



Large shrubs partly compensate negative effects of grazing on hydrological function in a semi-arid savanna

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Abstract

Semiarid woodlands and savannas are globally important biomes that provide ecosystem goods and services such as habitat for biota and sinks for carbon, support millions of people that rely primarily on pastoralism, and supply livelihoods for about a third of the global human population. Savannas, however, are prone to degradation by overgrazing, and encroachment by woody plants, reducing their capacity to produce forage that pastoral enterprises depend on. We examined the impacts of livestock grazing and woody encroachment on soil hydrological processes, hypothesizing that heavy grazing by livestock would reduce hydrological function, whereas woody plants would increase hydrological function, therefore, partially offsetting any negative effects of overgrazing by livestock. Understanding the major drivers of soil hydrology in savanna ecosystems is important because water is a critical, yet limited resource in savannas. We found that livestock grazing reduced the early (sorptivity) and late (steady-state infiltration) stages of infiltration under both ponding and tension, and attributed this to a reduction in porosity caused by livestock trampling. Steady-state infiltration and sorptivity under ponding were greater under the canopies of woody shrubs than in open areas, partly compensating for any negative effect of grazing. Structural equation modeling revealed a direct positive effect of shrub height on hydrological functions, and an indirect effect via increases in litter cover. Our results suggest that woody plants can play important roles in driving hydrological function in savannas, counteracting the suppressive effect of livestock overgrazing on infiltration processes. Management strategies in semiarid savannas should aim to reduce trampling by livestock and retain large woody plants in order to maintain hydrological function.

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Introduction

Drylands occupy about 40% of the terrestrial land surface and support about 38% of the global human population (Millennium Ecosystem Assessment, 2005). Currently, about

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half of all drylands are degraded due to inappropriate land management practices such as overgrazing by European livestock, and this degradation will likely be exacerbated by the predicted global changes in climate (Cook, Ault, & Smerdon, 2015; Fu & Feng, 2014). These forms of degradation include erosion, reduced soil structure and loss of topsoil, thereby intensifying desertification (García-Orenes et al., 2012; Graetz & Tongway, 1986; Ravi, Breshears, Huxman, & D'Odorico, 2010). By the end of this century, global drylands are likely to expand by 11–23%, substantially altering the livelihoods of its resident human populations (Huang, Yu, Guan, Wang, & Guo, 2016).

Drylands also support about 50% of the global livestock pool and are therefore highly susceptible to overgrazing (Eldridge, Soliveres, Bowker, & Val, 2013). The sparse vegetation cover in drylands makes it critically important to understand how livestock grazing affects dryland plants and soils (Puigdefábregas, 1998). The impact of livestock grazing on ecosystem functioning is caused by two separate yet related processes: herbivory and trampling (Eldridge, Poore, Ruiz-Colmenero, Letnic, & Soliveres, 2016). Herbivory alters plant communities, for example, by selective grazing, reducing plant cover and biomass, and shifting the balance between grasses and woody vegetation (Blaum, Seymour, Rossmanith, Schwager, & Jeltsch, 2009). Selective grazing of perennial grasses also reduces fuel loads and therefore fire intensity (Van Langevelde et al., 2003). Additionally, trampling by large-bodied, hard-hooved ungulates can cause severe effects on soil properties (Manzano & Nívar, 2000; Yong-Zhong, Yu-Lin, Jian-Yuan, & Wen-Zhi, 2005).

Many studies have shown, that trampling reduces litter and biocrust cover, and increases soil compaction (Byrnes, Eastburn, Tate, & Roche, 2018; Daryanto, Eldridge, & Wang, 2013; Eldridge et al., 2016). Trampling also reduces soil porosity, its structural complexity and water flow, thereby increasing runoff and erosion processes, which intensify desertification (Aubault et al., 2015; Eldridge, Beecham, & Grace, 2015; Houlbrooke & Laursen, 2013; Pulido, Schnabel, Contador, Lozano-Parra, & González, 2018). Herbivory, in particular overgrazing by ungulates, has been found to cause even more far-reaching impacts on ecosystem functioning through different feedbacks, e.g. by altering habitat and food availability for soil fauna, thereby negatively affecting organic matter decomposition (Abril & Bucher, 1999; Holt, Bristow, & Mcivor, 1996; Sankaran & Augustine, 2004). These cascading effects can have long-term impacts on dryland ecosystems, reducing production and resilience (Fernández, Gil, & Distel, 2009; Monger et al., 2015; Schlesinger et al., 1990). These impacts are particularly evident in systems that have not co-evolved with ungulates, where relatively low stocking densities can still have relatively large impacts on ecosystem functions.

