allowed access of grazing animals to the area beneath their canopy. Indeed the canopies of these trees are often used as resting or camping sites for kangaroos and domestic livestock (Eldridge and Rath, 2002; Wilson et al., 2007). Large eucalypt trees deposit substantial quantities of litter (up to 2.2 t ha⁻¹), and have high levels of organic matter (4.4%) beneath their canopies (Eldridge and Rath, 2002). These canopies are substantially larger (area up to 300 m²) and denser than those of the shrubs (area up to 10 m²); thus more shade is expected under tree than under shrub canopies. In spite of their positive effect on soil fertility and of their previously reported facilitative effects (Eldridge and Rath, 2002; Soliveres et al., 2011a), Eucalypt litter is known to have allelopathic effects on nutrient uptake and germination of some species (e.g. May and Ash, 1990). These allelopathic effects could substantially reduce their positive effects for some species and/or increase the species-specific nature of plant–plant interactions (Callaway, 2007).

We sampled thirty 0.5 m × 0.5 m quadrats within each microsite and site. The quadrats were distributed among at least three trees and five shrubs at each plot, which were of similar size and separated by distances of more than 2 m. In each quadrat we measured the cover and number of individuals of every perennial plant species. Annual plant composition in arid and semi-arid areas may substantially change through the year and among different years (Whitford, 2002). Thus, we did not include annual species in our

observational design to avoid confounding effects in the differences among study sites derived from sampling “incomplete” communities depending on the timing or the year of sampling. From these data we assessed interactions at both community and pairwise levels (see below). We acknowledge that plant density and cover (our surrogates of plant performance) might not be the best possible measurements for plant performance, and that it would have been preferable to measure directly either survival or growth. However, the recruitment of semi-arid plants, including those studied here, is mainly limited by seedling survival (Eldridge et al., 1991). Thus, the sole presence of an adult plant, and therefore the number of individuals, is a good surrogate of its survival, regardless of their size. Conversely, plant cover is related to productivity in semi-arid environments (Flombaum and Sala, 2009) and is a reasonable surrogate of plant performance, particularly if we consider the large amount of pairwise interactions assessed here and the logistic constraints of measuring directly plant performance in all of them.

Assessing plant–plant interactions and measuring species-specific factors

We divided all of the pairwise interactions included within our 27 plots into four “interaction-status” groups: Shrub-selective, Tree-selective, Non-selective (those facilitated by either shrubs or trees), and non-facilitated species. We performed χ^2 tests by microsite pairs (Shrub vs. Open and Tree vs. Open; to assign each species to a given group). We did not consider the difference in cover between the different microsites in the plot since we sampled exactly the same number of quadrats and therefore the sample effort was identical. Those species with significantly more individuals than expected under Shrub or Tree microsites than in the open (*i.e.* a significant χ^2 for Shrub vs. Open but not for Tree vs. Open or *vice versa*) were considered as Shrub or Tree-selective, respectively. Those species with significantly more individuals than expected under Shrub and Tree microsites than in the open (*i.e.* significant χ^2 for Shrub vs. Open and for Tree vs. Open) were considered as Non-selective. The remaining species were considered as non-facilitated. When a given species had fewer than 15 individuals in a given plot, no statistical test was performed, and we considered as Shrub or Tree-selective those species found only within a Shrub or Tree microsite with no individuals in the open. When species with fewer than 15 individuals were found under the canopy of both nurses (Shrub and Tree), but not in the open, were referred to as a Non-selective. Among the species with fewer than 15 individuals, those with individuals in the open were referred to as non-facilitated, regardless of the number of individuals located under Shrub or Tree microsites. Since we had the same sampling effort for each microsite, it is very unlikely that these species with low abundances affected our results either by over- or underestimating the effect of nurse plants on the species richness of the community because they should have exactly the same probability of occurring under a given microsite by chance.

