Biotic communities cannot mitigate the negative effects of grazing on multiple ecosystem functions and services in an arid shrubland

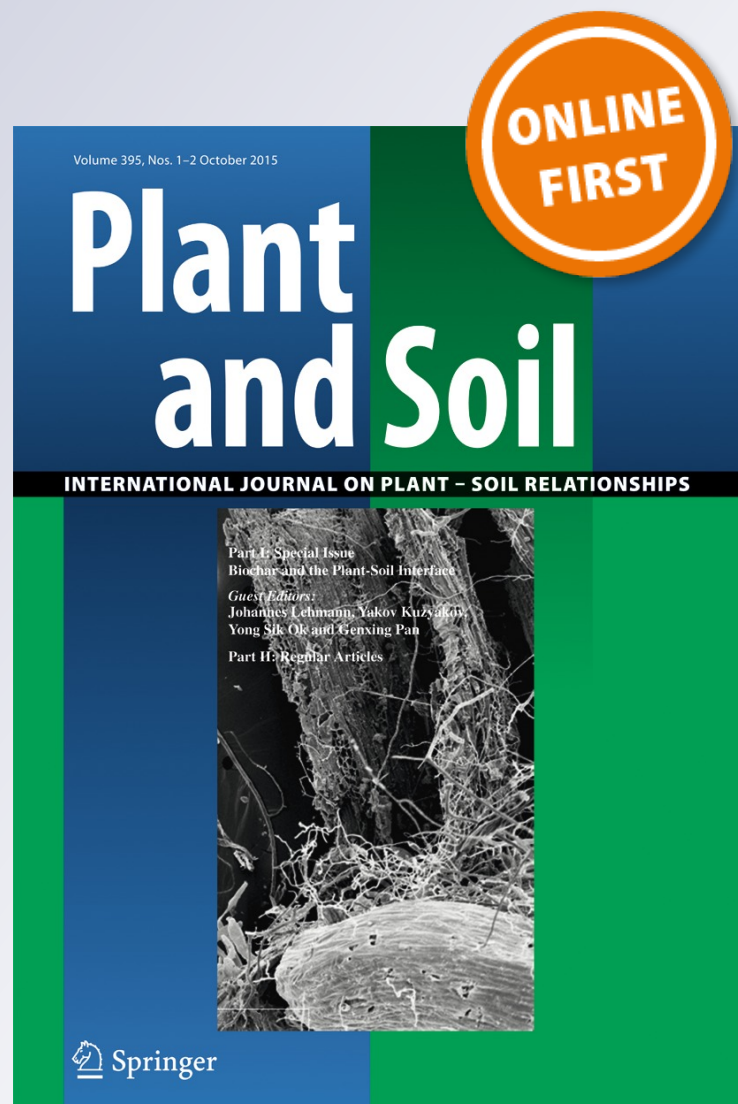## Jing Zhang, David J. Eldridge & Manuel Delgado-Baquerizo

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Biotic communities cannot mitigate the negative effects of grazing on multiple ecosystem functions and services in an arid shrubland

Jing Zhang · David J. Eldridge · Manuel Delgado-Baquerizo

Abstract

Aims Dryland biotic communities (plants and biocrusts) are known to maintain multiple functions (multifunctionality) and services (multiservices) that decline with overgrazing by domestic livestock. Here, we evaluate the role of biotic communities in controlling the responses of multiple functions and services to grazing in an arid shrubland.

Methods We compared nine ecosystem functions and services associated with carbon and nitrogen cycling, and water infiltration at grazed and ungrazed sites in eastern Australia. We hypothesized that overgrazing would reduce individual functions, but that effects on multifunctionality and multiservices would be tempered by shrubs, vascular plants and biocrusts.

Results Grazing reduced biocrust cover, soil phosphatase, β-glucosidase and potential mineralization, but not plant richness, soil respiration, infiltration measures nor dissolved inorganic N. In our models, grazing had the largest and most negative effects on multifunctionality and multiservices. Structural equation modelling showed that grazing reduced biocrust cover. Unlike the univariate analyses, grazing reduced plant cover and suppressed any positive effect of these biotic communities on multifunctionality and multiservices.

Conclusions Our results suggest that any positive buffering by plant richness, shrubs and plant cover on multifunctions or multiservices will not offset the negative effects of grazing. Strategies to improve functionality of arid shrublands should focus on the management of total grazing pressure.

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Introduction

Human activities such as overgrazing have had substantial negative impacts on key ecosystem functions and services such as the provision of clean air and water, nutrient cycling, carbon storage, climate regulation, and cultural and recreational values (Cardinale et al. 2012). which are all critical for human well-being. These

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ecosystem functions and services are difficult to differentiate, and have often been lumped under a common theme. Here we consider those ecosystem functions and services that contribute to overall ecosystem performance in response to long-term grazing by domestic livestock. By grazing we mean the many effects of large herbivores on ecosystem processes, including the direct removal of plant biomass via herbivory. Functions such as enzyme activity and mineralization rates are related to broad processes of organic matter decomposition, which in turn contribute to ecosystem services such as nutrient cycling, carbon storage and plant production. Similarly, shading by plant canopies provides a direct ecosystem service to organisms that use these shaded environments for foraging during high daytime temperatures (e.g. Margarey 1999). Shaded environments also provide a service to understorey plants through facilitatory mechanisms (Howard et al. 2012).

Grazing by domestic livestock is expected to increase, and meat production likely to double by the middle of this century (World Bank 2008) in order to support the demand for food and fibre by a continuously growing population. To date, two closely related gaps in the current literature limit our understanding of the patterns and mechanisms that control grazing effects on ecosystem functions and services. First, we lack an integrative approach that considers how grazing affects multiple ecosystem functions (multifunctionality; Maestre et al. 2012) and services (multiservices; Gamfeldt et al. 2013). Previous studies have highlighted how grazing reduces specific functions (e.g. soil respiration; Eldridge et al. 2010; Thomas 2012; Daryanto et al. 2013a, b; Eldridge et al. 2015, 2016) or services (e.g. soil stability; Eldridge et al. 2013). but the influence of grazing on multifunctions and multiservices is poorly known. Second, the effects of grazing on multifunctions and multiservices may be driven by multiple and complex interactions with biotic and abiotic components, but we have only a limited understanding of the exact mechanisms whereby it effects multifunctionality and multiservices.

Over the past decade the multifunctionality approach has gained widespread acceptance in ecology and soil science (Maestre et al. 2012; Bradford et al. 2014; Wagg et al. 2014; Lundholm 2015) because it provides a straightforward and logical measure of the capacity of ecosystems to sustain multiple functions simultaneously (Byrnes et al. 2014). This approach can be extended to services, so that individual attributes providing an ecosystem service can be combined into a multiservice index. Together, both indices are extremely useful for reducing complex processes into more tangible concepts, and they provide more information than can be obtained from single functions alone.