The effects of both herbivory and trampling are often concentrated in resource-rich patches that support productive and nutrient-rich plants (Augustine, McNaughton, & Frank, 2003). These fertile patches are dominated by woody

plants (trees and shrubs) and are also important sinks for water, which is a limiting resource in drylands (Noy-Meir, 1979; Rango, Tartowski, Laliberte, Wainwright, & Parsons, 2006). Compared with the interspaces, woody patches conduct and store relatively large quantities of water (Ludwig, Wilcox, Breshears, Tongway, & Imeson, 2005). Their capacity to conduct water depends on many factors including litter and biocrust cover, grazing history and large pores (>70 μm , macropores) created by soil-burrowing invertebrates or plant roots (Eldridge & Freudenberger, 2005). The positive effects of invertebrate-derived macropores on infiltration processes in drylands have been shown for various insect groups such as ants (Cerdà & Jurgensen, 2008; Eldridge, 1993) and termites (Bargués Tobella et al., 2014; Elkins, Sabol, Ward, & Whitford, 1986; Mando, Stroosnijder, & Brussaer, 1996). Biocrusts, complex communities of bryophytes, lichens and cyanobacteria can also affect the infiltration of water (Faist, Herrick, Belnap, Van Zee, & Barger, 2017) and litter cover has been shown to be positively correlated with infiltration, by increasing soil organic matter and soil aggregation (Blackburn, 1975; Bronick & Lal, 2005; Meeuwig, 1970). Grazing-induced disturbance has marked effects on infiltration because it alters the levels of litter, biocrusts and macropores in dryland soils, but the extent to which these changes vary between interspaces and woody resource-rich patches is still relatively poorly understood. Patches with an extensive cover of woody vegetation might play a vital role in mitigating degradation caused by future climate scenarios. In drylands, shrubs may function as water sinks, increasing the overall water infiltration capacity of the ecosystem particularly in areas with low precipitation and few heavy rain events annually that are predicted to become more intense, but less in their total amount (Kirtman et al., 2013; Tadross, Jack, & Hewitson, 2005) and where droughts are predicted to occur more frequently.

We examined the effects of livestock grazing, litter and biocrust cover, and the density of macropores on infiltration both under shrubs and in the interspaces, in a savanna ecosystem in eastern Australia. Australian ecosystems have not co-evolved with ungulates, and in many systems, particularly drylands, even relatively low levels of livestock grazing can have substantial impacts on ecosystem functions. We compared the early (sorptivity) and late (steady-state infiltration) stages of infiltration at sites that had either been disturbed by high levels of cattle grazing or located within a large livestock-free conservation reserve. We compared total infiltration (when all pores in the soil conduct water) with sorptivity (where infiltration is restricted to small matrix pores) to investigate the influence of macropores on the infiltration process. Soil porosity is a critically important determinant of infiltration capacity and is known to be reduced by overgrazing and enhanced around perennial plants. We predicted, therefore, that ponded infiltration, which includes water flow through large, biotically-produced pores, would be greater under shrubs and at sites that are ungrazed than at grazed or shrub-free microsites. We also