Although the degree of co-occurrence has successfully been used as a proxy of facilitation in numerous studies worldwide (*e.g.* Tewsby and Lloyd, 2001; Valiente-Banuet et al., 2006), assuming that a higher level of co-occurrence is solely related to positive interaction between the species involved is risky. Plant spatial patterns are not only driven by these interactions but by a variety of different processes such as resource heterogeneity or dispersal (Alados et al., 2006). Regrettably, our observational study does not allow us to tease apart these different processes; however the results from empirical studies and mathematical models are in agreement in that both dispersal and facilitation/competition shifts are the major drivers of the spatial co-occurrence among species under semiarid conditions (*e.g.* Tirado and Pugnaire, 2005;

Gómez-Aparicio, 2008; Pueyo et al., 2008; Soliveres et al., 2012). We pooled different dispersal mechanisms into two classes: vertebrate-dispersed and dispersed by other vectors. This improved our interpretation of the co-occurrences by discriminating between (1) species found beneath a given nurse plant as a result of dispersal and facilitative mechanisms from (2) species occurring solely through facilitative processes. Plants dispersed by vertebrates (mostly birds and small mammals) were those with fleshy fruits or adhesive appendages (adapted to attach to fur, hair or feathers of vertebrates). These seeds are more likely to be dropped close to the canopies of woody plants, leading to a nucleation process (Dean et al., 1999). Conversely, seeds dispersed by wind, ants or gravity (classified in our study as “dispersed by other vectors”), do not contribute to this nucleation process. Wind-dispersed seeds are also likely to accumulate beneath nurses such as our Shrub microsites, which capture wind-blown sediments. Other patch-types (*e.g.* dead branches or grass patches) also retain these wind-dispersed seeds and. Although these other patch-types are smaller than *Eucalyptus* or shrub canopies, they are fixed permanently to the soil surface, making them equally effective as traps for wind dispersed seeds compared with *Eucalyptus* trunks or shrub canopies. We believe, therefore, that wind-dispersed seeds are less likely to co-occur more than expected by chance with woody plants by dispersal alone. The primary dispersal mechanisms of each of our species were determined by consulting literature sources, and were assigned to one of our two groups (Appendix B).

We used three categories to define the life strategy of all the species sampled: drought tolerator, competitor under wetter conditions, or generalist. We based our classification of “competitor” or “stress-tolerator” specifically on the adaption to water scarcity (drought tolerators) or the ability to compete with neighbors under wetter conditions (competitor) of each species. Since ecological traits indicating these adaptations for all species found in the 27 plots were unavailable in the literature, we developed a simple indicator based on our own observations. We defined drought tolerators as those species that: (1) were able to produce more biomass (indicated by higher cover in the quadrats) at the driest end of the gradient (see below), or (2) occurred only in the driest part of the gradient, suggesting that their recruitment is limited by factors other than low water availability. In the latter case we considered only those species with at least five occurrences in this extreme of the gradient. Competitor species were defined in a similar way: those with higher cover in the wettest part of the gradient or that only occurred in the wettest plots. We measured the limitation on biomass production (cover) under each rainfall level with χ^2 tests, with average cover of each species by rainfall level as the response variable (considering cover as count data for biomass sections) and rainfall level as the predictor. Unfortunately, we could not exclude the possibility that some species were overlooked because they were grazed; however, we pooled the data of the three different levels of grazing studied to perform these χ^2 tests. Thus, the possibility of overlooking grazing-sensitive species should wane as these species should appear at least in the ungrazed plots. Thus, a strong effect of herbivory on this analysis is unlikely. To avoid confusion with the facilitative effect of nurses *per se*, only individuals growing in the Open microsite were considered for both classifications. Any species that failed to meet these requirements (*i.e.* non-significant χ^2 test and fewer than five individuals sampled in any of the rainfall extremes) was characterized as “generalist strategy” (see classification summary in Table 2). To increase the confidence in our classification, we compared it with data of specific leaf area (SLA) obtained for over 80 species from the published literature (Westoby and Wright, 2003; Wright et al., 2004; Taylor and Eamus, 2008) by using ANOVA (drought-tolerator/competitor/generalist classification as predictor and SLA

Table 2
Summary of the different classifications used to define the pairwise interactions included in the study.