The effects of grazing on ecosystem functions and services are likely to be important in less productive, resource-poor ecosystems such as drylands (arid, semi-arid and dry-subhumid ecosystems; Eldridge et al. 2013), which are highly susceptible to desertification and global environmental change. Drylands occupy about 40 % of Earth's surface and support about 40 % of its human population (Maestre et al. 2012). Vascular plant cover is typically sparse and spatially variable, and plants are generally replaced by a variable cover of biocrusts; assemblages of lichens, mosses and cyanobacteria that occur within the interspaces between perennial plants such as grasses and shrubs (Eldridge and Tozer 1997). Thus, any assessment of the effects of grazing on multiple ecosystem functions and services in drylands needs to consider the multiple biotic communities inhabiting these ecosystems. Different microsites such as perennial plant patches, bare interspaces, and interspaces occupied by biocrusts have been shown to provide different levels of multifunctionality (e.g. Bowker et al. 2013). For example, dense patches of litter associated with perennial shrubs are associated with higher concentrations of organic matter and soil nutrients (Soliveres et al. 2014). and greater infiltration and soil moisture (Colloff et al. 2010; Eldridge et al. 2015), leading to patches of enhanced microbial, invertebrate and vertebrate activity (Schlesinger et al. 1990). Similarly, biocrusts have been shown to be associated with enhanced functions such as soil stabilisation, water infiltration, nitrogen mineralization and organic matter-rich soils compared with areas of bare soil (Eldridge et al. 2010; Bowker et al. 2013; Delgado-Baquerizo et al. 2015). Because of their unique legacy effects (e.g. concentrations of organic matter), different microsites would be expected to respond differently to grazing.

The negative effects of grazing on multifunctionality and multiservices may be mediated by multiple biotic and abiotic attributes of a system. For example, grazing is known to reduce the richness of plants and of biocrusts (Eldridge et al. 2013; Kutt et al. 2012). two of the major drivers of multifunctionality in drylands (Maestre et al. 2012). Apart from diversity, grazing also affects plant community structure by reducing the cover, spatial arrangement and biomass of vegetation and

biocrusts (Muscha and Hild 2006; Daryanto et al. 2013a, b, c; Eldridge et al. 2016). thus compromising their ability to maintain functions and services (Maestre et al. 2011; Bowker et al. 2013; Delgado-Baquerizo et al. 2013; Soliveres et al. 2014). A question that remains unanswered is, to what extent can the biotic components mitigate the negative effects of grazing on multiple ecosystems functions and services? Our definition of grazing includes the many effects of large herbivores on ecosystem processes, including the direct removal of plant biomass via herbivory. Although the direct effects of grazing have been widely reported in the literature, relatively little is known about how different biotic and abiotic components mediate the effects of grazing on ecosystems (indirect effects). An analysis that considers the total system improves our understanding of how grazing and microsites influence multiple ecosystem functions and services. Understanding the biological feedbacks among grazing, plant richness and multiple functions and services is fundamentally important if we are to understand the potential effects of overgrazing on land degradation, which currently threatens about 250 million people across 20 % of drylands worldwide.

Here we used the chenopod shrublands in arid eastern Australia as a model to evaluate the effects of long-term grazing by domestic livestock and shrubs on multiple ecosystem functions (activity of β-glucosidase and phosphatase, soil respiration, dissolved inorganic nitrogen and potential net nitrogen mineralization rates) and services (shading, steady-state infiltration, sorptivity and Infiltration index; *sensu* Maestre et al. 2012). These functions and services are associated with carbon and nitrogen cycling, and water infiltration. To clarify the direct and indirect effects of grazing on multifunctionality and multiservices, through shrub size, biocrust cover, and vascular plant cover and richness, we generated a structural equation model (Grace 2006) based on the known effects and relationships among grazing and the key drivers of ecosystem functionality and services (shown in the a priori model in Fig. 1). In this model, grazing is predicted to have negative effects on both multifunctionality and multiservices by reducing soil surface cover, thereby altering soil function (Table 1). Plant richness, however, is expected to have positive effects on ecosystem multifunctionality and multiservices (e.g. Maestre et al. 2011) simply because greater richness of plant species will be associated with a greater variety of microbes and the microbial processes they are associated with. Biocrust
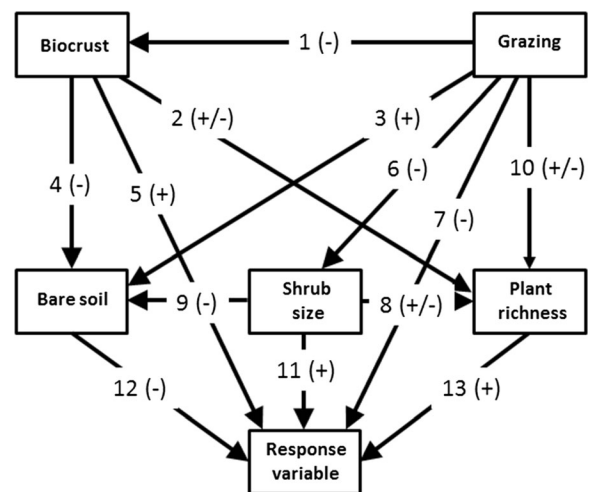

Fig. 1 Conceptual a priori meta-model (sensu Grace 2006) for the response variables multifunctionality and multiservices. Support for the mechanisms underlying these models is presented in Table 1

cover would be expected to promote the accumulation of nitrogen and carbon (Delgado-Baquerizo et al. 2015), and larger shrubs would be expected to provide physical protection against trampling, to have greater litter fall and therefore decomposition (Daryanto et al. 2012). and promote greater levels of infiltration.

Using this model we tested the following hypotheses: (i) grazing would reduce ecosystem multifunctionality and multiservices because of its direct and indirect suppressive effects via soil cover and plant species richness; (ii) declines in multifunctionality would be less pronounced under shrubs than in the interspaces. We expected such a response because shrubs act as nurse plants and moderate ecosystem processes through their effects on biotic and abiotic processes around canopies (the so-called "islands of fertility" effect; Schlesinger et al. 1990); (iii) reductions in ecosystem multifunctionality and multiservices with grazing would vary with shrub size. We expected greater reductions in multifunctionality and multiservices with declining shrub size simply because larger shrubs have a greater effect on ecosystem processes, produce more litter and provide greater physical protection against grazing by livestock.

Methods

Site description

The study was carried out at the Fowlers Gap Arid Zone Research Station, a pastoral research property located in

Table 1 Hypothesized mechanisms underlying the a priori metamodel (Fig. 1)

Path	Hypothesised mechanism
1	Trampling reduces biocrust cover (Eldridge et al. 2013) and alters composition (Dettweiler-Robinson et al. 2013)
2	Biocrusts are associated with increases (Hawkes and Menges 2003), decreases (Miller and Damschen 2013) and no change (Escudero et al. 2007) in vascular plant richness.
3	Grazing removes surface cover and increases bare soil (Daryanto et al. 2012)
4	Biocrusts colonise bare soils (Delgado-Baquerizo et al. 2013)
5	Biocrusts promote nitrogen and carbon accumulation (Delgado-Baquerizo et al. 2013).
6	Grazing-induced trampling and herbivory reduce the size of *Atriplex* and *Maireana* shrubs (Graetz and Wilson 1980)
7	Grazing-induced trampling compacts surface soils, reducing macroporosity, increasing soil bulk density (Laycock and Conrad 1981) and reducing soil microbial populations (Fterich et al. 2011) and therefore soil function.
8	(+) Shrubs provide physical protection against trampling by herbivores (Eldridge et al. 2013; Smit et al. 2007). (−) Shading and competition for light may alter plant cover and community composition (Pintado et al. 2005).
9	Litterfall and enhanced decomposition under shrubs reduces the cover of bare soil (Daryanto et al. 2012).
10	Grazing alters plant composition with variable effects on plant richness (Lunt et al. 2007).
11	Greater macroporosity, litter cover and depth, microbial community composition, and soil C and N under shrubs (Daryanto et al. 2012)
12	Bare soil characterised by low populations of soil microbes, reduced insolation, greater wind erosion leading to dysfunctional soils (Maestre et al. 2012, Delgado-Baquerizo et al. 2013)
13	Increased plant species richness leads to enhanced soil functionality (Maestre et al. 2012).