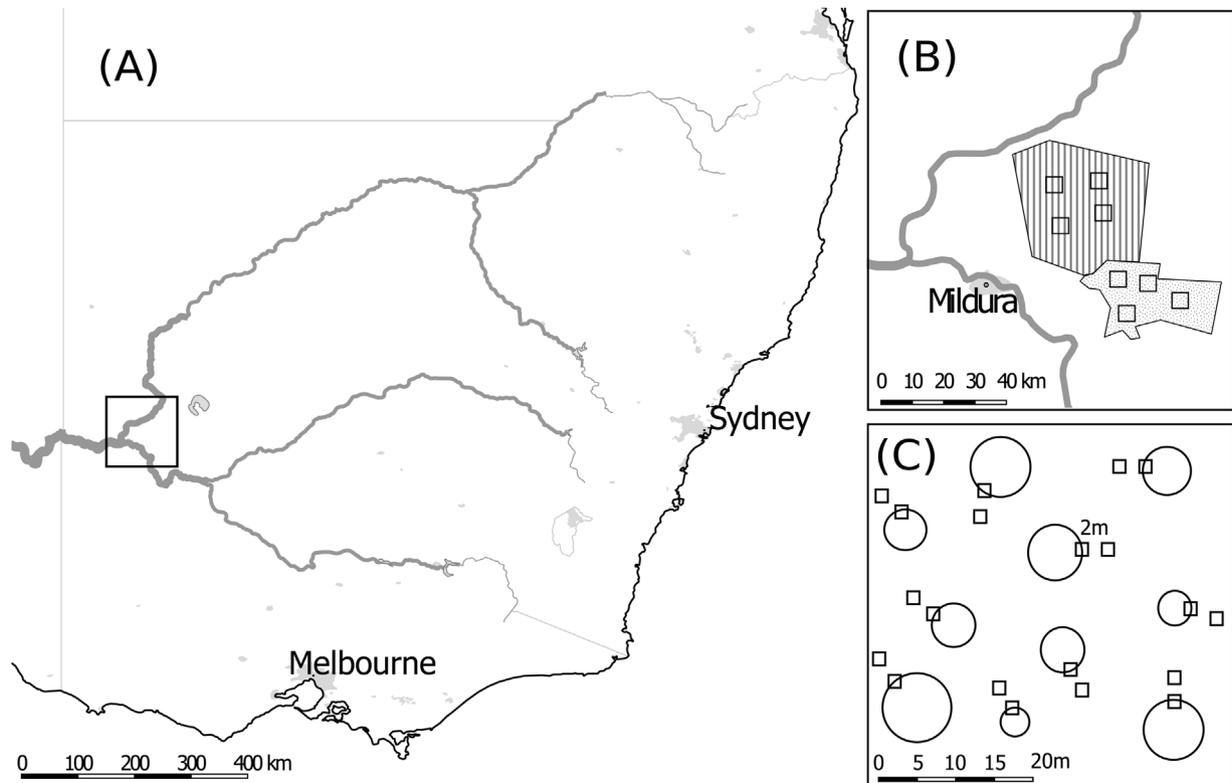


Fig. 1. (A) Schematic map of south-eastern Australia showing the location of the study area. (B) Schematic map of our study area with the two study locations, the livestock-free conservation area (Mallee Cliffs, dotted area) and the livestock grazed adjacent properties (striped area). The squares indicate the eight 50 m × 50 m study sites (not to scale). (C) Schematic representation of one study site with 10 different sized shrubs indicated by circles. At each shrub the paired plots are shown as two squares within a distance of 2 m.

expected that larger shrubs with more foliage and deeper larger roots would have more macropores around their roots and provide more habitat for macropore-producing biota such as ants and termites (Colloff, Pullen, & Cunningham, 2010).

Materials and methods

Study site description

Our study was conducted approximately 30 km north-east of Mildura (34°06'S, 142°06'E) in the livestock-free conservation area Mallee Cliffs and the neighboring grazing properties in the Murray basin in south-western New South Wales (NSW), Australia (Fig. 1A and B). Mallee Cliffs was managed as a pastoral lease and gazetted as a National Park in 1977. Stocking rates prior to gazettal varied according to vegetation community but were in the order of about 0.1 DSE ha⁻¹ (dry sheep equivalent i.e. one non-lactating ewe) in the belah woodland (Department of Lands, unpubl. Data, 2003). Current grazing rates for the surrounding grazed properties ranged from about 1.8 to 3.1 DSE ha⁻¹ and the area has had a long history of heavy grazing. Stocking rates were extremely low for Mallee Cliffs National Park (<0.1 DSE ha⁻¹ from occasional feral goats). The region is classified as semi-arid savannas (Aridity Index = 0.26–0.39) with a cli-

mate characterized by high variation in low annual rainfall ranging from 115 mm to 705 mm, temperatures ranging from a maximum daily temperature of 33 °C in hot dry summers to a daily minimum temperature of 4.5 °C in cool winters, and high potential evapotranspiration (~1500 mm/year). The soils are classified as Hypercalcic Calcarosols (McDonald, Isbell, Speight, Walker, & Hopkins, 1998) and textural class is fine-textured loam, which support the formation of biocrusts (Eldridge et al., 2010). The vegetation community consists of grassland with scattered trees with a variable cover of shrubs such as *Eremophila sturtii*, *Senna artemisioides* and *Dodonaea viscosa*, and perennial grasses such as *Austrostipa* spp. and *Austrodanthonia* spp. (Keith, 2004). The area between the grasses and shrubs range of bare soil (under cattle grazing) to a rich community of biocrusts (in the conservation reserve).

Study design and field measurements of soil hydrological properties

We randomly selected eight 50 m × 50 m sites with shrubs, four grazed by cattle (grazed sites) and four ungrazed (conservation sites) (Fig. 1B). Sites were located at least 5 km apart, and the grazed sites spanned several paddocks across neighbouring grazing properties. At each of the eight sites

we selected 10 paired plots centered on 10 *Eremophila sturtii* shrubs. The 10 plots comprised the shrub and its nearest interspace at least 2 m from any shrub canopy, which was dominated by either grasses, generally *Austrostipa*, or annual forbs and herbs (Fig. 1C). To test for the effects of shrub height on infiltration, the 10 shrubs within each site were haphazardly selected to emulate a gradient in shrub height from small short shrubs to large tall shrubs (see Supplementary Appendix A: Table 1). The minimum distance among the 10 paired plots at each site was 10 m.

