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Do changes in grazing pressure and the degree of shrub encroachment alter the effects of individual shrubs on understorey plant communities and soil function?

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Summary

1. Shrub canopies in semi-arid environments often produce positive effects on soil fertility, and on the richness and biomass of understorey plant communities. However, both positive and negative effects of shrub encroachment on plant and soil attributes have been reported at the landscape level. The contrasting results between patch- and landscape-level effects in shrublands could be caused by differences in the degree of shrub encroachment or grazing pressure, both of which are likely to reduce the ability of individual shrubs to ameliorate their understorey environment.

2. We examined how grazing and shrub encroachment (measured as landscape-level shrub cover) influence patch-level effects of shrubs on plant density, biomass and similarity in species composition between shrub understories and open areas, and on soil stability, nutrient cycling, and infiltration in two semi-arid Australian woodlands.

3. Individual shrubs had consistently positive effects on all plant and soil variables (average increase of 23% for all variables). These positive patch-level effects persisted with increasing shrub cover up to our maximum of 50% cover. Heavy grazing negatively affected most of the variables studied (average decline of 11%). It also altered, for some variables, how individual shrubs affected their subcanopy environment with increasing shrub cover. Thus, for species density, biomass and soil infiltration, the positive effect of individual shrubs with increasing shrub cover diminished under heavy grazing.

4. *Synthesis*: Our study refines predictions of the effects of woody encroachment on ecosystem structure and functioning by showing that heavy grazing, rather than differences in shrub cover, explains the contrasting effects on ecosystem structure and function between individual shrubs and those in dense aggregations. We also discuss how species-specific traits of the encroaching species, such as their height or its ability to fix N, might influence the relationship between their patch-level effects and their cover within the landscape.

Key-words: competition, ecosystem function, facilitation, herbivory, landscape functional analysis, open woodland, semi-arid, shrub encroachment

Introduction

Increases in the density or cover of woody plants in former grasslands (woody encroachment or thickening) is a phenomenon that affects the composition and diversity of plants and other organisms, and influences multiple ecosystem functions and services in drylands world-wide (reviewed in van Auken 2000; Eldridge *et al.* 2011). Although woody encroachment has frequently been linked to land degradation and desertification processes (MEA 2005), this view is at odds with the extensive body of evidence reporting generally positive effects of individual shrubs (patch-level effects) on their understorey plant

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communities and soil conditions in semi-arid environments (Tewskbury & Lloyd 2001; Maestre & Cortina 2005; Holzapfel *et al.* 2006; Soliveres *et al.* 2011a). However, reports of the effects within dense or extensive patches of shrubs (landscape-level effects) are varied, ranging from positive to negative or neutral (Eldridge *et al.* 2011). Many studies have reported reductions in soil nutrients and plant diversity, and increasing erosion following encroachment (Schlesinger *et al.* 1990; Parizek, Rostagno & Sottini 2002; Báez & Collins 2008). Other studies, however, have shown that woody encroachment can substantially enhance soil nutrient acquisition at the landscape level or increase plant, animal and soil biota diversity (Hughes *et al.* 2006; Throop & Archer 2008; Maestre *et al.* 2009).

The differences in effects of shrub encroachment identified at individual plant and landscape levels may be due to differences in (i) the degree of woody encroachment (i.e. the percentage of the landscape that is encroached; Breshears 2006; Riginos *et al.* 2009) or (ii) prevailing environmental conditions (e.g. differences in available moisture, soil texture or grazing intensity among studies; Knapp *et al.* 2008; Eldridge *et al.* 2013). The relative importance of how different environmental conditions or densities of woody plants at landscape scales alter patch-level effects of individual woody plants on their understorey remains, however, poorly understood.

The effects of individual plants have been shown to vary as plants aggregate to form dense landscape-level patches (Riginos *et al.* 2009). Increases in woody cover or density across entire landscapes affect the heterogeneity of soil nutrients and light availability, and likely reduce the capture of run-off by patches of woody plants (Breshears 2006; but see Turnbull *et al.* 2010). Thus, the tendency for woody plants to enhance fertility and productivity beneath their canopies (i.e. local, individual, or patch scale effect) may be compromised when plants occur within densely aggregated, homogeneous stands. The waning of the positive effects of individual shrubs on their subcanopy environment when they occur in dense stands could explain the net negative effect of woody encroachment on ecosystem structure and functioning apparent in studies of dense woody stands (Báez & Collins 2008; Riginos *et al.* 2009; but see Eldridge *et al.* 2013). Conversely, less dense stands are less likely to reduce heterogeneity in light and soil nutrient availability. Thus, the positive effect of individual shrubs is more likely to persist, potentially explaining the positive effects of encroachment reported in sparsely vegetated stands (e.g. Maestre *et al.* 2009).