the arid shrublands about 110 km north of Broken Hill, NSW, Australia (31°05'S, 141°43'E). The climate is characterised by hot dry summers and mild winters, with mean temperature ranging from 7° C in winter to 33° C in summer and an annual mean of 21 °C. The annual rainfall is approximately 220 mm, falling evenly throughout the year.

The study area comprised ranges and footslopes of low topographic relief, characterised by a clearly-defined banded pattern (Macdonald 2000). These bands are made up of a shelf area dominated by rounded quartzose gravel overlying shallow red duplex loams (desert loam), and a depression dominated by self-mulching clays (Eldridge and Tozer 1997). The vegetation is characterized by a discontinuous cover of shrubs, with annuals in favorable years, and widespread soil crusts; physical crusts interspersed with biocrusts (Eldridge and Tozer 1997). The vegetation community was predominantly open chenopod shrublands, with bluebushes (e.g. *Maireana sedifolia* and *M. pyramidata*) and bladder saltbush (*Atriplex vesicaria*; (Macdonald 2000) as the dominant species. Biocrusts were dominated by cyanobacteria (Rogers 1995). sparse mosses of the family Pottiaceae (Eldridge and Tozer 1997) and cyanolichens such as *Peltula* and *Collema* spp. (Eldridge 1996)..

Experimental design

This study was conducted in an area with a long history of grazing by livestock (merino sheep) and red kangaroos (*Macropus rufus*). Within a large paddock of about 3.5 km² we selected two areas; one of 15 ha that has experienced moderately and continuous grazing by sheep and kangaroos, and an exclosure of 14 ha that had been ungrazed for more than 50 years. In both areas we selected 70 locations to undertake detailed measurements of soils, plants and ecological processes. Half of the sites were (1) canopy microsites, dominated by the perennial shrub (*Maireana sedifolia*) and the other (2) were open (interspace) microsites. To select the 35 canopy and 35 interspace locations inside and outside the exclosure, we chose sampling locations that represented the largest possible gradient in biocrust cover across canopy and interspace microsites. This non–random design allowed us to maximise the chance of discerning the relative importance of the direct effects of the two different microsites on multifunctionality and multiservices, while decreasing correlation among these players as much as possible in a non–experimental setting (Eldridge et al. 2010). Because there is only one long-term exclosure, and it was not possible to replicate the treatment elsewhere, the design is therefore pseudoreplicated, and does not allow generalization about the effects of grazing beyond the study site. Nevertheless, a single replicate of a unique long-ungrazed exclosure such as this represents a valuable opportunity to gain information about the effects of grazing and shrubs on multiple functions and services.

Measurements of individual ecosystems functions and services

At each of the 140 locations we assessed five ecosystem functions (activity of phosphatase and glucosidase, soil respiration, dissolved inorganic N, potential net N mineralisation rate) and four ecosystem services (shading by plant canopies, steady-state infiltration, sorptivity and an infiltration index). All these measurements were made within a circular quadrat of 0.03 m^2 (20 cm diameter). We selected these variables because they have been shown to be good proxies of nutrient cycling, biological productivity, and buildup of nutrient pools. For example, phosphatase is related to the release of inorganic P from organic matter, and β-glucosidase supports sugar degradation (Bell et al. 2014). Taken together, they are strong indicators of multiple functions and services provided by shrublands (see Maestre et al. 2012; Wagg et al. 2014; Delgado-Baquerizo et al. 2015).

Within each of the 140 locations rings we assessed the surface cover of biocrusts and bare soil using high resolution photographs taken of each circular ring with a grid of 314, 1-cm^2 cells. Plant richness was assessed as the total number of species present in the circular quadrat 3-weeks following a rainfall event of 12 mm. Within each ring we also recorded eight soil surface attributes: soil surface roughness, biocrust resistance, biocrust cover, crust stability (biocrust and physical crusts), litter cover, litter origin, degree of litter incorporation and soil texture. Together these values were used to derive an index related to how the soil conducts water (Infiltration index). This index has been shown to be strongly related to a range of ecosystem functions estimated with widely accepted laboratory techniques (Maestre and Puche 2009) and has been widely used in many dryland systems. Apart from the infiltration index, we also measured two primary components of infiltration; sorptivity, the early phase of infiltration, which is dependent upon soil water content and diffusivity, and steady-state infiltration, the rate of infiltration per unit cross-sectional area and unit hydraulic gradient. In an operational sense, steady-state infiltration is the rate at which water flow through the soil becomes constant. Sorptivity and steady-state infiltration were measured with paired disk permeameters (Eldridge et al. 2010).

Soil respiration was assessed in situ using a portable LI-8100 Automated Soil CO$_2$ Flux System (LICOR, Lincoln, Nebraska, USA). The soil was primed with the equivalent of 10 mm of rainwater the evening before carbon flux measurements were made in order to simulate a rainfall that occurs three to five times per year at the study site. This allowed us to measure soil respiration and therefore potential carbon flux over a period of maximum potential soil biological activity. To avoid strong diurnal fluctuations, measurements were made between 8:00 and 10:00 h. Photosynthetic photon flux density (PPFD) was measured at ground level at each location with a light meter to obtain a measure of photosynthetically active radiation (PAR). These PAR values were then multiplied by −1 to provide an index of shading.

At each of the 140 locations we collected soil from the top 3 cm of the surface. Soil was air dried at constant temperature, passed through a 2 mm sieve to remove litter and rock, and stored at 4 °C. Nitrogen mineralization and dissolved inorganic N were determined from soil extracts following Delgado-Baquerizo and Gallardo (2011). In brief, dissolved inorganic N was measured from K$_2$SO$_4$ 0.5 M soil extracts in a ratio 1:5 (2.5 g of soil). Soil extracts were shaken in an orbital shaker at 200 rpm for 1 h at 20 °C and filtered to pass a 0.45-μm Millipore filter. The filtered extract was kept at 2 °C until colorimetric analyses were conducted (655 nm) 24 h after extraction. For potential net N mineralization rate, air-dried soil samples were re-wetted to reach 80 % of field water holding capacity and incubated in the laboratory for 14 days at 30 °C (Allen et al. 1986). This rate was estimated as the difference between initial and final dissolved inorganic N concentrations, respectively Delgado-Baquerizo and Gallardo (2011). Phosphatase activity was measured by determining the amount of p-nitrophenol (PNF) released from 0.5 g soil after incubation at 37 °C for 1 h with the substrate pnitrophenyl phosphate in MUB buffer (Tabatabai and Bremner 1969). The activity of β-glucosidase was assayed following the procedure for phosphatase, but using p-nitrophenyl-β-D-glucopyranoside as a substrate and Trishydroxymethyl aminomethane instead of NaOH when preparing the buffer (Tabatabai 1982).