At each microsite (shrub, open), we measured soil hydrological properties with two disc permeameters, one under ponded conditions (+10 mm) and one under a negative tension (−40 mm). The two disc permeameters were placed about 30 cm apart so that we could directly compare the results from both permeameters. The permeameter under tension was placed on a thin bed of sand to provide uniform contact with the soil surface and the ponded permeameter was placed on a steel ring (diameter: 23 cm) above a 2 cm deep pond of water. Measurements were run for 15 min, or until steady-state infiltration had been achieved. In addition to the infiltration measurements, we measured three soil attributes: (1) the percentage of the soil within the ponded reading that was covered by detached plant material (litter), (2) the percentage of the soil surface that was covered by biocrusts, and (3) the number and size of biologically produced pores on the surface (macropores). To measure macropores, we carefully removed the litter from the surface after conducting the hydrological measurements and counted the number of pores and measured their maximum diameter using vernier calipers. These pores are produced by ants, termites and other soil-resident invertebrates. All measurements were conducted within a period of two consecutive days in December 2016.

Sorptivity is independent of gravitational forces and is dominated by the tendency of soils to transmit water by capillarity. There are various estimates for how long sorptivity is the driving force of infiltration, but it mostly lasts for less than 10 min and depends on soil type (Perroux & White, 1988). Once the infiltration rate becomes constant and the water flow is dominated by gravitational forces, steady-state infiltration occurs. The tension permeameter with −40 mm negative pressure measures only water flow through soil micropores with a diameter less than 75 μm, i.e. infiltration only occurs between individual soil particles within the soil matrix. The ponded infiltration permeameter, on the other hand, measures water flow through micropores of the soil matrix, as well as larger biogenic soil pores (macropores), created by roots or soil-burrowing animals with a diameter >0.7 mm. With these measures, a macroporosity index was calculated, as the ratio of sorptivity at the two applied tensions: $MI = (\text{sorptivity}_{+10 \text{ mm}} / \text{sorptivity}_{-40 \text{ mm}})$. This index reveals the extent to which macropores contribute to total water flow (White, 1988). It is indicative of conductive, functional soils

with high levels of biological activity (Perroux & White, 1988).

Statistical analysis

Rather than use a model selection process to find the optimal model design, we designed our model to test our specific hypotheses. We used mixed-effects models in R Version 3.5.1 (R Core Team, 2018) to analyze the additive fixed effects of grazing (grazed vs. ungrazed) and the size/presence of shrubs (shrub vs. open; diameter of open sites = zero) and their interaction on five hydrological values: sorptivity and steady-state infiltration under both tension and ponding, and the macroporosity index. Sites and pairs were used as random effects, with pairs nested within sites. Prior to analysis all hydrological values were \log_{10} transformed to meet the assumptions of linear models and results presented as back-transformed means. Our models were fitted using REML and p-values were derived using Kenward-Roger approximations for degrees of freedom. Diagnostic tests available in R (e.g. normality, homoscedasticity etc.) were examined prior to analyses.

In a second set of analyses we used structural equation models to examine the direct and indirect effects of grazing, shrubs (using height as our attribute), litter cover, biocrust cover and the number of pores on our measure of hydrology. This approach allowed us to simultaneously analyse how the relationships between multiple connected variables impact the hydrological processes. The understanding of the tested system thereby determines the respective causal relationships and their direction. Structural equation models use variance and co-variance matrices to iteratively estimate unknown parameters of the model as variances of endogenous parameters, path coefficients and total effects (the sum of direct and indirect effects of one variable on another). Five models were performed. Our a priori model predicted that shrubs, litter and the number of pores would have positive effects, whereas grazing would have negative effects, on our five measures of hydrological function (see Supplementary Appendix A: Fig. S1). Our model is based on our expected understanding of hydrology in semiarid savanna systems, i.e. larger shrubs have more litter (Eldridge, Wang, & Ruiz-Colmenero, 2015) and a greater number of larger macropores beneath their canopies (Marquart, unpublished data), and grazing reduces litter and biocrust cover (Daryanto, Eldridge, & Wang, 2013) and the number of macropores (Colloff et al., 2010). Infiltration is known to be reduced by overgrazing (Houlbrooke & Laurenson, 2013), and thought to increase with increasing shrub height (Eldridge, Wang et al., 2015), litter, biocrust cover (Blackburn, 1975; Faist et al., 2017), and the density of macropores (e.g. Mando et al., 1996). Specifically, we expected that livestock grazing would have direct effects on our hydrological measures and indirect effects, mediated by changes in litter and biocrust cover and number of biogenic pores. Our data were z-transformed (standardized) prior to all

Table 1. Mean (\pm SE) values for the five measures of hydrology for the four combinations of grazing (grazed, ungrazed) and microsite (shrub, open).