Alternatively, differences between patch- and landscape-level effects of shrubs may be explained by differences in the prevailing environmental conditions among studies. It is known that the effects of woody plants at both patch and landscape scales depend, in part, on environmental and management conditions (Smit *et al.* 2007; Knapp *et al.* 2008; Dohn *et al.* 2013; Eldridge *et al.* 2013), particularly grazing pressure. First, grazing is a major driver of encroachment (Scholes & Archer 1997; van Auken 2000) and is the predominant land use in grasslands with a variable degree of woody encroachment (e.g. savannas, shrublands, open woodlands; House *et al.* 2003; Riginos & Grace 2008). Secondly, grazing dampens the positive effects of woody plants at the landscape level (Eldridge *et al.* 2013) and also alters the positive effects of woody plants at the patch level; the latter peaking at intermediate levels of grazing pressure (Smit *et al.* 2007; Soliveres *et al.* 2012). Moreover, woody plant density and cover influence patterns of herbivore usage. Although domestic livestock seem generally insensitive to changes in woody densities, native herbivores prefer low-density stands and this differential usage may influence the structure of their understorey plant community (Riginos & Grace 2008).

Although differences in the degree of shrub encroachment or grazing pressure could explain the contrasting effects of shrubs found at patch and landscape scales, very few studies have addressed how shrub effects vary at these two markedly different spatial scales (but see Riginos *et al.* 2009; Sitters, Edwards & Olde Venterink 2013). Moreover, to our knowledge, no studies have considered how grazing alters the relationship between the degree of shrub encroachment and the effects of individual shrubs on their understorey environment. We aimed to do this by assessing simultaneously the effects of increasing shrub cover and contrasted grazing pressure on how individual shrubs influence multiple attributes of the soil and understorey vegetation. We tested the following hypotheses: (i) individual shrubs enhance both soil function (infiltration, nutrient cycling and stability) and plant performance (biomass, species density) beneath their canopies while increasing grazing pressure reduces these functions; (ii) the positive effects of individual shrub canopies on their subcanopy environment wane when individual shrubs coalesce to form dense stands; and 3) given that grazing can shift interactions from competitive to facilitative (e.g. Smit *et al.* 2007; Soliveres *et al.* 2011b), and denser woody stands can restrict access to certain herbivores (Riginos & Grace 2008), we expected that increasing grazing pressure would dampen the rate of decline in patch-level effects with increasing shrub cover. Thus, we expected that the positive effects of individual shrubs on soil and plant attributes would peak under a higher shrub cover in heavily grazed than in lightly grazed environments.

Materials and methods

STUDY SITES

We studied two areas with similar climate and plant composition in western New South Wales (Australia): Buronga (34°06′S, 142°06′E) and Scotia (33°43′S, 143°02′E). Average annual rainfall at both areas is *c.* 230 mm, with average temperatures of 30 °C and 17 °C in summer and winter, respectively. Soils are classified as Hypercalcic Calcarosols (McDonald *et al.* 1990), with surface textures dominated by loams and clay loams at Buronga and sandy to sandy loams at Scotia. The vegetation at both areas is an open woodland dominated by medium-sized (*c.* 2 m tall) shrubs such as *Eremophila sturtii* (representing *c.* 20% of shrub cover), *Senna artemisioides* (*c.* 20% of shrub cover) and *Dodonea viscosa* (*c.* 60% of shrub cover). Plant community below the shrub strata averages 30% cover and is dominated by perennial grasses (e.g. *Austrostipa* spp., *Austrodanthonia* spp.), and ephemeral forbs such as *Sclerolaena* spp., *Maireana* spp., or *Sida* spp.