Classification	Category	Description	
Interaction status	Shrub-selective	Species with more co-occurrences under shrubs than in open areas or under trees	
	Tree-selective	Species with more co-occurrences under trees than in open areas or under shrubs	
	Non-selective	Species with more co-occurrences either under shrubs or trees than in open areas	
	Non-facilitated	Those species with significantly less occurrences under shrubs or trees than in the open, or with non-significant χ^2 tests	
Species-specific factors	Dispersal mechanism	Vertebrate	Species with fleshy fruits or structures to assist dispersal by mammals
		Other	Species dispersed by vectors other than birds or mammals (ants, wind, gravity)
	Life strategy	Drought-tolerators	Species only occurring in the driest part of the gradient, or with significantly more cover under the driest conditions
		Competitors	Species only occurring in the wettest part of the gradient, or with significantly more cover under the wettest conditions
		Generalists	Species not fulfilling the requirements to be either drought-tolerators or competitors

as response variable). Specific leaf area is a widely used functional trait, known to be strongly related to drought and shade tolerances, growth rate and other important ecological functions (Westoby and Wright, 2003; Wright et al., 2004). High SLA values are found in shade tolerant, highly competitive plant species and low SLA values found in less competitive but drought-tolerant species (Wright et al., 2004). We found that SLA increased significantly from drought-tolerators ($60.6 \pm 10.7 \text{ cm}^2/\text{g}$, $n = 10$) to generalists ($112.1 \pm 14.7 \text{ cm}^2/\text{g}$, $n = 53$) to competitors ($161.2 \pm 17.4 \text{ cm}^2/\text{g}$, $n = 19$; $F_{2,81} = 7.42$; $P = 0.001$). Our metric of plant–plant interactions at the community level was the percentage of facilitated species in each plot. Facilitated species were considered as those species with more occurrences under any nurse than in the open (*i.e.* Shrub-selective, Tree-selective and Non-selective species).

Statistical analyses

We used log-linear models to assess the role of environmental (grazing and rainfall) and species-specific (dispersal and life strategies) factors in determining the outcome of specialist and generalist pairwise plant–plant interactions. We had balanced replication within the different grazing and rainfall levels, but our data were based on natural occurrences of each life strategy and dispersal class, which are known to change along abiotic gradients (Grime, 1977; *e.g.* more drought-tolerant species were found under lower rainfall levels). Thus, we had to account for this in our analyses. For doing so, we analyzed changes in the relative frequency of facilitated/unfacilitated cases, rather than the absolute number. Separate analyses were performed for the relative frequency of Shrub-specialist, Tree-specialist, and Generalist interactions. As neither the life strategy nor SLA data could be considered completely independent of rainfall level (given that rainfall was used to determine life strategy, see above, and SLA significantly increased with water availability), we used separated log-linear models for species-specific and environmental variables to avoid multicollinearity. Since we were interested in assessing the different role played by species-specific and environmental factors as drivers of each of the interaction-types considered (Shrub- and Tree-selective and Non-selective species), we ran separated analyses for each of them. Thus, six different hierarchical log-linear models were used. Three of them included Grazing and Rainfall as categorical predictors, with separate models each for frequency of non-selective, or Shrub or Tree-selective as response variables. The remaining models included Strategy and Dispersal as categorical predictors,

with the same three different interaction-status attributes (non-selective, or Shrub or Tree-selective) as response variables.