Hydrological attribute	Grazed				Ungrazed			
	Shrub		Open		Shrub		Open	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Sorptivity under ponding (+10 mm)	113.0	± 10.34	76.0	± 6.56	160.5	± 12.55	112.1	± 7.10
Sorptivity under tension (−40 mm)	10.2	± 0.82	9.4	± 0.69	19.4	± 1.27	19.6	± 1.38
Steady-state infiltration (+10 mm)	34.6	± 3.57	16.8	± 2.15	51.1	± 4.02	36.7	± 3.74
Steady-state infiltration (−40 mm)	2.4	± 0.21	2.1	± 0.13	6.0	± 0.75	5.8	± 0.67
Macroporosity index	17.0	± 3.26	13.0	± 3.37	10.0	± 1.17	6.7	± 0.64

analysis. Standardized coefficients are model parameter estimates based on the analysis of standardized data, in the sense that all variables are supposed to have unit variance. Standardized data are affected less by the scales of measurement and can be used to compare the relative impact of variables (Kwan & Chan, 2011). All structural equation modelling was carried out using the lavaan package (version 0.5-22) in R Version 3.5.1 (R Core Team, 2018; Rosseel, 2012).

Results

All four measured hydrological variables were significantly lower at the grazed than the ungrazed sites (Table 1). Livestock grazing reduced steady-state infiltration under tension by $61.5 \pm 8.8\%$ ($F_{1,6} = 11.63$, $P < 0.05$) and under ponding by $41.4 \pm 8.3\%$ ($F_{1,6} = 14.61$, $P < 0.01$). On grazed sites sorptivity was $49.7 \pm 5.5\%$ lower under tension ($F_{1,6} = 18.92$, $P < 0.01$) and $30.7 \pm 7.3\%$ under ponding ($F_{1,6} = 7.09$, $P < 0.05$) (Fig. 2).

At the level of the microsites (shrub canopy vs. open soil), sorptivity and steady-state infiltration under ponded conditions were significantly higher under shrub canopies, than in the open (mean steady-state infiltration: under shrub: 42.85 mm/h, open soil: 26.76 mm/h; $F_{1,79} = 33.52$, $P < 0.001$; Sorptivity: under shrub: $136.73 \text{ mm h}^{-0.5}$, open soil: $94.04 \text{ mm h}^{-0.5}$; $F_{1,79} = 22.65$, $P < 0.001$). The presence of shrubs partly compensated for the negative effects of grazing on steady-state infiltration (Fig. 2D), but this was only marginally significant ($F_{1,78} = 2.92$, $P = 0.091$). Under tension, the presence of shrubs had no effect.

The average macroporosity index was about one-third greater under shrub canopies than in the open ($F_{1,79} = 9.92$, $P = 0.002$). The lowest average values were recorded for open soil at ungrazed sites (6.71) and highest values under shrub canopies at grazed sites (16.95) (Fig. 3A). Both average litter cover and surface macropore density were greater under shrub canopies than in the open, while the effect of grazing on both variables was negligible (Fig. 3A and C). Biocrust cover, conversely, was higher in the open than under the canopy (Fig. 3D).

Our structural equation models showed that grazing had an overall negative effect on hydrology, while shrubs had a strong positive effect, and therefore larger shrubs enhanced water flow (Fig. 4). The only effects of biocrusts were a negative effect on sorptivity under tension and a positive effect on the macroporosity index (Fig. 5). Contrary to expectation, we found no effects of macropore size or density on hydrological properties, and no effects of litter cover.

Discussion

In this study we examined the combined effects of grazing and shrub size on hydrology in a semiarid Australian savanna. We found clear evidence that infiltration rates were greater under shrubs and that the effect increased with increasing shrub size, but only under ponded conditions when water was allowed to flow through both small matrix pores and large, biogenically-produced macropores. We also found a strong suppressive effect of grazing on hydrology, of a similar, but opposite, magnitude to that of the shrub effect. Together our results indicate that the retention of shrubs in savanna environments might partially offset any negative effects of grazing on hydrology.