At each area, we selected plots with contrasting levels of grazing and shrub cover. We selected sites subjected to low levels of grazing within Mallee Cliffs National Park (Buronga) or within the Australian Wildlife Conservancy exclosure (Scotia) where the density of feral and native herbivores is controlled and no livestock grazing is permitted. This, together with their distance from permanent water points (>1·5 km in both cases), resulted in relatively low levels of grazing. We selected plots under a high grazing level among pastoral properties close to the low grazing sites. Apart from the presence of livestock (mostly sheep, but also cattle and goats), densities of native and feral herbivores are not controlled on these pastoral properties, and the distances to water points are shorter (<1 km). We converted the densities of different herbivores present within each site to a common scale (dry sheep equivalents [DSE]·ha^{-1}; see Eldridge *et al.* 2013 for further details), resulting in rates of grazing of 0·9 and 0·1 and 2·5 and 3·8 DSE ha^{-1} for low and high grazing levels in Buronga and Scotia, respectively.

SAMPLING DESIGN

Within each combination of Area (Buronga, Scotia) and Grazing (low, high), we selected 16 plots of 50 × 50 m (40 000 m^2 sampled for each Area × Grazing combination), representing a gradient in shrub cover and density from no shrubs to maximum values of about 50% canopy cover (equivalent to *c.* 5000 shrubs ha^{-1}). Plots within each grazing levels were separated >1 km from each other, while sites among grazing levels were separated by ca. 10 km at Scotia and 13 km at Buronga. We quantified shrubs cover and density using the line-intercept method in each plot within three 50 m long by 2 m wide transects per plot (established at the centre and the outside edges of the plot). To reduce confounding effects caused by the presence of woody species other than shrubs, we avoided trees when establishing the plots in order.

Within each of the 64 plots, we sampled eight 0·5 × 0·5 m quadrats placed entirely beneath the canopy of shrubs and the same number of quadrats in open areas, but only on plots where shrub cover was >5%. For plots with <5% shrub cover, we could not find sufficient independent shrubs, so we established only four quadrats for each microsite (shrubs and open). In all quadrats, we measured six attributes: (i) species density; that is, the number of different plant species found within the 0·5 × 0·5 m quadrat, (ii) plant biomass, using a semi-quantitative double sampling method (Friedel & Shaw 1987) that is strongly related to the dry-weight of clipped above-ground biomass. Estimated biomass yields were highly positively correlated with actual biomass (r = 0·86 and 0·94 for Buronga and Scotia, respectively; P < 0·001 in both cases, N = 113 per area), (iii) the similarity (%) in plant composition between shrub and open microsites (pooling all the quadrats per plot; see below) and (iv) three indices of soil condition (infiltration, surface stability and nutrient cycling; see below).

Collectively, the first three response variables give us a comprehensive and integrated view of the effects of shrubs on an important and widely studied component of plant diversity (species density), plant productivity (biomass) and the degree of niche heterogeneity provided by shrubs (similarity). For niche heterogeneity, we assumed that a greater difference between available niches beneath shrubs compared with open microsites would translate into less similarity in plant communities between shrubs and their interspaces (e.g. Tewskbury & Lloyd 2001). The three LFA soil indices were calculated by assessing 13 soil surface attributes including variables such as the state of the biological and physical soil crusts, the origin and degree of decomposition of litter, or plant cover, using a semi-quantitative, field-based procedure (Tongway 1995; Table S1, Supporting information). These three indices provide measures of soil function, specifically, the extent to which the soil accepts water (infiltration index), captures and cycles nutrients (nutrient-cycling index) and resists erosion (stability index). These indices have been shown to be strongly related to quantitative and widely used laboratory and field techniques used to measure soil infiltrability, fertility and erosion in different drylands world-wide, including the open woodlands studied here (Holm *et al.* 2002; Rezaei, Arzani & Tongway 200; Maestre & Puche 2009).

STATISTICAL ANALYSES

We calculated the patch-level effect of shrubs using the relative interaction index (RII; Armas, Ordiales & Pugnaire 2004). RII was calculated as:

$$\mathrm{RII} = \left(X_{\mathrm{sh}} - X_{\mathrm{op}}\right) / \left(X_{\mathrm{sh}} + X_{\mathrm{op}}\right) \qquad \text{eqn 1}$$

where X is the value of a given response variable measured beneath the shrub (X_{sh}) or in the open (X_{op}). These indices are limited to values between −1 and 1, with values above or below zero indicating a positive or negative effect of shrubs, respectively, at the patch level on the response variable. We calculated the RII values for five of the six response variables (plants: species density and biomass; soils: infiltration, nutrient-cycling and stability indices).