Statistical analyses

We used two different approaches to assess the effects of grazing and shrub size on important biogeochemical processes controlling nitrogen, carbon and phosphorus pools and fluxes, and on indices of multifunctionality and multiservices, which we refer to henceforth as multifunctionality and multiservices because they are indices. In Stage 1 we used separate, mixed-models ANOVAs to examine potential effects of grazing (grazed,

ungrazed) and microsite (shrub, interspace) and their interaction, on separate soil functions (phosphatase, β-glucosidase, mineralisable N, dissolved N, soil respiration), services (sorptivity, steady-state infiltration, the Infiltration index, photosynthetically-active radiation [PAR-1]), the endogenous variables (plant richness, bare soil and biocrust cover), and our derived multifunctionality and multiservice indices (see below). In these analyses, the first stratum of the mixed-models ANOVA examined potential grazing effects ($n = 2$) and the second stratum microsite ($n = 2$) and its interaction with grazing. Data were tested for normality and homogeneity of variance (Levene's test) and transformed, where necessary, prior to analyses. *Post–hoc* differences in means were tested with Least Significant Difference tests. Differences in shrub size (volume of a half-sphere) were tested using one-way ANOVA after log_{10} transformation.

In Stage 2 we used Structural Equation Modelling (SEM; Grace 2006; see below) to explore the direct and indirect impacts of grazing, and four endogenous variables (shrub size, plant richness, biocrust cover and bare soil) on average functionality using a multifunctionality approach (Maestre et al. 2012). It is important to notice that, even when we also analysed all functions and services separately, we still used the multifunctionality approach with SEM because is allowed us to summarize multiple functions and services into two variables: multifunctionality and multiservices. These indexes were assessed as the average value of the previously of individual functions that have previously been standardized (z-transformed; Maestre et al. 2012). Multifunctionality and multiservice indices provide a conceptual framework that allows multiple functions, such as soil processes, to be included in the one measure or index. In our case, the multifunctionality index was calculated as the arithmetic mean of values for soil phosphatase, β-glucosidase, mineralisable N, soil respiration and dissolved N after standardization. The multiservices index was calculated as the arithmetic mean of values for the three measures of infiltration (steady-state infiltration, sorptivity, infiltration index) and a measure of shading provided by shrubs (1-PAR).

Structural Equation Modelling is useful for investigating the complex networks of relationships found in natural systems. It is used to test the plausibility of a causal model, based on a priori information (a priori model Fig. 1), of the relationships among particular variables of interest. In our case, we proposed that grazing would have a direct suppressive effect, and indirect effects on multifunctionality and multiservices,

mediated by biocrust cover, vascular plant richness and bare soil. We also expected that grazing would alter multifunctionality and multiservices indirectly by reducing the size of the shrubs (Fig. 1). This model included grazing, the four endogenous variables, and either multifunctionality or multiservices.

This approach is largely used in the current literature (e.g. Maestre et al. 2012; Wagg et al. 2014) and provides a straightforward and easily interpretable measure of the ability of different communities to sustain multiple functions simultaneously. Prior to calculating our index of multifunctionality, we examined the distributions of the four endogenous variables and tested their normality. In most cases, individual values were log_{10}-transformed. Values for soil respiration were also transformed (squared). Before fitting empirical data to our a priori models, we examined univariate correlations among our observed and response variables, developing a model that retained those variables that showed the strongest signals and therefore had the greatest predictive power.

Overall goodness of fit probability tests were performed to determine the absolute fit of the best models. The goodness of fit test estimates the long-term probability of the observed data given the a priori model structure. Thus high probability values indicate that these models are highly plausible causal structures underlying the observed correlations. Separate models with the strongest measures of fit (e.g., low χ^2, high goodness of fit index [GFI], and high normal fit index [NFI]) were interpreted as showing the best fit to our data. To aid interpretation of our data, we calculated the standardized total effects of grazing, bare soil cover, biocrust cover, plant richness and shrub size, on multifunctionality and multiservices. The net influence that one variable has upon another is calculated by summing all direct and indirect pathways between the two variables. If the model fits the data well, the total effect should approximate the bivariate correlation coefficient for that pair of variables. All SEM analyses were conducted using AMOS Software Version 20.

Results

Grazing and microsite effects on individual functions and services

Grazing significantly reduced the cover of biocrusts ($F_{1, 68} = 23.1$, $P < 0.001$; Fig. 2a), increased the cover
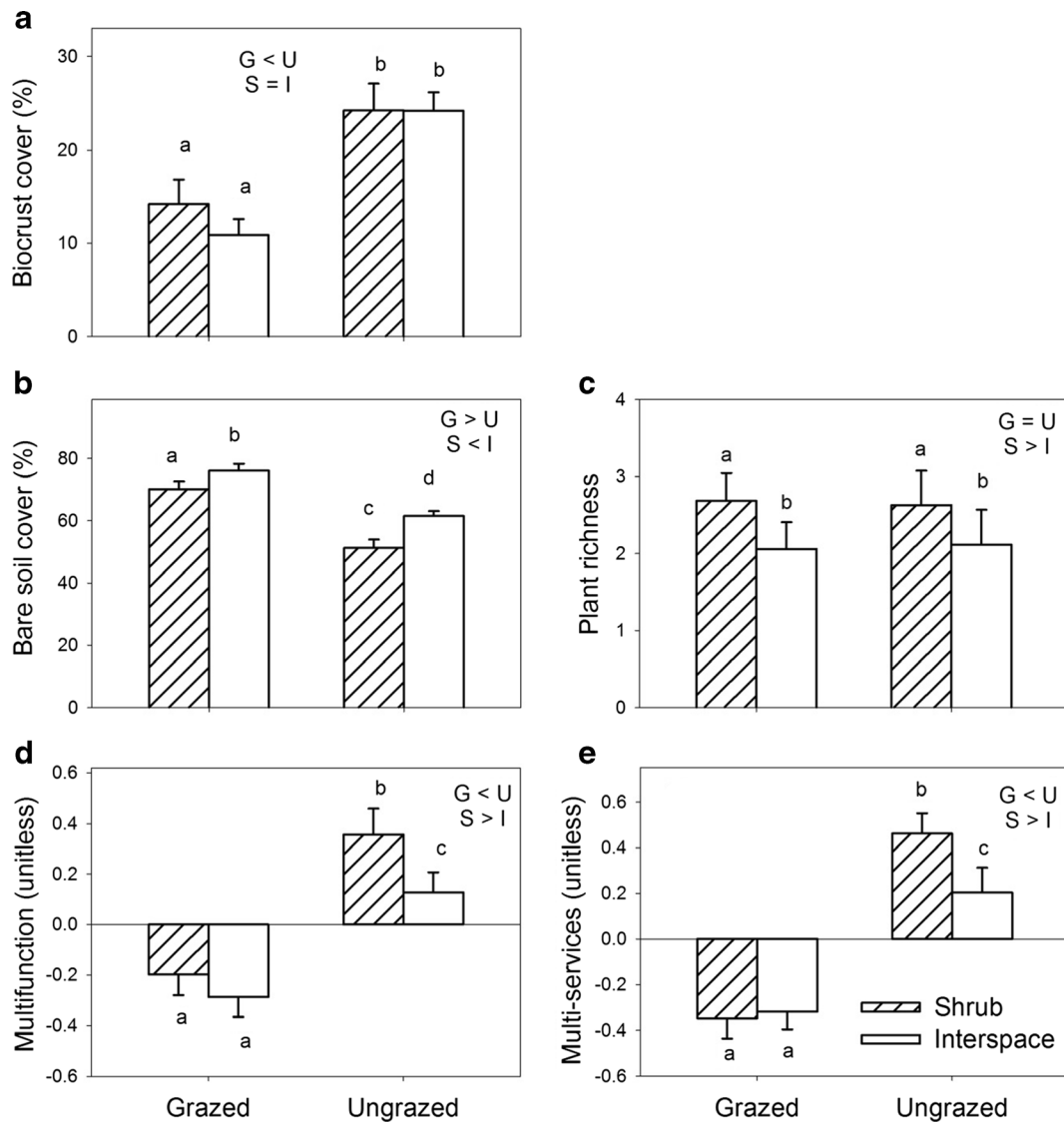
Fig. 2 Mean (± SE, $n = 35$) biocrust cover, bare soil cover, plant richness, multi-functionality and multiservices in relation to shrubs and their interspace for grazed and ungrazed sites. G = grazed, U = ungrazed, S = shrub, I = interspace. *Different letters* indicate significant differences among the four grazing by microsite combinations at $P < 0.05$

