Grazing dampens the positive effects of shrub encroachment on ecosystem functions in a semi-arid woodland

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Summary

1. The encroachment of woody plants into grasslands, open woodlands and savannah has been widely reported over the past few decades. Overgrazing is a probable cause of shrub encroachment and could be a stronger driver of declining ecosystem structure and functioning in shrublands than encroachment *per se*. We examined the relative effects of changes in shrub cover and grazing rate on ecosystem functions at sandy and loamy sites in eastern Australia varying in shrub cover and grazing. Our aim was to test the notion that the negative effects on ecosystem functioning commonly attributed to encroachment are more likely due to grazing than to increase in shrub cover *per se*.

2. Structural equation modelling indicated a generally strong positive effect of increasing shrub cover, and a generally negative, or slight effect of grazing on multiple measures of ecosystem function related to plant productivity, water infiltration, nutrient cycling and surface stability.

3. On loamy soils, grazing generally dampened the positive effects of increasing shrub cover on most response variables. On sandy soils, however, although there were generally stronger effects of grazing, most attributes did not change in response to increasing shrub cover.

4. *Synthesis and applications.* Our results indicate that, contrary to the prevailing opinion, increasing shrub cover was generally associated with increases (or no change) in functional and structural measures indicative of healthy systems. The dampening of the positive effects of shrub cover caused by grazing was site (soil texture) specific, reinforcing the notion that the effects of increasing shrub cover and their interaction with grazing are context dependent. Our study provides the basis for improved understanding and management of shrublands for a number of competing goals and suggests that managing grazing rates is a better strategy than focusing on shrub removal. Using low levels of grazing is likely to maximize the benefits from shrublands, such as the maintenance of biodiversity, water infiltration and C sequestration, while maintaining a productive herbaceous community.

Key-words: biodiversity, carbon, habitat management, infiltration, plant communities, shrubland, soil, structural equation modelling, woody thickening

Introduction

Shrub encroachment is a global phenomenon characterized by an increase in the density, cover and biomass of generally indigenous, woody or shrubby plants, particularly in arid and semi-arid grasslands (van Auken 2000; Archer, Boutton & Hibbard 2001). Encroachment is thought to result from complex interactions among grazing, burning, increased concentrations of atmospheric carbon dioxide and competition between woody seedlings and grasses (van Auken 2000; Archer, Boutton & Hibbard 2001; Knapp *et al.* 2008). Some symptoms often attributed to the shrub encroachment phenomenon include declines in

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grass cover and biomass, reduced pastoral productivity, altered habitat value, spatial distribution of soil nutrients, and levels of soil function such as respiration, decomposition and infiltration and soil water redistribution (Archer, Boutton & Hibbard 2001; Bhark & Small 2003; Schlesinger, Tartowski & Schmidt 2006). All of these changes further reinforce the persistence of shrublands at the expense of grasslands and are thought to lead to ecosystem degradation and desertification (Schlesinger, Tartowski & Schmidt 2006).

Although the causes of encroachment are relatively well known, its effects on ecosystem processes deserve more scrutiny in a greater number of ecosystems. The contemporary view of encroachment as a process leading to degradation has recently been shown not to be universal, with reports of positive or neutral effects of shrub encroachment in most of the studied variables in more comprehensive studies including the diversity and composition of different taxa (plants, ants, birds, biological soil crusts or soil microorganisms), different ecosystem types and different ecosystem attributes and functions (Maestre *et al.* 2009; Eldridge *et al.* 2011). Supporting this view of the positive effects of shrub encroachment in semi-arid environments is the extensive literature reporting facilitative effects of shrubs on their understorey vegetation and on soil fertility in many different semi-arid ecosystems world-wide (Holzapfel & Mahall 1999; Soliveres *et al.* 2011). An important consideration therefore is how to reconcile the conundrum of the well-known positive effects of shrubs at patch scale with the oft-reported pejorative view of shrub encroachment at landscape or ecosystem scales.

The overgrazing hypothesis, often invoked as an explanation of shrub encroachment, is based on the premise that sustained heavy grazing, and therefore forage (mostly grass) removal, shifts the balance of resources in favour of the germination and establishment of woody plants at the expense of grasses, resulting in feedback processes on reduced fire intensity and frequency (Archer, Boutton & Hibbard 2001). Even small increases in grazing can increase the emergence of woody seedlings (Brown & Archer 1989) by reducing the capacity of grasses to compete for soil moisture (Walker, Moore & Robertson 1972). Continuous grazing is likely to alter soil carbon and nitrogen pools through compositional changes in the vegetation community and reduced biomass (Archer, Boutton & Hibbard 2001). Irrespective of its effect on shrub encroachment, overgrazing is a well-known cause of land degradation in semi-arid environments. Among its effects, changes in the composition and reduction in cover of vegetation and biological soil crusts (hereafter biocrusts) and indirect effects (mediated by its influence on plants and biocrusts) and direct (e.g. trampling) degradation of the soil structure and its nutrient composition, are commonly reported world-wide (Fuhlendorf & Smeins 1999). Consequently, apart from its role in the initiation of shrub encroachment, grazing could explain the contrasting effects of shrubs at patch and landscape scales because the most strongly shrub-encroached sites might also be the most overgrazed. Despite the large number of studies focussing on shrub encroachment, the effects of encroachment and grazing on ecosystem functions have not been studied as partially independent drivers.