Shrubs enhance infiltration

Our results show that shrubs were a strong driver of infiltration in savanna soils, consistent with a large body of literature comparing water flow under the canopies of woody plants with that in the open (e.g. Bhark & Small, 2003; Eldridge, Wang et al., 2015; Ludwig et al., 2005; Lyford & Qashu, 1969; Vandendorj, Eldridge, Travers, Val, & Oliver, 2017). In our study, this effect was only found under ponded conditions, when all soil pores conduct water, indicating the importance of macropores in the infiltration process. This result is also consistent with the measured macroporosity index, which increased under shrub canopies on both grazed and ungrazed sites, implying that the differences in infiltration were caused by a larger number of water-conducting macropores. These biologically generated voids created mainly by soil burrowing arthropods and dead plant roots are to a large

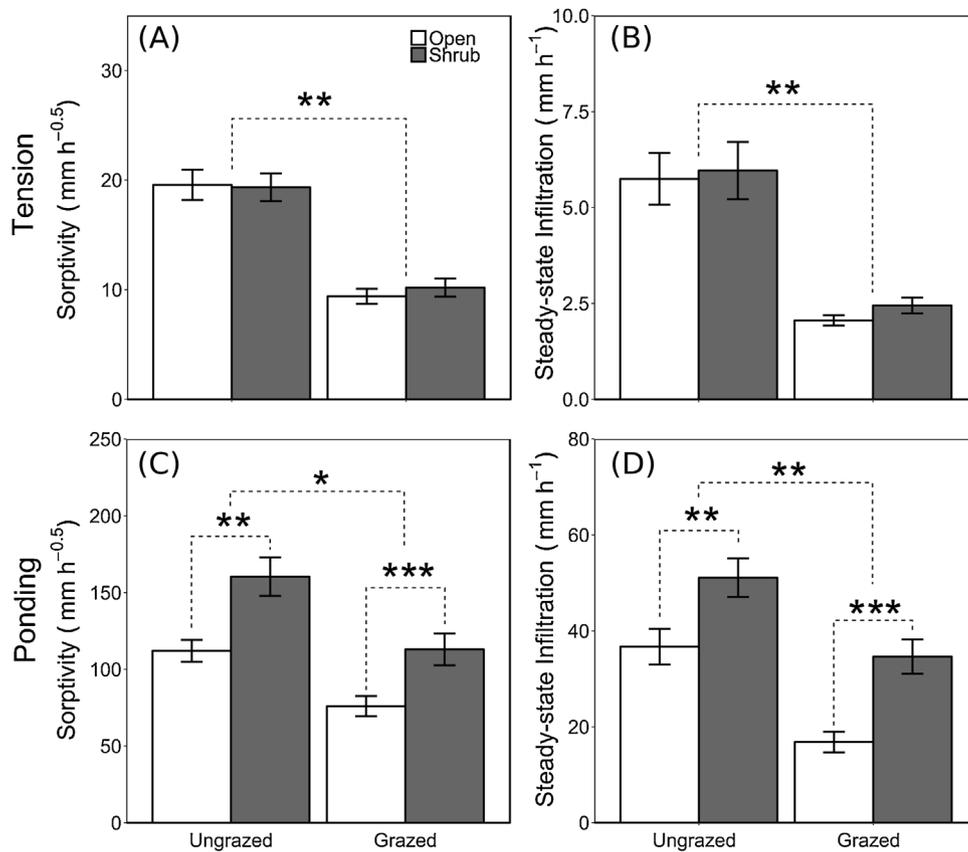


Fig. 2. Back-transformed means (\pm SE, $n = 40$) for sorptivity ($\text{mm h}^{-0.5}$) and steady-state infiltration (mm h^{-1}) under -40 mm tension (A & B) and under $+10$ mm of ponding (C & D) for the two grazing regimes and microsites. Pairwise comparisons between the means were calculated using our generalized linear models with Kenward-Roger approximations for degrees of freedom. Significant differences are indicated by asterisks (*: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$).

extent found beneath perennial vegetation such as grasses and shrubs (Colloff et al., 2010).

We expected, therefore, that shrub size would be highly correlated with soil hydrological function, given that larger shrubs have deeper roots, and produce a greater cover and mass of litter, which can increase infiltration by promoting aggregation and soil organic matter (Bronick & Lal, 2005) and are known to provide habitat and nutrition for a wide range of soil-disturbing animals such as termites and ants that are advantaged by the increased availability of food resources (Boeken & Orenstein, 2001; Daryanto et al., 2013b; Martínez-Yrizar, Núñez, & Búrquez, 2007). Increases in the density of subterranean arthropods lead to a greater number of tunnels and biopores, feeding back on soil properties and leading to greater infiltration rates (Léonard & Rajot, 2001; Mando et al., 1996). In our study we found a positive effect of shrub size on the number of visible surface macropores, but no meaningful relationships between total surface macropore density or area and hydrology. This was surprising, but is not clear evidence that our results are not driven by differences in soil macropore status or that surface pores are indicative of subsoil porosity. Dryland savanna communities in Australia support abundant communities of subterranean termites (Noble, Diggle, & Whitford, 1989;