To calculate plant similarity, we used only those plots with shrub cover >5% because of the relatively low number of shrub and open quadrats sampled in the plots with shrub cover <5%. This limited our data set for this analysis to 14 sites for each of the four treatments (N = 56). To examine plant similarity between shrub and open communities, we analysed a matrix of species abundance data with the PERMANOVA+ package for PRIMER (Anderson, Gorley & Clarke 2008). We square-root transformed the data, then converted to a similarity matrix using the Bray–Curtis distance and analysed it using 9999 permutations with Type III error.

To analyse the relationships among grazing, shrub cover and shrub patch-level effects, we used two complementary statistical analyses performed sequentially. First, we analysed the raw data (not RII) of soil and plant variables using a mixed-models (split-plot) ANOVA, with two error terms. The first stratum of the analysis tested for potential differences between the two study sites, that is, area (Buronga, Scotia) and Grazing (low, high), and their interaction, and the second stratum examined microsite (shrub, open; nested within Area and Grazing) effects, and its two- and three-way interactions with Area and Grazing. ANOVA results revealed strong interactions among study site and the remaining factors (Table 1), so we evaluated the relationship between patch-level effects and the cover of shrubs within the landscape separately for Buronga and Scotia in a second procedure. To do this, we performed linear regressions between the effects evaluated at the patch level, measured with the RII and similarity values, as the response variables, and shrub cover as the predictor. We performed these regressions separately for each grazing level (low vs. high grazing) and compared their slopes using Student's t-tests to assess the influence of grazing in the relationship between the effects of shrubs at the patch level and their cover within the landscape. Diagnostic tests revealed that our data did not require transformation to achieve the assumptions of the analyses. We ran the analyses using Minitab statistical software (Minitab, Inc. 2010). The data from this study is deposited in the Dryad repository: http://dx.doi.org/10.5061/dryad.gg3c9 (Soliveres & Eldridge 2013).

Table 1. ANOVA results for the mixed-models analysis of Area, Grazing, Microsite and their interactions

Source	Stability		Infiltration		Nutrient-cycling		Similarity		Species density		Biomass		Summary of the response found
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	
Area	8·11	ns	4·21	*	2·81	ns	1·22	ns	0·37	ns	0·42	ns	
Grazing	22·81	***	1·09	ns	7·62	**	0·61	ns	6·23	*	4·38	*	LG > HG
Area × Grazing	9·84	**	0·01	ns	2·77	ns	0·82	ns	0·25	ns	4·63	*	Greater effects of grazing at Scotia
Microsite	90·75	***	244·49	***	173·02	***			21·38	***	25·04	***	Shrub > Open
Microsite × Grazing	3·73	ns	3·27	ns	1·23	ns			4·34	ns	1·77	ns	
Microsite × Area	0·11	ns	11·21	**	6·20	*			0·28	*	5·47	*	Greater effects of shrubs at Scotia
Microsite × Area × Grazing	3·44	ns	0·01	ns	0·02	ns			2·30	ns	9·39	**	

NS, non-significant; LG, lightly grazed; HG, heavily grazed.
Degrees of freedom for all response variables (except Similarity) = 1, 52. $^{***}P < 0{\cdot}001$, $^{**}P < 0{\cdot}01$, $^{*}P < 0{\cdot}05$.

Results

We found significant interactions between Area (study site) and the other factors (grazing and patch-type) in the mixed-models ANOVA for most of the response variables (Table 1). Increasing grazing pressure reduced four of our six response variables (soil stability [−6%] and nutrient cycling [−7%], and plant species density [−16%] and biomass [−22%]; ANOVA: $F > 4{\cdot}38$ and $P < 0{\cdot}041$ for all of them). These negative effects were area dependent for biomass and stability, with a stronger negative effect of grazing at Scotia (average reduction of *c*. 16% in the variables studied) than at Buronga (average reduction of *c*. 5% in the variables studied). We also found a consistent positive effect of shrubs on all the response variables tested (biomass [+32%], species density [+25%], infiltration [+26%], nutrient-cycling [+26%] and stability [+8%]; ANOVA: $F > 25{\cdot}1$, $P < 0{\cdot}001$). These results were also supported by the positive RII values generally found (Figs 1 and 2). The positive effects of shrubs were stronger at Scotia (31% of average increase in all the studied variables) than at Buronga (17% of average increase).