Here we test the relative effects of changes in shrub cover and grazing rate on ecosystem functions in an encroached woodland in eastern Australia. Woody plants are believed responsible for reducing ecosystem functions and exacerbating degradation processes in eastern Australia, Africa (Snyman 2012) and the western United States (Torell *et al.* 2005). Consequently, legislation and policy in eastern Australia promote removal of woody plants if they are thought to behave 'invasively' (Native Vegetation Act 2003). In the western United States, woody encroachment has been identified as a significant causal factor for non-achievement of land health in the Bureau of Land Management's Land Health Reporting Standards Program (S. Karl, personal communication). Here we argue that the impacts resulting from encroachment *per se* and the grazing levels that promote such shrub encroachment might often be confounded, and it is generally difficult to disentangle the two. Thus, whereas land managers typically see the presence of shrubs as leading to deleterious ecosystem outcomes, others attribute declines in function to grazing rather than shrubs.

Our aim was to use a novel study design that would allow us to separate potential effects of both shrub cover and grazing on (i) herbage biomass and biocrust cover, (ii) three indicators of landscape function (soil infiltration, nutrient cycling and surface stability; Tongway 1995) and (iii) two direct measures of ecosystem function (infiltrability, an empirical measure of infiltration capacity, and soil labile carbon). Our analyses tease apart the direct effects of shrubs and grazing on these response variables. Our ability to separate the effects of grazing from those of shrubs would improve our understanding and management of shrublands where grazing and biodiversity conservation are often competing environmental goals.

Materials and methods

SITE DESCRIPTION

Our research was conducted at two sites; near Buronga (34°06′S, 142°06′E) and in the Scotia region (33°43′S, 143°02′E), both in south-western New South Wales (NSW), Australia (see Fig. S1 in Supporting Information). The climate at both sites is characterized by low and variable rainfall (220–280 mm; mean annual rainfall), high evapotranspiration (~1500 mm year^{-1}), hot dry summers (daily mean temperature: 30 °C) and cool winters (daily mean: $\leq$ 17 °C). The landscape at both sites is predominantly Quaternary sandy and calcareous sediments on slightly undulating plains to 1% slope, often with low aligned west–east trending dunes. The soils are classified as Hypercalcic Calcarosols (McDonald *et al.* 1990) and ranged from fine-textured loams and clay loams (Buronga) to sands and sandy loams (Scotia). The

soils supported a rich community of cyanobacteria, lichens, mosses and liverworts (biocrusts; Eldridge *et al.* 2010).

The vegetation community comprised an open woodland; grasslands with interspersed trees (~15% cover) with varying degrees of shrub encroachment. Our study sites were typical of encroached woodlands in semi-arid eastern Australia and elsewhere where open patches between trees have become encroached or infilled by shrubs of a range of species (*Eremophila sturtii, Senna artemesioides* and *Dodonaea viscosa*). Often, open woodland has been converted into a shrubland with variable cover of perennial grasses *Austrostipa* spp., *Austrodanthonia* spp.), and ephemeral forbs such as *Sclerolaena* spp. Shrub encroachment has occurred episodically, generally following periods of heavy overgrazing (e.g. following the droughts of the early 1900s, or periods of high rainfall (La Niña) such as 1955 and 1973/74, which stimulated germination of large cohorts of seedlings. Shrubs tend therefore to be dominated by individuals of a single size (age) class.

SELECTION OF SITES

We employed a novel sampling strategy to treat grazing and degree of shrub cover as largely independent influences on ecosystem function. Sites without trees were selected to avoid confounding effects of the presence of other woody species. At Buronga, a set of sites was established at Mallee Cliffs National Park. Mallee Cliffs National Park has been managed as a pastoral grazing lease for about 150 years, but was designated a National Park in 1977. After its gazettal as a National Park, domestic stock were removed from the Park resulting in an immediate reduction in grazing pressure. Since 1990, the progressive decommissioning of ground tanks that were previously used to water stock has occurred in accordance with park management strategy to reduce the densities of kangaroos *(Macropus* spp.) and feral goats *Capra hircus*. The lack of free water helps to self-regulate grazing pressure, although access to water outside the Park means that routine mustering and trapping are required to keep goat densities at low levels. To reduce rabbit numbers to low levels, ripping of warrens and poisoning have been used intensively. As a consequence, the Park experiences very low levels of grazing. An additional set of sites was selected from adjacent pastoral properties, and represented relatively high rates of stocking and extensive development of surface waters that are typically imposed in these areas. We used the same approach for site selection in the Scotia area. A set of very lightly grazed sites was selected from within the Australian Wildlife Conservancy (AWC) exclosure. The area was only open to grazing in the middle of the 20th Century. Feral herbivores and carnivores were removed from the site in 2000, and a small number of locally extinct omnivorous animals were introduced. Another 16 sites from adjacent pastoral properties supported high, but variable populations of grazing animals. Overall, these sites provided us with a range of independent levels of both shrub encroachment and grazing intensity. Within these four groups differing in grazing history, we selected 16 sites per group representing a gradient in shrub cover and density from no shrubs to maximum values of about 50% canopy cover and 5000 shrubs ha^{-1}, which are within the range of values reported for shrub-encroached sites. The 64 study sites were separated by distances of more than 1 km, and we therefore consider them to be statistically independent. All 64 sites were selected within a single land unit (flats and depressions) to avoid confounding influence of landform on-site attributes.