The total number of species (richness), and the percentage of facilitated species were analyzed using a split-plot ANOVA, with rainfall and grazing as fixed factors. The first stratum considered rainfall, and the second stratum the grazing \times rainfall interaction. The ranges of grazing intensity changed substantially across the rainfall gradient (Table 1). Hence, to control for the different grazing ranges along the rainfall levels, we introduced the exact DSE ha^{-1} (dry sheep equivalents) as a covariate in the ANOVA. Diagnostic tests indicated that the data met assumptions of homoscedasticity and normality, and therefore were not transformed. ANOVA analyses were performed using Minitab, while Log-linear models were performed using SPSS 13.0 for Windows (SPSS Inc., Chicago, Illinois, USA).

Results

Species-specific and environmental factors as drivers of plant–plant interactions

The frequency of non-selective positive interactions (18% of the 681 pairwise interactions studied) changed significantly in relation to both species-specific (life strategy and dispersal) and environmental (rainfall and grazing) factors (Table 3). The frequency of positive generalist interactions increased linearly with decreasing rainfall or increasing grazing pressure (LOG-LINEAR: rainfall $\chi^2 = 8.97$; DF = 2; $P < 0.05$, grazing $\chi^2 = 6.91$; DF = 2; $P < 0.05$; Table 3A). These positive interactions were also less frequent for species following a “drought tolerator” strategy than for those following “competitor” or “generalist” strategies ($\chi^2 = 14.52$; DF = 2; $P < 0.001$), and for vertebrate-dispersed species than for those dispersed by other mechanisms ($\chi^2 = 5.10$; DF = 1; $P < 0.05$; Table 3B).

Shrub and Tree-selective interactions represented 25% and 19% of all 681 pairwise interactions studied, respectively. Shrub-selective positive interactions increased with grazing pressure ($\chi^2 = 7.19$; DF = 2; $P < 0.05$; Table 3A), and marginally increased with aridity ($\chi^2 = 5.71$; DF = 2; $P = 0.058$). However, they were only marginally affected by the life strategy \times dispersal mechanism interaction ($\chi^2 = 5.47$; DF = 2; $P = 0.065$), with a slightly higher frequency of positive interactions for drought-tolerator beneficiaries when those were vertebrate dispersed. Conversely, tree-selective interactions were only significantly affected by the life strategy of the beneficiary species, with a lower frequency of positive

Table 3

Percentage of positive interactions by category in relation to environmental (A) or species-specific (B) variables ($N=681$ species). Life strategies are species more abundant in (1) high rainfall plots [Competitors], (2) low rainfall plots [Drought-tolerators] and (3) neither Competitors nor Drought-tolerators [Generalists]. Dispersal mechanism: species dispersed by birds or mammals [Vertebrate] or by other vectors, such as gravity, wind or ants [Other]. Shrub- and Tree-selective beneficiaries = species only found beneath Shrub or Tree canopies, respectively, and Non-selective beneficiaries = species found beneath Shrub and Tree canopies but not in the open.

Rainfall	Grazing	Shrub-selective	Tree-selective	Non-selective
(A) Environmental variables				
High	High	21.9	21.0	16.2
	Moderate	15.4	17.9	15.4
	Low	10.8	26.5	9.8
Moderate	High	29.0	18.8	30.4
	Moderate	23.0	35.6	14.9
	Low	14.3	23.2	17.0
Low	High	22.9	20.0	28.6
	Moderate	24.5	30.6	26.5
	Low	27.1	18.8	18.8
Life strategy	Dispersal mechanism	Shrub-selective	Tree-selective	Non-selective
(B) Species-specific variables				
Competitor	Other	17.9	18.3	19.1
	Vertebrate	17.1	17.1	35.4
Drought-tolerator	Other	19.1	17.6	8.8
	Vertebrate	34.8	13.0	4.3
Generalist	Other	23.5	30.4	15.2
	Vertebrate	12.0	52.0	16.0

interactions for drought-tolerator species ($\chi^2=25.60$; $DF=2$; $P<0.001$). Neither the dispersal mechanism of the beneficiary species, nor the levels of rainfall or grazing, affected the frequency of tree-selective positive interactions ($P>0.1$ in all cases; Table 3A).