Spain, Okello-Oloya, & Brown, 1983). Studies over the past five years at Mallee Cliffs, the site of our conservation reserve, reveal a high density of termite-constructed pavements; up to 15 ha^{-1} (James Val, unpublished data, 2018). Other biopore-forming invertebrates are also common in these landscapes (e.g. Delgado-Baquerizo et al., 2018), and are likely responsible for the observed higher rates of infiltration under the shrubs. The fact that we did not detect differences in macropore densities in our plots can be attributed to the characteristic channels built by these invertebrates that conduct water, but rarely open at the surface.

Impacts of cattle grazing on hydrology

We found strong suppressive effects of cattle grazing on our four measures of hydrology. For those measurements under ponded conditions, the strength of the grazing effect was very similar, but opposite, to that of the shrubs. Effectively, this means there are two competing drivers of hydrology in this system; shrub canopies and grazing. Apart from any macropore-driven effects, we would expect infiltration to be greater under shrub canopies because they provide a physical barrier to the movement of livestock. Irrespective of their

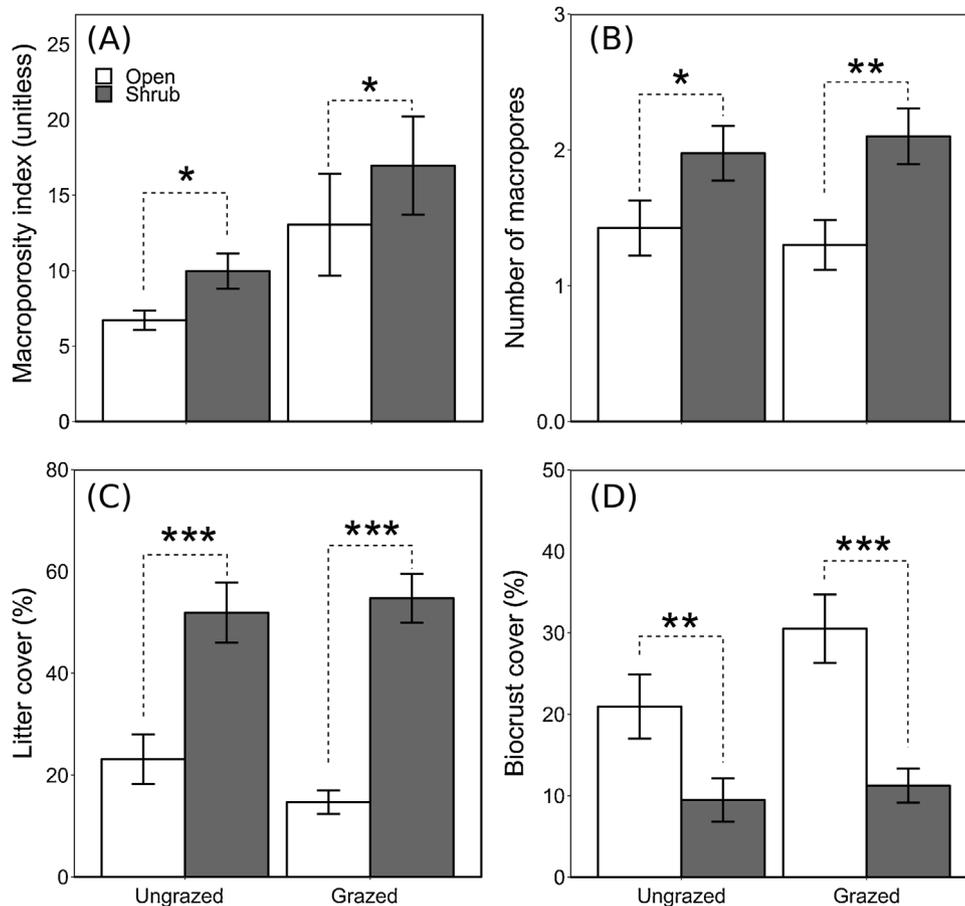


Fig. 3. Back-transformed means (\pm SE) of (A) macroporosity index, (B) number of macropores (C) litter, and (D) biocrust cover for the two grazing regimes and microsites. Pairwise comparisons between the means were calculated using our generalized linear models with Kenward-Roger approximations for degrees of freedom. Significant differences are indicated by asterisks (*: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$).

body size, all herbivores including cattle would have access to open savanna sites. Densely-woody, plant-covered sites have been shown to restrict the entry of large-bodied herbivores such as cattle (Eldridge, Delgado-Baquerizo, Travers, Val, & Oliver, 2018). These herbivores have been shown to alter vegetation community composition and soil surface condition, and therefore, the capacity of soils to conduct water (Yates, Norton, & Hobbs, 2000).