SITE-LEVEL MEASUREMENTS

A 50 × 50 m plot was sampled at each of the 64 sites. Within each plot, we placed three 50-m transects, one located centrally, and the others located 20 m on either side of the central transect. Along each transect, we measured (i) the interception of shrub canopies (by species) to assess canopy cover and (ii) the density of shrubs within a 2 m belt on one side of the transect. At all sites, we established a number of 0·5 × 0·5 m quadrats (depending on the relative cover of shrubs and open interspaces) in which an experienced observer (JV) estimated total above-ground herbage biomass (excluding shrubs) using a portfolio of photographic standards of known weight. The number of quadrats assessed increased with increases in shrub cover, but there was always a minimum of five (maximum 15) paired shrub and interspace quadrats per site. At the completion of measurements, we estimated the biomass within a further five quadrats at each site, clipped all above-ground material and dried it at 60° C for 72 h to determine the relationship between estimated and actual biomass. Separate regression equations were derived for Buronga and Scotia and their predictive powers were relatively strong (R^2 = 0·74–0·89; $P < 0·001$, $N = 113$).

ASSESSMENT OF GRAZING INTENSITY

We used two measures of grazing intensity; stocking rate (dry sheep equivalents; DSE – the number of animals expressed in terms of a non-lactating ewe) was calculated using data on herbivore densities, and distance to permanent surface water measured using ArcGIS Spot Imagery (see Appendix S1, Supporting Information).

To more closely approximate the probable grazing intensity experienced on a plot, we combined paddock-level stocking rate information (DSE) within-paddock proximity to a water source, and their interaction. To create the interaction term, distance to water source was first reflected to create a variable that increased with closeness to water source. Secondly, we put DSE and closeness to water on a common scale of 0–1 by dividing each value by the maximum value. Thirdly, we cross-multiplied these two variables to create an interaction term. This creates a number that is maximized at the highest stocking density and the closest distance to water, and is minimized if either of these components is minimal. Separate Student's *t*-tests indicated that there were significant differences in grazing rate, expressed as DSE ha^{-1} and the interaction between DSE and Distance to water, for both Buronga ($P < 0·01$) and Scotia ($P < 0·001$), but no differences in the Distance to water at either site ($P > 0·15$; see Table S1, Supporting Information).

ASSESSING MEASURES OF LANDSCAPE FUNCTION

We used a mixture of indices including low-resolution information and more empirical, quantitative information that incorporates a narrow set of high resolution information. Our justification for doing this was threefold; (i) it was not possible to measure many empirical attributes at high resolution, (ii) qualitative indices provide a broader view of functional changes outside our short list of key quantitative data and (iii) qualitative indices have been used extensively in the literature, are relatively easy to collect and are moderately well correlated with quantitative data (e.g. Maestre & Puche 2009).

We made detailed measurements of the morphology of the soil surface from under a number of shrub hummocks and their paired interspaces using simple, quadrat-based methods (Tongway 1995). Within each 0·25-m² quadrat, we assessed 13 attributes; surface roughness, crust resistance, crust brokenness, crust stability, biocrust 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 (Appendix S2; Table S2, Supporting Information). These values were used to derive three indices related to soil functions in terms of water flow (infiltration index), nutrients (nutrient-cycling index) and surface stability (stability index). These three indices (infiltration, nutrient cycling and stability) have been shown to be strongly related to a range of laboratory assessed ecosystem functions (Maestre & Puche 2009; see Appendix S2, Supporting Information).

Within three of the paired quadrats described above, we collected an undisturbed soil core (0·84 cm³, 5 cm depth) for assessment of bulk density and soil labile carbon. The three samples were pooled for each site resulting in one site-level sample each for shrub hummocks and interspaces. Labile carbon which represents the smallest, most bioavailable soil carbon pool, is a sensitive indicator of management-induced changes in soil quality (Wander & Bidart 2000). It was determined using a simplified laboratory method (Weil *et al.* 2003). Infiltrability, our empirical measure of infiltration, was assessed in the laboratory using the syringe method (Mills *et al.* 2006). Infiltrability is an empirically based measure of the infiltration capacity of the soil, which is related to the tendency of the soil to break down, disperse and form a surface seal (Mills *et al.* 2006). The infiltration index, however, relates more to the tendency of the soil to accept water, and will depend on other soil attributes such as porosity. It is derived from eight soil surface features measured within small quadrats on the soil surface (Appendix S2, Supporting Information) and has been validated in numerous studies globally (e.g. Razaei, Gilkes & Andrews 2006; Maestre & Puche 2009). Data were area adjusted to account for the relative proportion of shrubs and interspaces at each site.

STATISTICAL ANALYSES

We used a two-stage approach to examine the effects of shrubs on ecosystem processes in relation to grazing. Stage one used structural equation modelling (SEM; Appendix S3, Supporting Information) to estimate the overall sign and magnitude of the effects of shrub cover and grazing intensity on various ecosystem functions. Although SEM is often applied to understand system structure or to test complex hypotheses, it can also be used as a flexible linear model with some beneficial capabilities. Our application mimicked multiple regression models with three important distinctions: (i) Parameters were estimated using maximum likelihood rather than least squares techniques. (ii) Our models employed composite variables, enabling us to additively pool the effects of multiple such indicators into a single grazing effect, so that its magnitude can be compared with the effect of shrub cover (Grace & Bollen 2008). Composite variables are analogous to multiple regression models within the larger model. We created three continuous variables describing grazing intensity. In practice, we found that we could not include all three grazing variables without inducing a multicollinearity problem. However, this did not present a major problem because preliminary multiple

regressions indicated that variance explained was nearly maximized in the majority of response variables if closeness to water and DSE × closeness to water were used as predictors. (iii) Our models used a multi-group modelling approach, considering the two sites, Buronga and Scotia, as groups (Appendix S3, Supporting Information). Path coefficients were assigned to pathways linking grazing, shrub cover and each of the response variables. These coefficients are directly mathematically analogous to partial correlation coefficients or regression weights. In their standardized form, they are bounded between 0 and 1, and can be interpreted, as in a regression context, as the strength of the effect one variable exerts on another.