Community level responses to grazing and rainfall

Species richness differed significantly in relation to rainfall but was not significantly affected by grazing, the dry sheep equivalents (DSE), or the rainfall \times grazing interaction (Fig. 1A). Richness was greatest under high or medium rainfall (~ 30 species by plot) and lowest under low rainfall (~ 15 species). Interestingly, the lack of effect of both grazing and the rainfall \times grazing interaction was caused by the introduction of DSE as covariate, which was non-significant ($P=0.358$). Even after controlling by the different ranges in grazing intensity across the rainfall/grazing categories, the percentage of facilitated species was significantly affected by rainfall, grazing and their interaction. A reduction in the percentage of facilitated species was found under high rainfall levels (from $\sim 70\%$ at moderate-low rainfall levels to $\sim 50\%$ under high rainfall; Fig. 1B). The increase in grazing pressure (either to moderate or high levels) increased the percentage of facilitated species, from $\sim 55\%$ at low grazing levels to $\sim 69\%$ at moderate and high grazing levels. However, this grazing effect disappeared under the highest rainfall availability. It must be noted that the widest range in grazing density (DSE) was precisely found under this high rainfall availability (Table 1).

Discussion

Species specificity in plant–plant interactions

The low frequency of positive co-occurrences when beneficiary species were drought-tolerators is consistent with the literature (e.g. Hoffmann, 1996; Gómez-Aparicio et al., 2005; Gross et al., 2010). These species are more likely to be outcompeted beneath nurse canopies by either other facilitated species or the nurse itself, and are less likely to benefit from greater water availability beneath the nurse canopy (Liancourt et al., 2005; Holmgren and

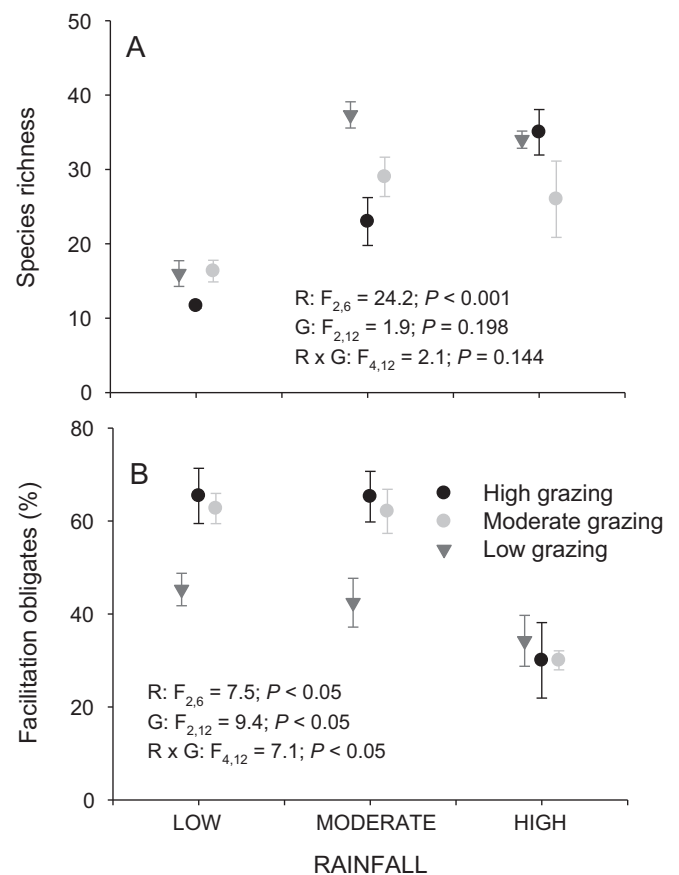


Fig. 1. Species richness (A) and percentage (B) of facilitated species at the community level at different rainfall and grazing levels. Statistical significance of the ANOVAs performed is shown in each panel. Degrees of freedom [factor, error] were 2, 6 for rainfall; 2, 12 for grazing; and 4, 12 for rainfall \times grazing interaction. Abbreviations are: R = rainfall, G = grazing and R \times G = rainfall \times grazing interaction. Data are means \pm SE ($n=3$).