Contrary to expectation, the positive effects of shrubs on soil and plant variables at the patch level did not decline with increasing shrub cover, but either remained constant or increased with increasing shrub cover (Figs 1 and 2). Grazing altered this relationship for species density at Buronga and Scotia, and for the infiltration index at Scotia. In these cases, grazing dampened the positive patch-level effect with increasing shrub cover. Similar, but insignificant, trends were found for biomass at both areas (Fig. 2) and for stability at Buronga (Fig. 1). Again, the strength of the grazing effect differed between Scotia and Buronga, with generally weaker effects at Buronga than at Scotia.

Discussion

Our results question the commonly held belief that any positive effects of individual shrubs on ecosystem structure and function are always reversed at high shrub densities. In contrast to the previous studies of different encroaching species from different study areas (Báez & Collins 2008; Riginos *et al.* 2009), we showed that the effects of shrubs on plants and soils at the patch level remained positive for stands up to 50% cover. We illustrated for the first time how elevated levels of grazing alter the relationship between patch-level effects of shrubs and their cover within the landscape. Overall, our results can provide valuable insights into the ecological consequences of woody encroachment by demonstrating how these effects might depend on the specific features of the encroacher species or intensity of the prevailing land use, that is, livestock grazing.

Despite some inconsistencies in our results between Buronga and Scotia, we found generally positive effects of shrubs on all the response variables at the patch level, consistent with previous literature (Facelli & Temby 2002; Soliveres *et al.* 2011a; Howard, Eldridge & Soliveres 2012) However, contrary to expectation, the positive patch-level effects of shrubs did not decrease with increasing shrub cover. Rather, the influence of individual shrubs on plant composition (similarity) and species density increased with increasing shrub cover at both areas, and for soil infiltration at Scotia, and were constant for the remaining variables. Our findings are in contrast to other studies (Báez & Collins 2008; Riginos *et al.* 2009), which showed a reduction in the positive effects of woody plants with increasing shrub or tree density. However, our results accord with those of Hoffman (1996) and Salazar *et al.* (2012), who recorded greater recruitment, survival and density of different woody species with increasing tree density in a neotropical Brazilian savanna.

Both positive and negative relationships between patch-level effects and the degree of woody encroachment have been detected across broad woody density gradients similar to those found in our study areas, and under contrasting rainfall regimes (*c*. 200 mm to >500 mm; Báez & Collins 2008; Riginos *et al.* 2009; Salazar *et al.* 2012; this study). Consequently, the contrasting effects that we