of bare soil ($F_{1, 68} = 5.60$, $P = 0.021$; Fig. 2b), but had no effect on plant richness ($P = 0.99$; Fig. 2c) nor shrub size ($P = 0.45$, data not shown). Shrub microsites were characterised by less bare soil ($F_{1, 68} = 16.5$, $P < 0.001$, Fig. 2b) and greater plant richness ($F_{1, 68} = 6.3$, $P = 0.014$, Fig. 2c) but there were no significant effects on biocrust cover (Fig. 2a).

For individual functions, grazed sites had lower soil phosphatase ($F_{1, 68} = 6.1$, $P = 0.014$, Fig. 3a), and lower overall levels of β-glucosidase and potential mineralization rate ($F_{1, 68} > 4.94$ and $P < 0.03$) when averaged

over the two microsites (Fig. 3b and 3c, respectively). Microsite effects for β-glucosidase and potential mineralization rate varied in relation to grazing. For ungrazed sites, β-glucosidase activity was significantly greater beneath shrubs, but under grazing, was lower beneath shrubs ($F_{1, 68} = 4.94$, $P = 0.03$; Fig. 3a). Potential mineralization rates were greater beneath shrubs than in the interspaces, but only at the grazed sites ($F_{1, 68} = 8.75$, $P = 0.004$; Fig. 3c). There were no effects of grazing on dissolved inorganic N (Fig. 3d) nor soil respiration (Fig. 3e).
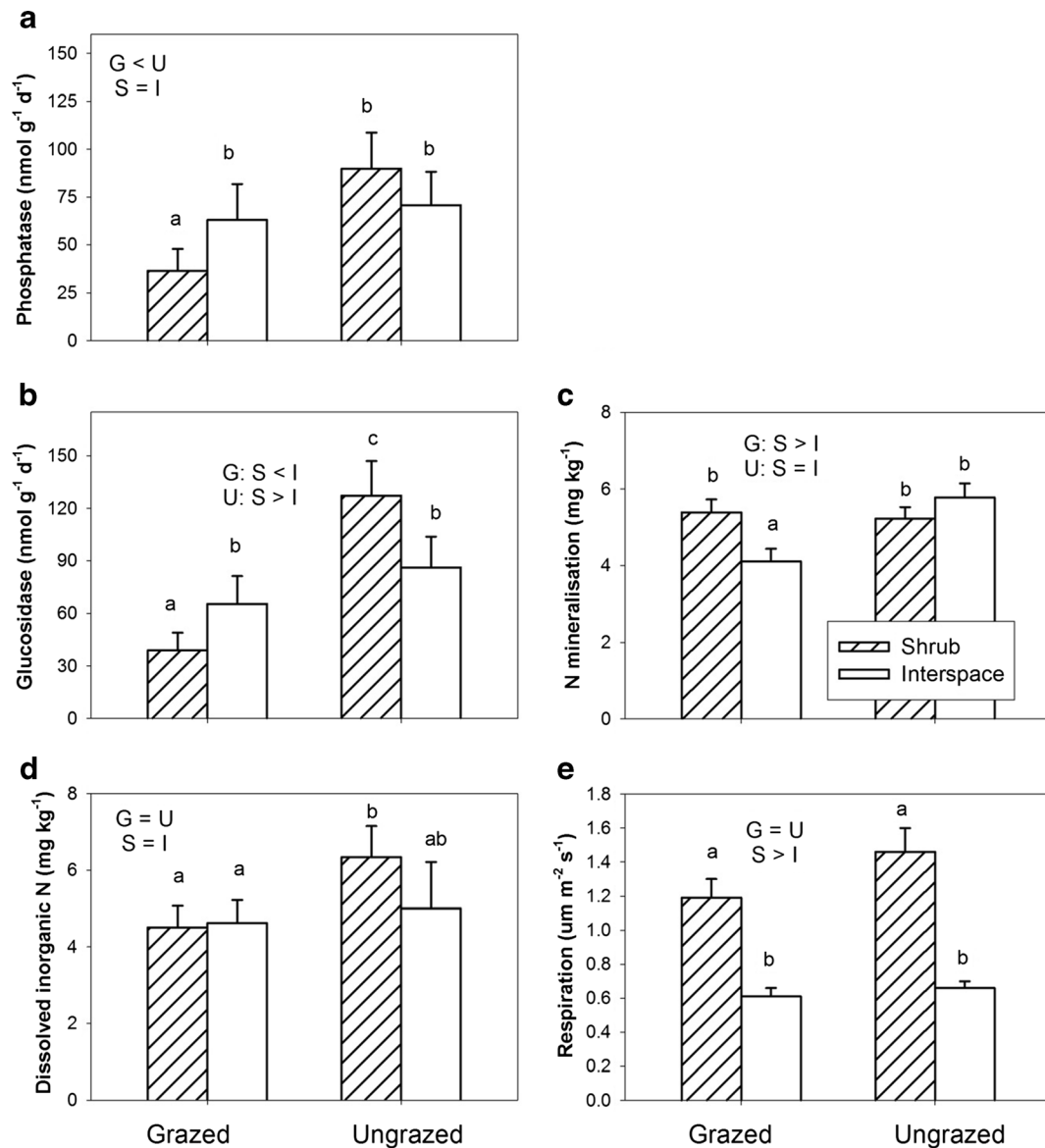
Fig. 3 Mean (± SE, $n = 35$) values for individual soil functions; soil phosphatase, glucosidase, N mineralisation, dissolved inorganic N and respiration measured under shrubs (S) and in the interspaces (I) at grazed (G) and ungrazed (U) sites. *Different letters* indicate significant differences among the four grazing by microsite combinations at $P < 0.05$

For individual services, grazing had no effect on sorptivity, infiltration (steady-state infiltration) or the Infiltration index (Fig. 4a–c; $F_{1, 68} < 4.04$, $P > 0.093$), but grazed sites were characterised by higher PAR (i.e. less shading; $F_{1, 68} = 69.26$, $P < 0.001$) than ungrazed sites (Fig. 4d). Microsites beneath shrubs had significantly greater sorptivity, infiltration and Infiltration index ($F_{1, 68} > 4.33$ and $P < 0.041$; Fig. 4a–c), but lower PAR ($F_{1, 68} = 117.32$, $P < 0.001$; Fig. 4d).