Scheffer, 2010). Furthermore, most adaptations to drought stress, such as hairy and thick leaves, lignified tissue or short stature are also related to grazing-resistance, reducing the probability of these species to be facilitated even by grazing protection (Baraza et al., 2006; Smit et al., 2009).

Most of criticism surrounding the use of co-occurrence measures as surrogates of biotic interactions in plants is based on habitat-sharing or seed trapping. Our study is not free of this criticism, since we are not able to differentiate between positive co-occurrences caused by dispersal, dispersal + positive interactions, positive interactions, or other factors (*i.e.* soil heterogeneity) from our observational dataset. However, we partially reduced the uncertainty of our results by considering the dispersal mechanism of the species studied. Interestingly, positive co-occurrence among species pairs was not related to the dispersal strategy of the target species, with the exception of drought-tolerator species. This suggests that the positive co-occurrences found for the remainder life strategies (competitors or generalists) are caused by facilitative interactions, and not by the role of the nurse species as bird perches or refugia for mammals. As stated above, drought-tolerator species are much less likely to benefit from the ameliorated microclimatic conditions and, therefore, the higher frequency of positive co-occurrence for vertebrate-dispersed species in this group found seems to reflect the important role of nucleation processes, rather than true facilitative interactions, to determine co-occurrence patterns among drought-tolerant species and their nurses.

Tree-selective species (involved in over 19% of all pairwise interactions, 30% for positive interactions only) were only significantly affected by species-specific attributes, which also played a major role in the outcome of interactions involving non-selective beneficiary species. Therefore, our results suggest that species-specific factors can be more important than environmental variables in defining a large number of the pairwise interactions in the studied ecosystem. Interestingly, an elevated number of the species facilitated by either shrubs or trees did not correspond to a specific life strategy (Table 3B), suggesting that species-specific attributes other than the life strategy play an important role in such interactions. These could include indirect facilitatory mechanisms (Levine, 1999; Soliveres et al., 2011a), or differential responses to the allelopathic effects of eucalypts, litter type and amount, or the nature of mycorrhizal associations among the beneficiary species (Callaway, 2007). Unfortunately, our experimental design does not allow us to disentangle the multiplicity of possible mechanisms driving the outcome of these species-specific interactions. Irrespective of the particular mechanism(s) involved, our results question the notion of the overwhelming importance of environmental factors as drivers of plant–plant interactions, which has pervaded current literature. In line with previous work (Callaway, 2007; Brooker et al., 2008), our study suggests that species-specific factors, such as life strategy and dispersal mechanisms, should also be considered when studying the relationship between plant–plant interactions and environmental gradients. The reduction in the relative abundance of competitor species (*sensu* Grime, 1977) with declining rainfall has been suggested as the mechanism responsible for the waning of facilitation at the community level under extreme conditions (Michalet et al., 2006), and could explain the reduced number of facilitated species detected at the low rainfall end of our gradient.

Community level responses to grazing and rainfall

Grazing affected plant–plant interactions at the community level at low to moderate, but not high, water availabilities. The greater influence of grazing on facilitative interactions under low and moderate, but not high, rainfall conditions (Fig. 1B) is at odds with current predictions (Smit et al., 2009; Holmgren and Scheffer,