In the second stage of our analysis, we investigated this grazing × shrub density interaction using a comparison of the slopes of the shrub density function models between high and low grazing intensity clusters at each site. We used linear regression to estimate the effect of increasing shrub cover on measures of landscape function based on lightly and heavily grazed sites separately, and Student's *t*-tests were used to explore potential differences in the slopes of the regression models between these two grazing classes.

To assess the overall effects of shrub cover and grazing, we tested shrub effects on average function by examining whether the individual slopes of the response variable by shrub cover relationships differed from zero using one-sample Student's *t*-tests. The mean slope would be expected to be positive if shrub effects were mostly positive. Six tests were performed; two considering all the seven response variables across both sites for lightly ($n = 14$) and heavily ($n = 14$) grazed sites, and four separate tests considering all response variables for each of the four sites by grazing combinations, i.e. Buronga lightly grazed, Buronga heavily grazed, Scotia lightly grazed and Scotia heavily grazed. Standardized slopes were used.

Results

INDICES OF SOIL FUNCTION

Our SEM models explained a substantial amount of variation (r^2 to 59%) in the three derived indices of soil function (Fig. 1). The large positive path coefficients indicate the generally strong positive effects of shrub cover on infiltrability and the infiltration and nutrient indices, at both locations, and the soil stability index at one location. There was, however, a non-trivial negative effect of shrub cover on the stability index (path coefficient = −0·35) at Scotia (Fig. 1). Overall, grazing had either a very little (<0·15) or negative (nutrients: −0·51, stability: −0·56) effect on our functional measures at both locations, but reasonable positive effects on infiltrability (0·28 and 0·44). Both grazing and shrub cover were associated with reduced plant biomass at Scotia (Fig. 2).

EFFECTS OF GRAZING ON SOIL AND PLANT RESPONSE TO INCREASING SHRUB COVER

Under low levels of grazing at Buronga, we detected significant increases in all response variables, except herbage biomass ($P = 0·76$), with increasing shrub cover
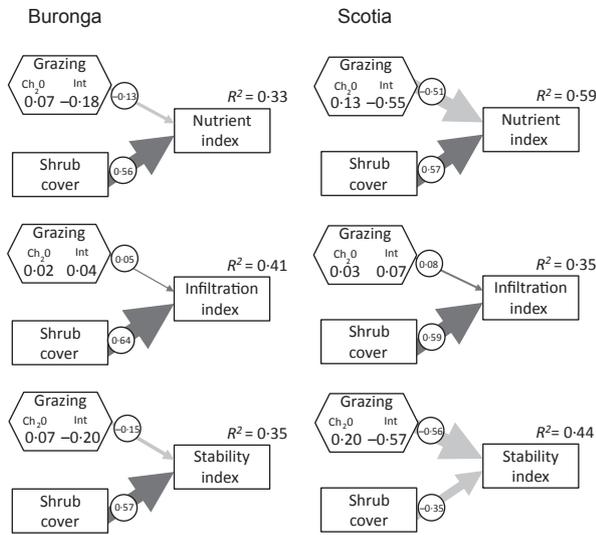
Fig. 1. Structural equation models showing relationships between grazing and shrub cover, and the three derived measures of soil function. The grazing effect is represented by the pooled effects of two grazing indicators: closeness to water and the interaction between distance to water and grazing intensity (dry sheep equivalents). CH_2O represents the path coefficient for closeness to water. Int represents the path coefficient for the interaction between distance to water and dry sheep equivalents. The coefficient of variation (R^2) is the net effect of all direct and indirect effects of grazing and shrub cover on each derived measure of soil function. The width of the pathways corresponds to the relative strength of the patch coefficients. Positive pathways are a darker colour (green) and negative pathways lighter (blue).

(Fig. 3). Heavy grazing at Buronga, however, dampened the positive effects of shrub cover on most response variables (Fig. 3). At Scotia, trends were less clearly defined (Fig. 4). Although some attributes increased with increasing shrub cover under low levels of grazing (nutrient index, $R^2 = 0.30$, $P = 0.016$; infiltration index, $R^2 = 0.26$, $P = 0.025$; infiltrability, $R^2 = 0.24$, $P = 0.031$), most showed no clear trend. There was a greater number of significant effects under grazing, with significant increases (nutrient index: $R^2 = 0.44$, $P = 0.003$; infiltration index: $R^2 = 0.28$, $P = 0.021$; infiltrability: $R^2 = 0.20$, $P = 0.048$) and two declines (herbage biomass: $R^2 = 0.49$, $P = 0.002$; stability index: $R^2 = 0.19$, $P = 0.055$; Fig. 4). However, unlike Buronga, there were no significant differences in the slope of the relationship between the response variables and shrub cover between heavily and lightly grazed sites at Scotia (Fig. 4).