Grazing and microsite effects on multifunctionality and multiservices

When separate functions were combined into the two indices, both the multifunctionality ($F_{1, 68} = 30.77$, $P < 0.001$) and multiservice ($F_{1, 68} = 52.41$, $P < 0.001$) indices were negative under grazing and positive under exclosure (Fig. 2d and 2e, respectively). The multifunctionality index was most highly correlated
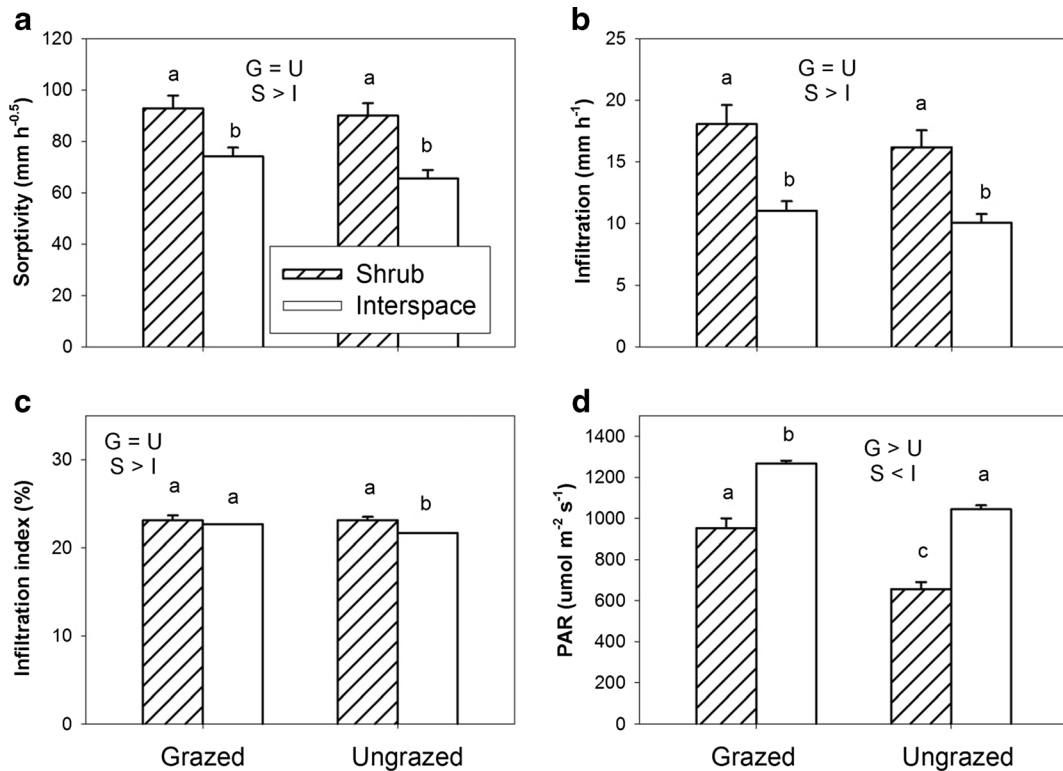
Fig. 4 Mean (± SE, $n = 35$) values for sorptivity, infiltration (steady-state infiltration), Infiltration index, and photosynthetically-active radiation (PAR) measured under shrubs (S) and in the interspaces (I) at grazed (G) and ungrazed (U) sites. *Different letters* indicate significant differences among the four grazing by microsite combinations at $P < 0.05$

with soil phosphatase and β-glucosidase, and the multiservice index with sorptivity and steady-state infiltration (Table 2). Both indices were greater under shrubs than in the interspaces (Fig. 2d and 2e; $F_{1, 68} > 21.0$, $P < 0.01$).

Table 2 Spearman's correlation coefficients (r) between the individual attributes and multifunctionality and multiservice

Attribute	Multi-functionality	Multi-service
Phosphatase	0.76	
β-glucosidase	0.75	
Mineralisable nitrogen	0.42	
Soil respiration	0.42	
Dissolved nitrogen	0.36	
Sorptivity		0.74
Steady-state infiltration		0.72
Infiltration index		0.67
Shading		0.47

All relationships were significant at $P < 0.001$

Structural equation modelling

Our structural equation models for multifunctionality and multiservices were very similar and a strong fit with the data ($\chi^2 = 0.342$, df = 2, $P = 0.843$, NFI = 0.998 and GFI = 0.999). Both models indicated (1) a strong and direct suppressive effect of grazing on the multifunctionality and multiservice indices, (2) a weaker, though direct, positive effect of shrub size on multifunctionality and multiservice indices, (3) suppressive effects of grazing on biocrust cover and plant richness, but a positive effect on the cover of bare soil, and (4) a weak indirect and negative impact of grazing (through plant richness) on ecosystem multifunctionality and multiservices (Fig. 5). Grazing had the strongest overall effect on both multifunctionality and multiservices (standardised total effect [STE]: -0.43 and −0.57, respectively) while the effects of shrubs (STE = 0.26–0.17) and plant richness (STE = 0.22–0.15) were always positive (Fig. 6). Separate SEM models for individual functions and