2010) and empirical research (Howard et al., 2012). In contrast to our results, previous research has demonstrated the crucial role of plant–plant interactions in the maintenance of plant species richness under grazing across a range of ecosystems and productivity levels (Callaway et al., 2000; Smit et al., 2007). However, other research clearly supports the notion of a higher grazing impact on plant performance, and therefore a higher importance of grazing-mediated facilitation, in water-limited environments (Illius and O'Connor, 1999; Rebollo et al., 2002; Gómez-Aparicio et al., 2008). It is difficult to explain these contrasting results in the literature, but we speculate that the interaction between grazing and abiotic stress could be idiosyncratic and depend on (1) the relative abundances of grazing-intolerant vs. drought-intolerant species, and (2) the degree of protection against grazing provided by nurse canopies (Baraza et al., 2006; Gómez-Aparicio et al., 2008; Vanderberghe et al., 2009). Put simply, if grazing-intolerant species are abundant and nurses provide a high degree of protection against herbivory, then a high importance of grazing-mediated facilitation should be expected under any abiotic condition. Conversely, if plants are more sensitive to drought than to grazing, or the degree of grazing protection provided by the nurses is insufficient to shield them from higher herbivory pressure caused by the lack of alternative food sources under harsh conditions, then grazing-mediated protection should wane under extremely high levels of grazing pressure (*e.g.* Smit et al., 2007; Soliveres et al., 2011b).

It must be noted, however, that our results and conclusions regarding the grazing effect on plant–plant interactions could be strongly affected by the unequal range of grazing densities (dry sheep equivalents [DSE]) over the rainfall gradient and within/between our categorical grazing levels (Table 1). Arguably, we believe that separating grazing levels by these categorical classes instead of using the DSE *per se* is a reasonable procedure by three main reasons: (1) our classification was also strongly supported by the other indicators of grazing intensity used (land use, plant composition and distance to water points). All of them repeatedly demonstrated to be good indicators of ecologically important differences in grazing intensity affecting plant communities, (2) plant productivity is much higher under higher rainfall levels and, therefore, a much higher density of grazers can be sustained regarding the low productivity of water-limited environments (Holechek, 1988). Therefore, the effect of a relatively low grazing density under water-limited conditions is expected to have the same effect on plants than a much higher grazing density under wetter conditions (~21 vs. ~13 DSE in the high vs. low rainfall level, Table 1; Osem et al., 2002). Hence, we believe that our categorical classification reflects better than the raw DSE numbers the ecologically significant effect of the different grazing intensities on plants, and how this effect changes across different water availabilities, (3) to properly analyze the grazing × rainfall interaction using the DSE we would need to have the same ranges of DSE across rainfall levels, which did not happen. However, when we controlled for these different grazing densities introducing DSE as a covariate in the split-plot ANOVA, the results did not change substantially and therefore we can be confident about our results and conclusions.

Concluding remarks

To our knowledge, this is the first study to assess how both grazing and abiotic stress influence plant–plant interactions at the community-level in a terrestrial system. Though based solely on observational data, our work provides a first assessment of how the species-specific nature of some plant–plant interactions can affect the role they play at the community level along contrasting environmental conditions. We found strong species-specific components in all pairwise interactions, with positive interactions

prevailing for less drought-adapted species or for vertebrate-dispersed species when these were tolerant to drought. These species-specific attributes were particularly important for Tree-selective and non-selective interactions, which accounted for ~37% of all the interactions studied, with some interactions independent of environmental conditions. However, and irrespective of the important role of species-specific attributes in defining the outcome of pairwise interactions, our results show shifts between plant–plant interactions at the community level depending on the environmental conditions. This could result from either the influence of the environmental conditions on the outcome of some pairwise interactions (non-selective and Shrub-selective beneficiaries) or, more likely, from changes in the relative abundances of the different life strategies along the gradient. These two factors could define the number of facilitated species at each plot, and therefore determine the response of the whole community.

Our study highlights two important issues: (1) the greater importance of species-specific attributes, regarding abiotic conditions, in defining the outcome of a large fraction of the pairwise co-occurrences evaluated, and (2) a greater dependence of grazing-mediated facilitative interactions under low to moderate, than under high, rainfall levels. Our results also suggest that the effects of plant–plant interactions on plant species richness are dependent on the relative predominance of their particular dispersal mechanisms or life strategies.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ppees.2012.09.003>.

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