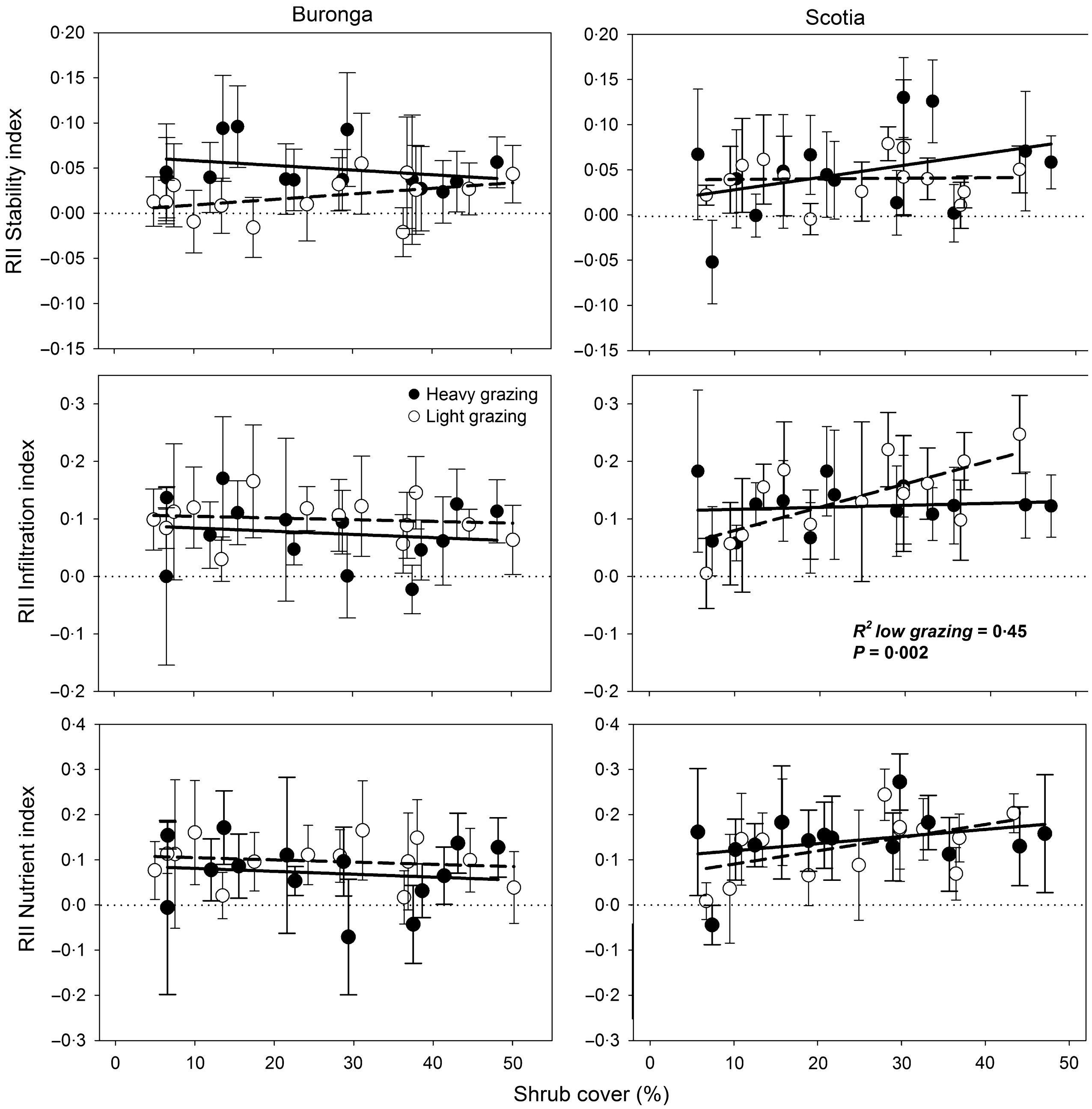

Fig. 1. Mean (± 95% confidence intervals [95%CI]; $N = 8$; 4 in plots with <10% shrub cover) values of RII (Relative Interaction Index) for the stability, infiltration and nutrient-cycling indices for both sites across the gradient in shrub cover. Values above zero for RII indicate positive patch-level effects of shrubs regarding open areas, while negative values of RII indicate negative shrub patch-level effects. Those with the 95%CI not overlapping with the zero-line can be considered statistically different from zero. The broken line represents the linear relationship for the lightly grazed sites and the solid line for heavily grazed sites. Regression results (R^2, *P*-values) are shown only for those relationships that were statistically significant.

observed in our study at different spatial scales cannot be attributed to differences in rainfall or site productivity. Rather, we speculate that they might depend on which variables are measured and on the functional traits of the encroaching plants such as their ability to fix nitrogen or their height (Breshears 2006; Sitters, Edwards & Olde Venterink 2013). The types of response variables measured could account for contrasting results, with generally positive effects of dense shrub or tree stands on the recruitment and density of other woody species (Hoffman 1996; Salazar *et al.* 2012), but less clear effects of woody encroachment on the abundance and performance of herbaceous species. While we detected positive relationships between shrub cover and plant diversity at Buronga and Scotia (Eldridge *et al.* 2013; this study), studies conducted in the Chihuahuan Desert (Báez & Collins 2008) and the African savanna (Riginos *et al.* 2009) have detected negative effects on these same attributes.