Fig. 5 Final structural equation models for **a** multifunctionality and **b** multiservices. The strength of relationships between variables is indicated by the magnitude and sign of the standardized path coefficients enclosed within *circles* embedded in the pathways and the thickness of the pathway *arrows*. A path coefficient is analogous to a partial correlation coefficient, and describes the strength and sign of the relationships between two variables. Negative pathways are shown as *broken red lines*, positive are *solid black lines*. Non-significant pathways are shown in *grey*. Our final model explained 31 % of the variation in multi-functionality and 41 % of the variation in multiservices ($\chi^2 = 0.342$, df = 2, $P = 0.843$, NFI = 0.998, GFI = 0.999)
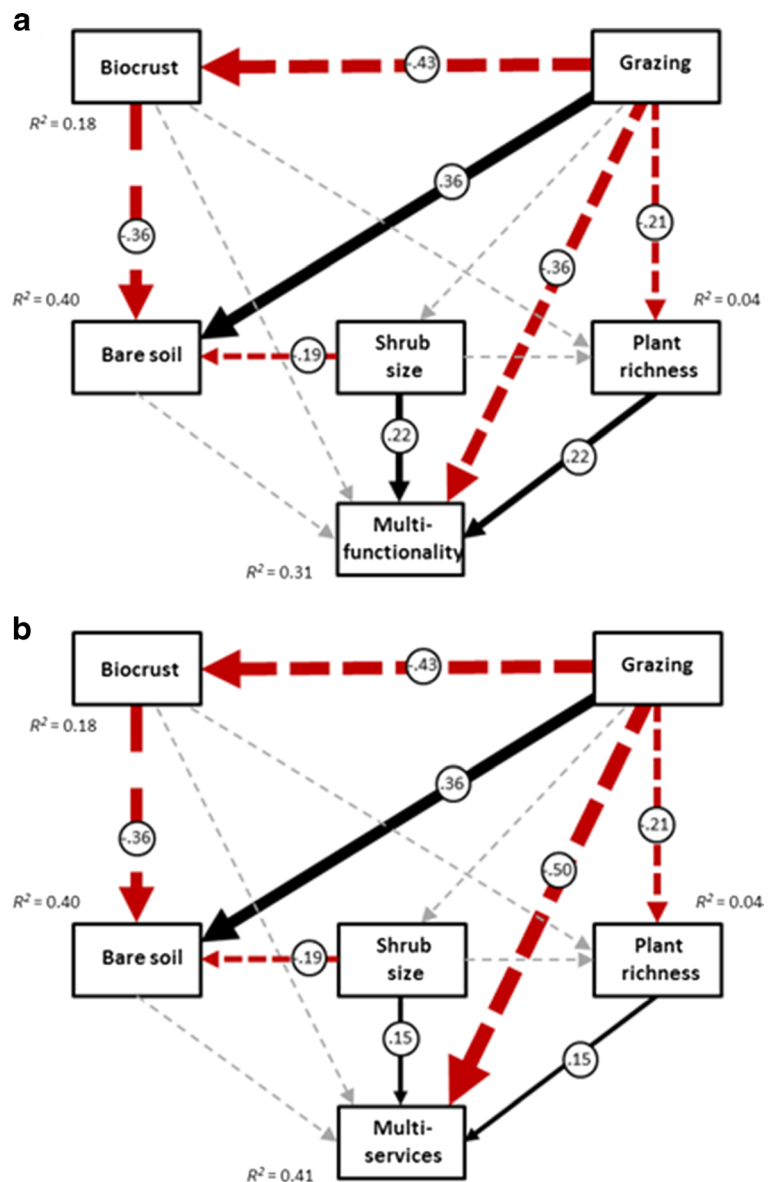

services showed some concordance. There were mostly neutral effects of biocrusts (except on respiration) while plant richness and shrub size had a few positive effects (Table 3). All effects of grazing were negative.

Discussion

Our results provide solid empirical evidence that grazing is associated with reduced multifunctionality and multiservices in our shrubland system, and suggest that these effects are only partly offset by increases in plant

species richness. They also reinforce the notion that grazing has strong negative effects on individual functions such as soil phosphatase, β-glucosidase and potential mineralization rate, that are associated with the phosphorus, carbon and nitrogen cycling, and services associated with the provision of shade and infiltration. Different microsites (e.g. bare areas *cf.* shrub canopies) had different effects on ecosystem functionality and services, providing support for our second hypothesis, and suggesting that it is critical to consider idiosyncratic effects of different microsites in order to understand community-level effects of grazing in drylands. We

Fig. 6 Standardised total direct and indirect effects of grazing (Gr), cover of bare soil (Ba), biocrust cover (Bi), plant richness (Ri) and shrub size (Sh) on **a** the multifunctionality and **b** multiservices indices
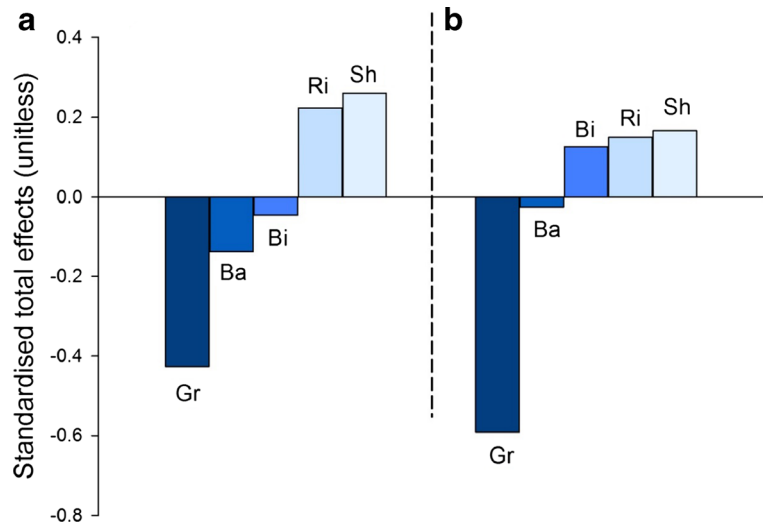
were unable to separate out the effects of domestic herbivores (sheep) from those of native herbivores (kangaroos), so our study represents the effects of total grazing pressure from all herbivores. The overriding effect of grazing in this system is consistent with our understanding of herbivore effects on chenopod shrublands across eastern Australia, many of which have had a long history of sustained overgrazing by sheep, kangaroos, and more recently, feral goats (Yan et al. 1996). Grazing had the largest (and negative) standardised total effect on our multifunctionality and multiservice indices in our structural equation modelling.

The message for land managers is that, despite some positive effects, the presence of shrubs, biocrusts, and to a lesser extent a diverse community of plants, will not offset the negative effects of total grazing pressure on multiple functions and services.

Direct and indirect effects of grazing on indices of multifunctionality and multiservices

In our study the direct effect of grazing on the multifunctionality and multiservices indices was predominantly unexplained by the measured environmental

Table 3 Path coefficients from separate structural equation models relating grazing, shrub size, bare soil cover, biocrust cover and plant richness to specific functions or services

Functions/services	Grazing	Shrub size	Bare soil	Plant richness	Biocrust cover
Functions					
Soil respiration	−0.16	0.46	−0.38		−0.52
β-glucosidase	−0.37	–	–	0.19	–
Phosphatase	−0.29	–	–	0.26	–
Dissolved nitrogen	–	–	–		–
Mineralisable nitrogen	–	–	–		–
Services					
Shading	−0.56	0.32	–	–	–
Steady-state infiltration	−0.38	–	–	0.18	–
Sorptivity	−0.29	–	–	0.26	–
Infiltration index	–	–	–	–	–
Multifunctionality	−0.36	0.22	–	–	0.22
Multiservices	−0.50	0.15	–	–	0.15

− not significant at $P < 0.05$

variables. Important biotic components such as biocrust cover, bare soil, shrub size and plant richness had only a very small role in mediating the grazing effects in our study site (~0.07 for multifunction; 0.09 for multiservice). The direct effects of grazing on multifunctionality and multiservices may also be driven by other important factors that were not measured in this study such as shifts in soil microbial communities (Eldridge et al. 2015). that can influence soil N content and mineralisation through consumption and deposition of plant material or through impacts on plant litter quality. Plant richness had a significant direct positive effect on multifunctionality (path coefficient: PC = 0.22), consistent with our first hypothesis. This is not surprising, given that plant richness is considered one of the major drivers of multifunctionality in drylands globally (Maestre et al. 2012). Plant richness has been shown to be highly correlated with soil functionality, particularly soil carbon, nitrogen and phosphorus cycling (Maestre et al. 2011). Our study reinforces our understanding about the importance of plant biodiversity in drylands, suggesting that species richness can be as important as other key biotic features such as community structure (e.g. cover of high resource patches) for modulating the effects of grazing on ecosystem functions and services.