Across all sites, the overall effect of shrubs on function was positive for lightly grazed ($t = 3.17$, $P = 0.007$), but not significantly different to zero for heavily grazed ($t = 1.44$, $P = 0.173$; Fig. 5). Separate analyses for Buronga and Scotia revealed three trends; (i) a generally strong positive shrub effect Buronga, but a much weaker positive effect at Scotia, (ii) a threefold greater positive effect of shrubs at Buronga under lightly than heavily grazed conditions and (iii) non-significant effects at Scotia (Fig. 5). Indeed, even if the average effect of shrubs on ecosystem
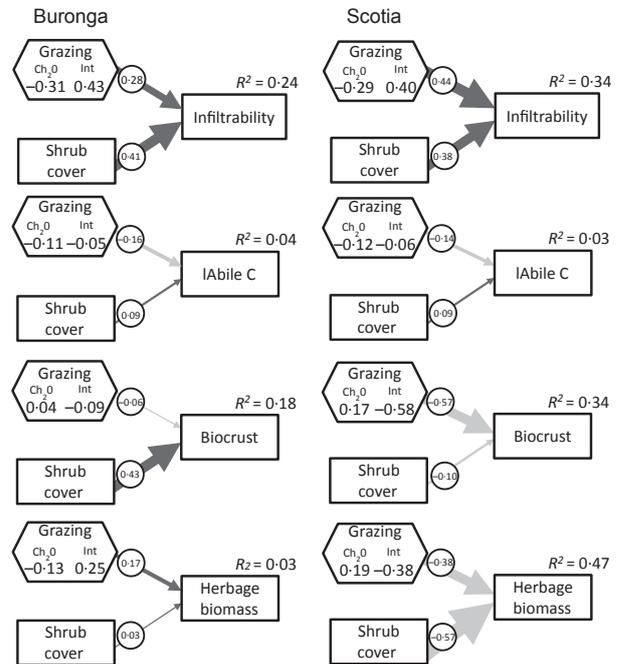
Fig. 2. Structural equation models for plant biomass, labile soil carbon and infiltrability. The grazing effect is represented by the pooled effects of two grazing indicators: closeness to water and the interaction between distance to water and grazing intensity (dry sheep equivalents). CH_2O represents the path coefficient for closeness to water. Int represents the path coefficient for the interaction between distance to water and dry sheep equivalents. The coefficient of variation (R^2) is the net effect of all direct and indirect effects of grazing and shrub cover on each derived measure of soil function. The width of the pathways corresponds to the relative strength of the patch coefficients. Positive pathways are a darker colour (green) and negative pathways lighter (blue).

measures was not significantly different from zero, the weight of evidence still suggests that the effects of increasing shrubs on ecosystem variables are generally not negative.