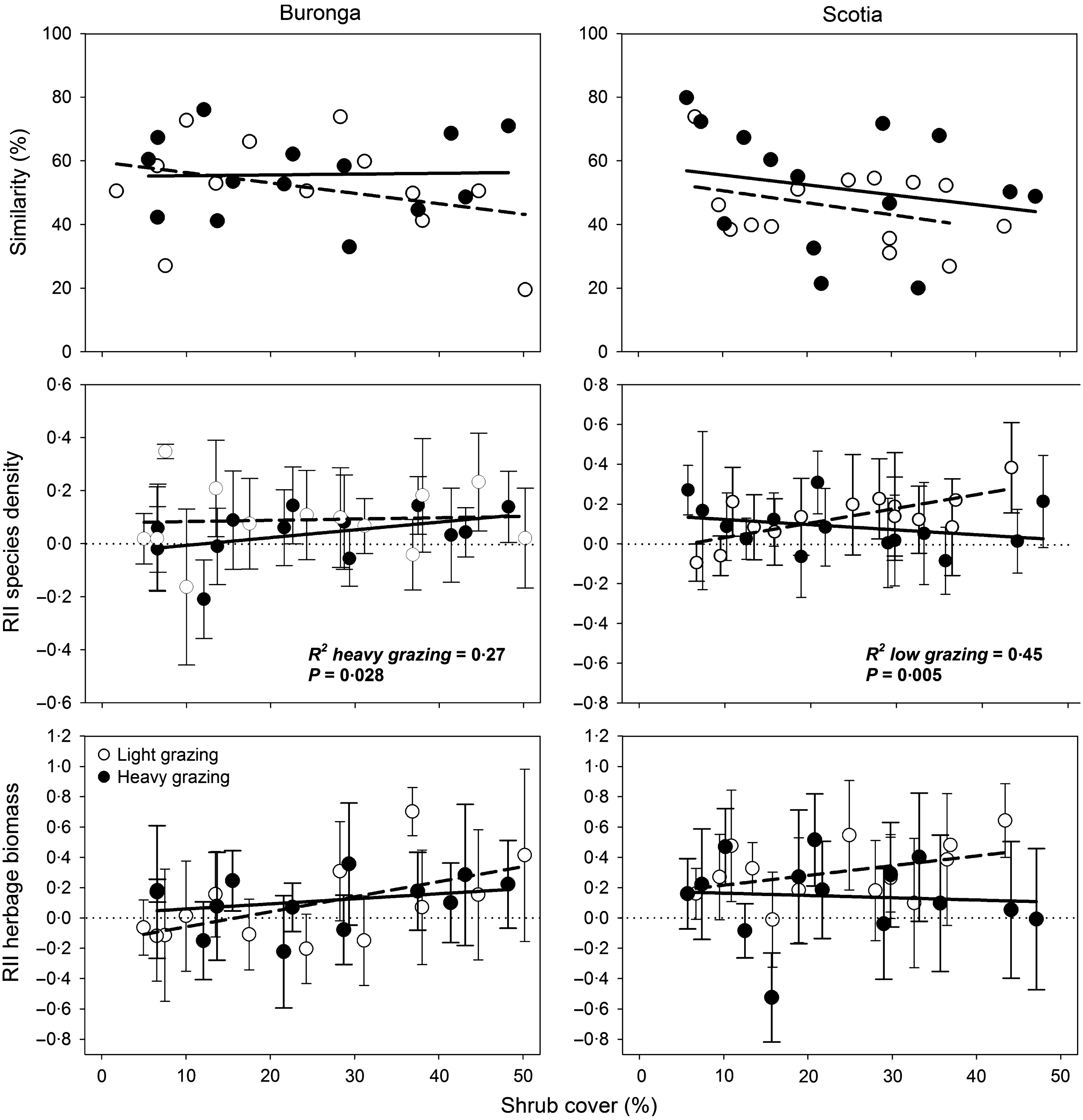

Fig. 2. Mean values of similarity (%) and mean (± 95%CI) values of RII (Relative Interaction Index) for understory species density and herbaceous biomass across a gradient in shrub cover. Values above and below zero for RII indicate positive and negative patch-level effects of shrubs regarding open areas, respectively. Those with the 95%CI not overlapping with the zero-line can be considered statistically different from zero. Broken and solid lines represent the linear relationships between response variables and shrub cover for lightly and heavily grazed sites, respectively. Regression results (R^2, *P*-values) are shown only for those relationships that were statistically significant.