In addition to reductions in biocrust cover and increases in bare soil (reduced plant cover), trampling of surface soil layers may explain the direct effects of grazing on ecosystem multifunctionality and multiservices. Livestock trampling disaggregates the soil, removes fine particles and therefore reduces organic matter levels. Fine sediment removed by trampling can clog surface pores, reducing macroporosity and therefore infiltration (Tongway et al. 2003; Daryanto et al. 2013a). Grazing-induced trampling is known to reduce surface roughness, a component of the infiltration index that is highly correlated with the tendency for water to pond on the surface (Tongway 1995). For example, in our study, ungrazed surfaces were significantly rougher (6.0 ± 0.37 mm; mean ± SE) than grazed (4.8 ± 0.26) surfaces ($P = 0.012$). Thus trampling would also account for the observed reductions in sorptivity and infiltration reducing important services such as groundwater recharge and promoting soil erosion. Trampling also increases soil compaction, reduces the resistance of surface soils to breakdown by wind and water, and ultimately reduces the structural complexity of surface soils (Tongway et al. 2003). That both multifunctionality and multiservices were reduced by grazing, in the absence of any mediating

effects through bare soil or biocrust cover, suggests that the principal mechanism involves surface compaction rather than any removal of surface soil *per se*. The direct suppressive effect of grazing could also be due to other potential reasons could be indirect impacts through litter quality such as changes in the arrangement, depth or cover of litter on the surface, which is known to harbour soil biota that maintain the integrity and connectivity of macropores to the surface (Colloff et al. 2010). Further evidence for a litter effect comes from the separate SEM models showing that soil respiration was highly positively associated with litter cover (data not shown). Association between soil respiration, organic carbon, microbial nitrogen and phosphatase activity are well known (Joergensen and Scheu 1999).

Correlation analyses indicated that multifunctionality was related most strongly to concentrations of soil phosphatase and β-glucosidase, enzymes that are associated with the release of inorganic P from organic matter and the cycling of carbon, respectively (Bell et al. 2013). These correlations were substantially larger than any correlations with nitrogen or carbon flux (Table 2). Reductions in the activity of phosphatase and β-glucosidase (Schimel and Weintraub 2003) can result in reduced bioavailability of phosphorus and carbon for plants and microbes. A direct effect of grazing in chenopod shrublands is to reduce plant richness, and plant and litter cover (e.g. Graetz and Wilson 1980). Given that vegetation type is an important indicator of phosphatase activity in soils (Bell et al. 2013). reductions in cover and reductions in diversity are likely to compromise the ability of drylands to function efficiently by reducing the availability of nutrients. Our results suggest therefore that grazing may promote considerable negative feedbacks on important functions such as net primary productivity and decomposition, potentially resulting in longer-term reductions in resilience of these systems to climate-induced change.

The role of microsites: shrubs vs bare interspaces

Although there were no effects of grazing on shrub size, larger shrubs had a direct positive effect on both multifunctionality (PC = 0.22) and multiservices (PC = 0.15), consistent with our third hypothesis. This effect was of a similar magnitude to those observed between plant richness and multiple ecosystem functions and services (Table 2). The effect of increasing shrub size on multifunctionality likely relates to the

tendency of shrub canopies to moderate environmental conditions and to provide physical protection against livestock grazing (Smit et al. 2007). Larger shrub canopies produce more biomass and therefore more litter (see Geddes and Dunkerley 1999; Daryanto et al. 2012) so that increasing shrub size would be expected to be associated with deeper litter layers and greater levels of organic matter decomposition (de Soyza et al. 1997). Larger shrubs would also be stronger nutrient pumps, depositing more nutrients through the accumulation of root exudates within the rhizosphere (Daryanto et al. 2012) and in the near surface layers (Throop and Archer 2008). Shrub size is therefore closely related to nutrient availability in dryland soils. Other evidence for greater functionality under large shrubs was the strong direct effects of shrub size on soil respiration and shading in separate models (Table 2).

The effect of soil-surface lichens on soil function has been shown to be due to the effects of secondary metabolites on nutrient uptake, and the formation of metallic complexes (e.g. norstictic acid; Hauck et al. 2009) and anti-herbivore defences through production of acids (e.g. usnic acid; Concostrina-Zubiri et al. 2014). However, contrary to expectation, and despite the negative relationship between grazing and biocrust cover, we failed to detect anything other than a very small mediating effect of crusts on multifunctionality (STE = −0.09) and multiservices (STE = 0.13; Fig. 3), and no significant effect of biocrust cover on multifunctionality. We did not assess biocrust richness, evenness, abundance nor spatial patterning; community properties that have been shown to be linked to multifunctionality (Bowker et al. 2013; Orwin et al. 2014). The crusts in our study area are all relatively species poor, even at high levels of cover, and dominated by cyanobacteria (Rogers 1995). sparse mosses (Eldridge and Tozer 1997) and cyanolichens (e.g. *Peltula* Eldridge 1996). The effect of these depauperate crusts on soil functions is therefore likely to be substantially less than that of biodiverse crusts of lichens and mosses (Pietrasiak et al. 2013; Delgado-Baquerizo et al. 2015). Had our biocrust surfaces been characterised by high species richness, random spatial pattern and low evenness (e.g. Maestre et al. 2012). the effects on multifunctionality might have been much stronger. In addition, we cannot reject the possibility that biocrust cover is positively related to other functions and services that were not measured at this study site, such as plant primary productivity.

Concluding remarks

Our results indicate that grazing had the largest negative effect on ecosystem multifunctionality and multiservices that are associated with the processing of organic matter and infiltration of water into the soil, respectively. These effects may be, at least in part, indirectly mediated by reductions in plant richness, which has been shown to be a major driver of multifunctionality in drylands. Interestingly, the grazing effect was not mediated by other important biotic features such as the presence of shrubs, suggesting that in this landscape, the size and structural configuration of shrubs is insufficient to protect the surface against the action of herbivores, possibly due to a long legacy effect of overgrazing. Different microsites, shrubs and their interspaces, had different effects on particular ecosystem functions and services, suggesting that at the landscape level, microsite type needs to be considered in order to adequately assess the ecosystem response to rapid environmental changes such as those resulting from grazing. Our results should be taken in context in that this represents only one ungrazed exclosure across a vegetation community that occurs over an extensive area of eastern Australia. Notwithstanding this limitation, however, there is strong evidence that these are not idiosyncratic effects, but are a common syndrome across grazed rangelands of eastern Australia. Despite this limitation, our results reinforce the notion that total grazing pressure, either through herbivory or surface disturbance, is a major degrading process that leads to reductions in ecosystem functionality.

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