Discussion

Over the past quarter century, a substantial body of research has tended to focus on the negative effects of shrub encroachment on ecosystem properties and processes as broad as suppression of understorey plant cover (Archer, Boutton & Hibbard 2001; Huenneke *et al.* 2002), reduced soil nutrient pools (Sparrow *et al.* 2003), altered nutrient distributions (Schlesinger, Tartowski & Schmidt 2006) and greater wind and water erosion (Abrahams, Parsons & Wainwright 1994). In direct contrast, we detected a positive effect of increasing shrub cover on average structure and function, and substantial increases in specific measures of structure and function indicative of healthy landscapes, with increasing shrub cover. This was particularly true under low grazing pressure although it varied between the two sites. Our SEM models of ecosystem behaviour indicated that increasing shrub cover had positive effects on most ecosystem
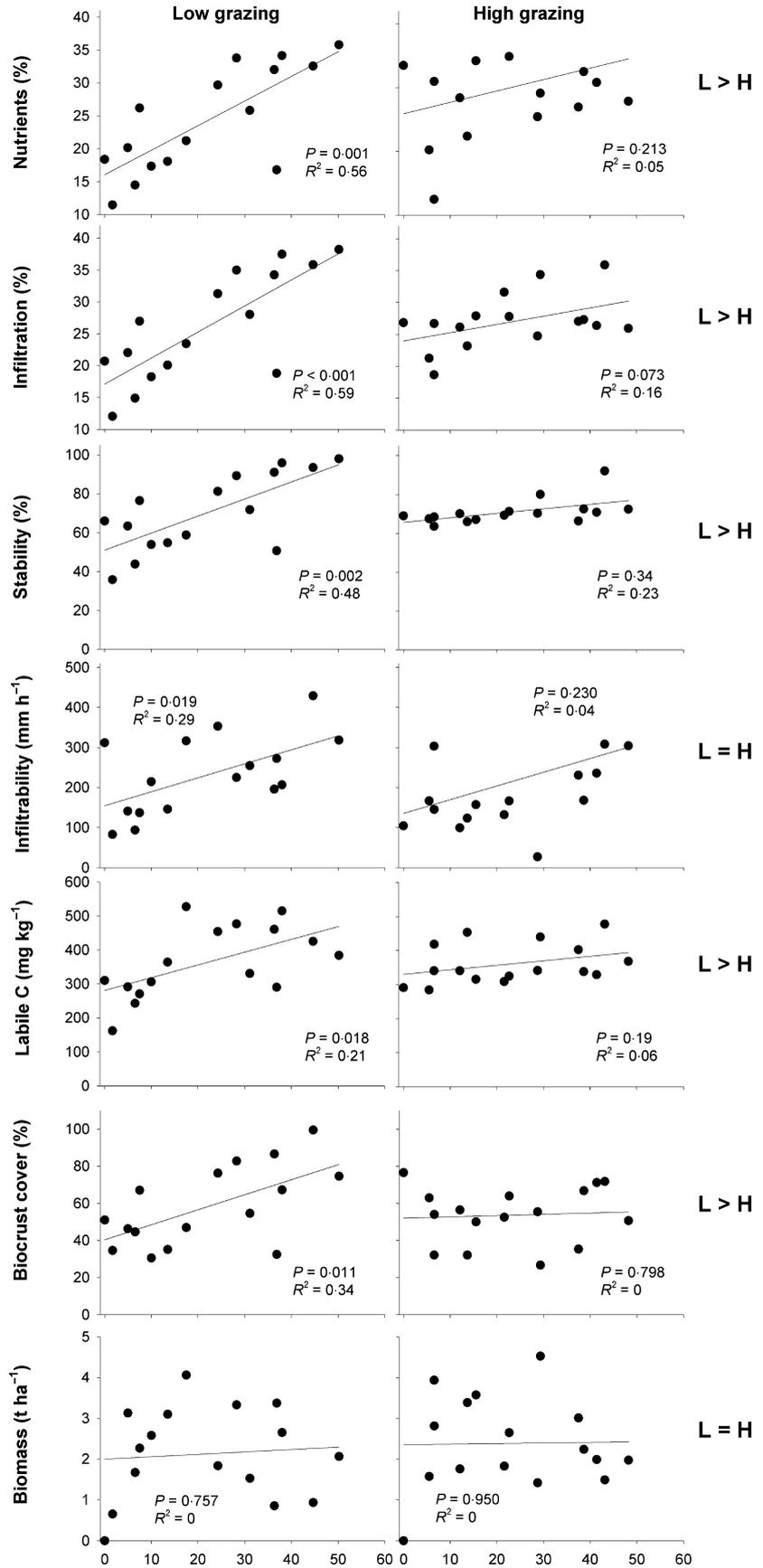
Fig. 3. Relationship among shrub cover (%) and a range of response variables for lightly and heavily grazed sites at Buronga. L > H indicates a significantly greater slope for the lightly (L) than heavily (H) grazed sites.
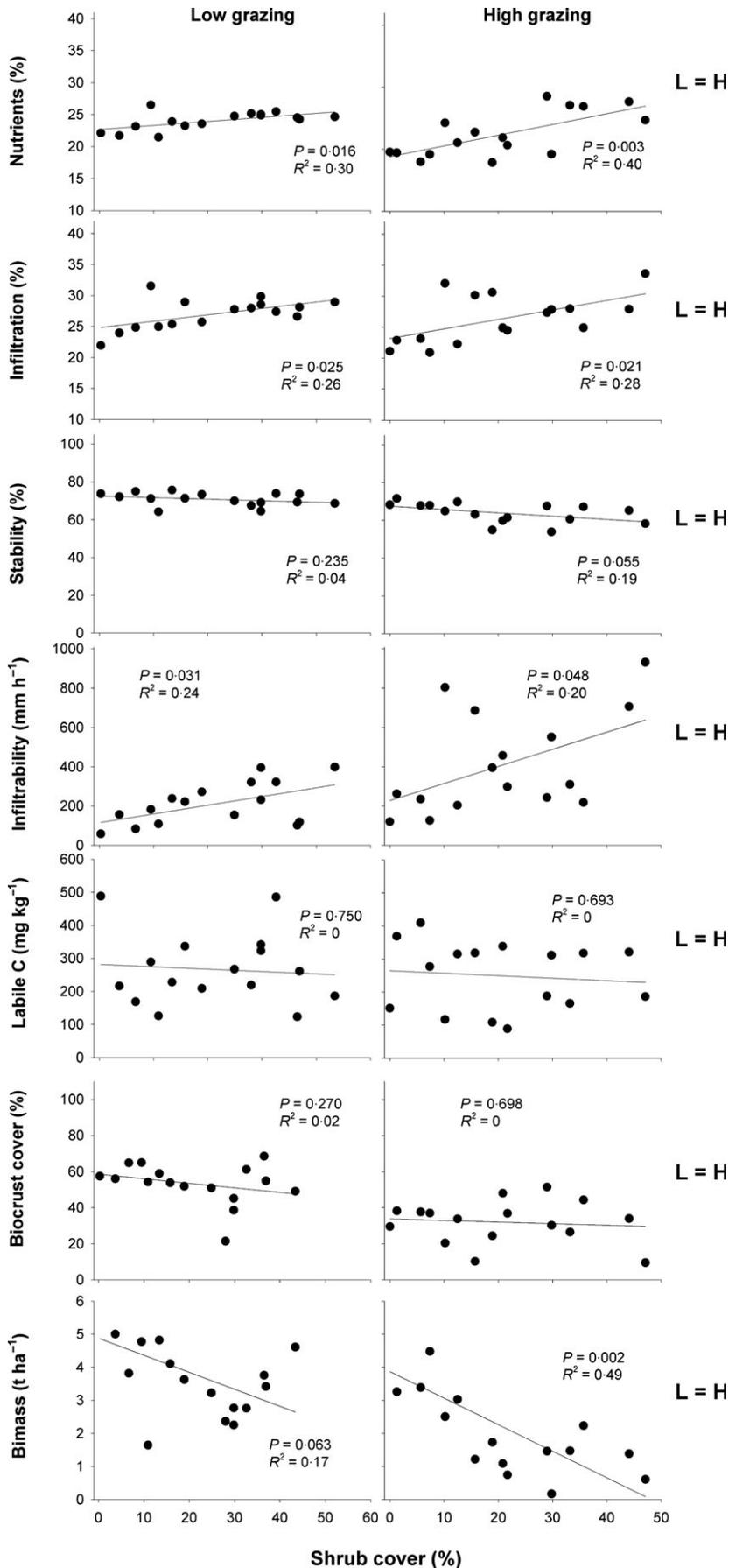
Fig. 4. Relationship among shrub cover (%) and a range of response variables for lightly and heavily grazed sites at Scotia. L > H indicates a significantly greater slope for the lightly (L) than heavily (H) grazed.
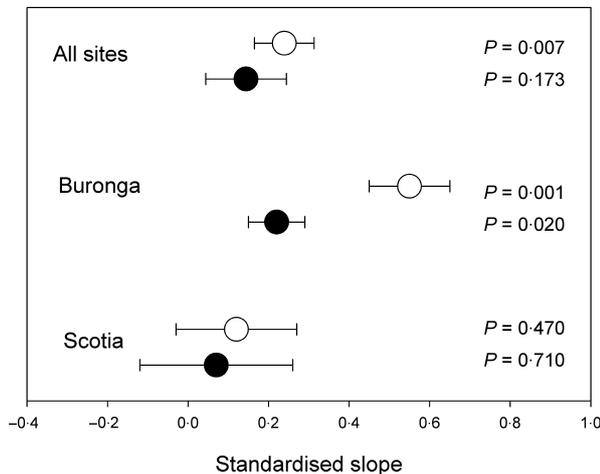
Fig. 5. Mean (±SE) of the standardized slopes derived from the seven response variables for lightly grazed (white) and heavily grazed (black) sites, and a comparison of the two sites by two levels of grazing.