Differences among studies could also be related to differences in the ability of target shrub to fix nitrogen. For example, N-fixing woody plants, when occurring at high densities, significantly reduce P availability limiting the productivity and forage quality of herbaceous plants growing beneath their canopies (Riginos *et al.* 2009; Sitters, Edwards & Olde Venterink 2013). These reductions on P availability, however, are less consistent when no N-fixing species are encroaching, with both positive and negative effects reported in the literature (e.g. Báez & Collins 2008; Maestre *et al.* 2009). Finally, the height of the encroaching woody plants could alter the relationship between woody cover and the effect of individual plants at the patch level. Increasing woody density hinders the positive effect of individual shrubs on their understorey by homogenizing levels of light and soil nutrients and reducing, therefore, the ability of individual shrubs to regulate microclimatic conditions beneath their canopies (reviewed in Breshears

2006). Hence, positive patch-level effects of woody species should wane under even relatively small increases in woody densities (from 5% onward; Riginos *et al.* 2009). This seems to hold true for trees or tall shrubs as, even at low densities or cover, their taller canopies and large root systems would shade and redistribute water even in the interspaces (Riginos *et al.* 2009). However, this may not be relevant for shrubs, which have shorter and narrower canopies, and would need to occur at higher densities to create the same effect (Breshears 2006). Indeed, Turnbull *et al.* (2010) showed that heterogeneity in water and nutrient re-distribution within the landscape increased, rather than decreased, with increasing shrub cover up to 25%. Our results suggest that the effects of increasing heterogeneity in light, soil moisture and nutrient availability within the landscape may well extend to cover levels as high as 50% when shrubs are encroaching. The latter view is supported, for example, by the lack of decline in the percentage of similarity between shrub-open plant communities across the gradient in shrub cover (Fig. 2). At shrub cover levels >50%, which are among the maximum encroachment levels that can be reached in semi-arid eastern Australia (Daly & Hodgkinson 1996), heterogeneity in light availability and water redistribution between shrub canopies and the open should hypothetically decline linearly (Breshears 2006). Therefore, a gradual reduction of positive patch-level effects of shrubs on soil and plant variables might be expected for shrub cover higher than 50%.

Grazing did not influence the patch-level effects of shrubs in any cases (non-significant Microsite × Grazing effect; Table 1). This is supported by the lack of a relationship between the positive patch-level effects of shrubs and increasing grazing intensity in the study area (Howard, Eldridge & Soliveres 2012). However, grazing significantly influenced the positive relationship between the patch-level effects of shrubs and shrub cover in some of the variables studied (species density at both study sites, infiltration at Scotia), and a similar trend was found for three other response variables (biomass at both study sites; soil stability at Buronga). If a reduction in the patch-level effects of shrubs is independent of grazing intensity, then how might we explain how, for some variables, the positive relationship between this effect and increasing shrub cover wanes with greater levels of grazing.

Grazing is known to reduce the pool of species available to colonize a given area, affecting the biomass and composition of plant communities (Lunt *et al.* 2007). Moreover, trampling by herbivores increases soil erosion and alters the redistribution of nutrients and water in the soil (Castellano & Valone 2007; Allington & Valone 2010). Indeed, grazing in our study reduced four out of the six soil and plant variables studied (Table 1). The sum of these well-known effects may likely have reduced the number of species that can be facilitated by shrubs, and the amount of soil and organic matter available to be captured in run-off by the shrubs. This would likely reduce the tendency of shrubs to enhance plant and soil heterogeneity at the landscape level and could be the reason for the waning of the positive relationship between patch-level effects and increasing shrub encroachment.

Conclusion

This is the first study, to our knowledge, to address the interactions among grazing, the degree of shrub encroachment, and the patch-level effects of shrubs on multiple plant and soil attributes. Our study clearly shows that higher levels of encroachment are not always associated with declines in ecosystem functioning, and that the positive effects of individual shrubs on plant and soil attributes can persist at levels of shrub encroachment representative of the maximum registered for the eastern Australian region (*c.* 50%; Daly & Hodgkinson 1996). Further studies are necessary to reveal why some plant-level effects change under higher levels of shrub cover. The reasons may relate to differences in the functional traits of the encroaching species, (Breshears 2006) or their ability to fix N (Riginos *et al.* 2009; Sitters, Edwards & Olde Venterink 2013). We also demonstrated that, compared with lightly grazed sites, heavy grazing dampens the effect that isolated shrubs have on their understorey environment across gradients of increasing shrub cover. Our work highlights the need to include the degree of encroachment and grazing pressure when studying effects of shrubs on their understorey in order to fully understand the implications of woody encroachment on ecosystem structure and functioning.

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Data accessibility

The data associated with this article are publicly accessible in the Dryad data repository, http://dx.doi.org/10.5061/dryad.gg3c9 (Soliveres & Eldridge 2014).

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Supporting Information

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

Table S1. Description of the 13 soils surface condition attributes recorded at each site and the indices in which each one is used.