properties (infiltration, stability and nutrient indices, infiltrability) whereas grazing had either negative or benign effects (Figs 1 and 2). Although the commonly held view is that encroachment suppresses herbaceous biomass (e.g. Knapp *et al.* 2008), we showed that this effect is not universal, with biomass declining at Scotia (path coefficient = −0·57), but remaining unchanged at Buronga (Fig. 2). We do not believe that this is due to rainfall, given the similar rainfall regime at both sites, but rather, to the many factors, and their inter-relationships that drive plant–plant interactions in drylands (see Callaway 2007). The results are consistent with recent research that questions the widely held view that encroachment is indicative of degraded systems (Maestre *et al.* 2009; Eldridge *et al.* 2011), providing strong evidence that woody plants, including shrubs, have positive, or neutral effects on the structure of dryland ecosystems and their biota. Our shrub species (*E. sturtii, S. artemesioides, D. viscosa*) are all medium-sized plants (up to 2 m tall) typical of woodland communities under varying levels of encroachment. Our conclusions, therefore, are applicable to extensive areas of Australia where these shrubland communities predominate.

GRAZING DAMPENS POSITIVE EFFECTS AND AMPLIFIES NEGATIVE EFFECTS OF SHRUB ENCROACHMENT

Higher levels of grazing in our study dampened the generally positive effects of shrubs on ecosystem functions, though the effect was site-specific, and mostly restricted to the Buronga sites (Fig. 5). We see two explanations for the differential grazing effect between sites. First, Scotia has had a shorter history of grazing (~70 years) than Buronga (>150 years), mainly because the Scotia sites were settled later and large areas were not watered before

the middle of the 20th Century. Secondly, the surface soils at the Scotia sites were sandier than those at Buronga, and the different effects could have been due to differences in soil hydraulic behaviour and water holding capacity, which are known to vary markedly with soil texture (Noy-Meir 1973). Also, physical and biological soil crusts are less evident on sandy soils, therefore the effect of trampling by herbivores would be lower. In most cases, the effect of grazing was to negate the generally increasing effect on most functional response variables, so that under grazing, there was little or no effect of increasing shrub cover (Fig. 3). A reduction in the positive effects of shrubs under high grazing levels could be due to a breakdown in the facilitatory effect of shrubs, or may relate to a change from many smaller, to fewer larger, shrubs, which would permit a greater access by herbivores (Smit *et al.* 2007).

The greatest grazing-induced changes in function were evident in our three soil functional indices, which, although highly variable at high grazing levels, showed values under low levels of grazing. The pronounced dampening effects of grazing on the positive shrub cover functional relationships suggests that the disparity in widely diverging reports of shrub and shrubland effects on ecosystem properties and processes could be explained, in part, by grazing.

Published accounts of the relative effects of grazing and increasing woody plant density are few, though there is some support for our finding of a moderating effect of grazing on function. Studies by Throop & Archer (2008), and results from an area closer to the studied areas (S. Daryanto, unpublished data) showed that heavily grazed sites had less soil organic carbon (SOC) under woody plant canopies than lightly and heavily grazed sites, supporting the notion that the strong positive effect of woody plant encroachment on SOC accumulation was partially offset by grazing. Enhanced soil infiltration, stability and fertility under woody canopies compared with open sites has been widely documented (the so-called 'islands of fertility' phenomenon), and the plant effect is known to extend far beyond the edge of woody canopies (Wu & Archer 1985; Maestre *et al.* 2009). Interception of rainfall by relatively dense canopies of *E. sturtii* and *D. viscosa* would be expected to reduce soil surface sealing beneath shrub canopies. Furthermore, sub-canopy litter is known to moderate raindrop energy, reducing the tendency of the soil to form a physical crust (Geedes & Dunkerley 1999) and enhancing water penetration and organic matter content, which is also enhanced by the retention of run-off by shrub canopies. This higher soil fertility, together with the shading produced by shrub canopies are often invoked as the main mechanisms driving positive interactions among shrubs and their understorey species (Pugnaire, Haase & Puigdefábregas 1996). Improved microclimatic conditions may allow the recruitment of species that are less adapted to stressful conditions (Prider & Facelli 2004), and this effect is known to extend to biocrusts, where more water-demanding species

grow prominently underneath plant canopies, but not in the open (Maestre 2003). The presence of these more productive species, together with the tendency for some plants to be protected from grazing and trampling under the canopies of dense shrubs, also explains the higher biocrust cover found under higher shrub covers.

A diminution of the well-known positive effects provided by shrubs under grazing might be due to several mechanisms. First, the scattering of litter into the interspaces by livestock, and exacerbated by wind or water can reduce the concentration of organic matter beneath shrub canopies (Li *et al.* 2009). Secondly, some of the species in our study (e.g. *D. viscosa*) are readily browsed by feral goats (Harrington & Johns 1990). Browsing reduces their capacity to intercept rainfall (Mills *et al.* 2009), and may affect their ability to retain litter (Bochet, Rubio & Poesen 1998). The differential effect of grazing on function could operate by altering the physical environment of the shrubs, by changing incoming levels of solar radiation (Yager & Smeins 1999) or by changing litter cover. Higher amounts of litter on the soil surface are expected to reduce the variability in soil temperature, which may in turn decrease soil organic matter decomposition rates and incorporation of carbon into deeper soil layers. Grazing therefore has substantial impacts on soil surfaces, altering their distribution, and ultimately affecting the infiltration of water in the interspaces beyond the shrub canopies. Grazing did, however, have a generally positive effect on infiltrability, which we attribute to the disruption to the biocrust, resulting in increases in infiltration (Eldridge *et al.* 2010). Thirdly, extremely high grazing levels lead to a weakening of positive plant–plant interactions (e.g. Smit *et al.* 2007), reducing the positive effect of shrubs on plants. Lastly, disturbance by some herbivores such as rabbits tend to be greater beneath shrub canopies; thus, the higher abundance of these grazers could overwhelm the positive effect of shrubs on biocrusts.

THE MANAGEMENT AND POLICY OF SHRUB ENCROACHMENT

In Australia's semi-arid woodlands, debate over the effects of shrub encroachment on ecosystems is highly polarized. Those whose livelihoods depend on livestock grazing argue that shrub encroachment threatens the viability of their pastoral enterprises, given the heavy reliance of grass production. Indeed, sections of the agri-pastoral lobby argue that encroachment is synonymous with land degradation, despite the conclusions of recent global review (Eldridge *et al.* 2011) and reports to government (Eldridge, Wilson & Oliver 2003), which have failed to identify any clear and unambiguous links between encroaching vegetation and degradation. Despite the existence of contrasting evidence, implicit in current NSW (Australia) government legislation (Native Vegetation Act 2003) is the premise that the removal or reduction in encroaching woody plants (*syn.* 'Invasive Native Scrub';

INS) is warranted to 'improve or maintain' environmental outcomes, a test under the NSW Native Vegetation Act (2003) http://www.legislation.nsw.gov.au. The listing of 'feral native plant species' as 'invasive' under NSW Legislation allows landholders to remove these plants under permit. The process for inclusion of species on the INS register has largely been based on their putative adverse effects on pastoral production. A similar situation exists in the western Cape of South Africa where the native shrub bankrupt bush *Seriphium plumosum*, has been listed as a Proclaimed Encroacher Plant (Regulation 16 of the Conservation of Agricultural Resources Act 43) because it displaces grasses and reduces the grassland grazing capacity (Wepener, Kellner & Jordaan 2008; Snyman 2012). In the United States, ranchers may apply for cost sharing from federal, state and local agencies to conduct brush removal on rangelands, with the stated purpose of enhancement of forage or water resources (Torell *et al.* 2005). An example is Texas SB1083 (Title 7 of the Agricultural Code), which establishes a fund to provide up to 70% cost sharing for brush removal, explicitly to promote groundwater recharge. Likewise, in New Mexico, substantial federal funding is being provided by the Bureau of Land Management to aerially apply herbicides to extensive areas of former grassland invaded by creosote bush (Restore New Mexico Program; http://www.blm.gov/nm/st/en/prog/restore_new_mexico.html).

An important issue identified in recent shrub encroachment models (Maestre *et al.* 2009; Eldridge *et al.* 2011) is the value that human society places on the ecosystem services provided by woody plants. Shrub encroachment can provide numerous conservation and societal benefits such as increased water recharge, habitat for organisms, carbon storage (Barger *et al.* 2011) and even autogenic regeneration at almost no cost to the community (Geddes *et al.* 2011). The extent of these benefits, however, has only recently been explored. For example, analyses of encroachment scenarios globally indicate that it is consistently associated with increases in the above- and below-ground carbon (Barger *et al.* 2011; Eldridge *et al.* 2011), and removal of shrubs may have little effect on recharge (Bazan *et al.* 2012). In Australia, the recent introduction of a price on carbon has provided renewed financial incentives for landholders to be involved in long-term carbon sequestration programmes such as the Carbon Farming Initiative (http://www.climatechange.gov.au/cfi) which allows farmers and land managers to earn carbon credits by storing carbon or reducing greenhouse gas emissions on the land. This new carbon price is expected to encourage the development of ecologically based, market-driven carbon plantings (Crossman, Bryan & Summers 2011). Because encroached communities are generally mixed-species stands, they are likely to offer additional biodiversity co-benefits that are not provided by monocultural plantings (Watson *et al.* 2000), and therefore may represent a superior C-storage strategy. It may be timely therefore to investigate alternatives to a predominantly grazing-centric

view of encroachment, and to possibly embrace other land uses, some of which may be more profitable than pastoralism under new carbon economies.

Our research has shown that shrublands are associated with increases in measures of ecosystem function that are indicative of healthy dryland ecosystems, though sometimes neutral responses, and our results provide a strong ecological platform on which to reassess the value of shrublands. Ultimately, however, the prevailing land use is likely to depend on social systems and human decisions, and how society reconciles competing valuations of ecosystem services related to soil carbon, grazing and wildlife habitat. Developing useful models that couple natural systems with social systems is a key to informing this process.

Acknowledgements

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Supporting Information

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

Appendix S1. Assessment of grazing rates and grazing conversions.

Appendix S2. Assessment of measures of landscape function and soil surface condition.

Appendix S3. Details of the Structural Equation Modelling.

Figure S1. Location of the study sites.

Table S1. Mean values of the three measures of grazing intensity.

Table S2. Soil surface features measured during the soil surface condition assessment.