Conversely, large shrubs provide protection from intense solar radiation, and cattle have been observed to actively move to shaded patches to avoid heat stress (Tucker, Rogers, & Schütz, 2008). Therefore, soil beneath large shrubs would likely be affected by trampling (Hiernaux, Biellers, Valentin, Bationo, & Fernández-Rivera, 1999). Hence, the positive effect of shrub height on infiltration would likely be moderated for larger shrubs on the grazed sites that provide shade for livestock. Surprisingly we did not observe an interaction between shrub size and livestock grazing, but this circumstance might to some extent explain the similar trends between open soil and shrub plots on livestock-grazed and

conservation sites for ponded sorptivity and steady-state infiltration.

Trampling by livestock can have profound effects on macropore structure and extent, and reduce pore connectivity (Mead & Chan, 1992). In our study, the standardized total effect of cattle on the macroporosity index was 0.20, indicating that cattle had an overall positive effect on the index (Table 2). This might at first seem counterintuitive, but given the way that the indices are calculated, high levels of sorptivity under tension would likely result in a reduction in the value of the index, meaning that a larger fraction of total infiltration is controlled by macropores. Grazing is known to compact surface soils (Byrnes et al., 2018; Graetz & Tongway, 1986; Tate, Dudley, McDougald, & George, 2004), so heavy levels of cattle grazing could conceivably compact the surface layers and therefore increase the matrix density without significantly reducing the macroporosity associated with subterranean termite and ant burrows. Our study did not find an impact of grazing on litter cover or the density/size of surface macropores, indicating that grazing under the lev-

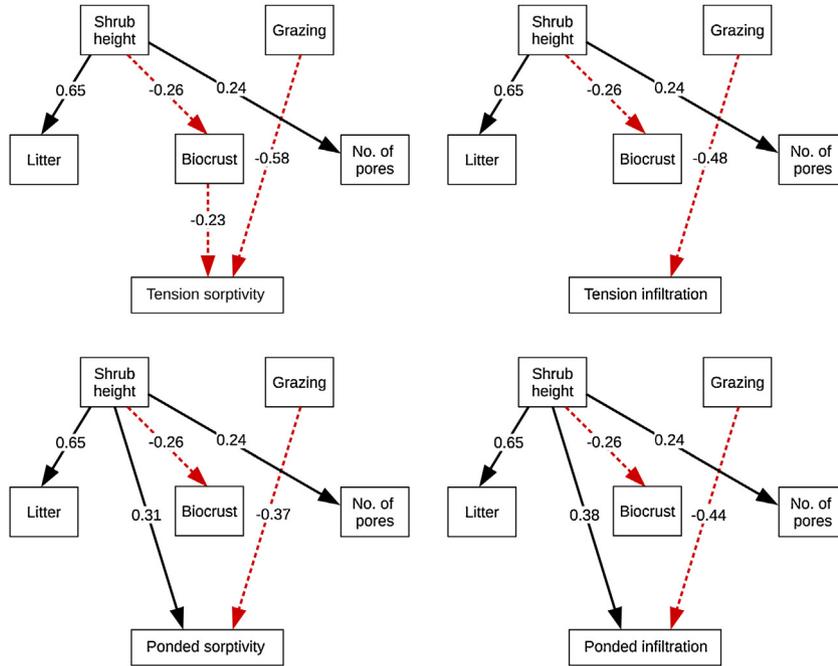


Fig. 4. Structural equation models for the four measures of hydrology. The value and sign of the standardized path coefficients indicate the strength of the effects among variables. Negative relationships are shown as broken red arrows and positive relationships are represented by solid black arrows. Non-significant pathways are not shown. The proportions of variance explained (R^2) are as follows: tension sorptivity: 0.38, tension infiltration: 0.25, pondered sorptivity: 0.29, pondered infiltration: 0.38. Model fit for all models: $\chi^2 = 0.48$, $df = 3$, $P = 0.92$, $NFI = 0.997$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2. Standardized total effects (sum of direct and indirect effects) of the different variables on the five hydrological measures. Only significant effects are shown ($P < 0.05$).

Attribute	Sorptivity		Steady-state infiltration		Macroporosity index
	Ponding	Tension	Ponding	Tension	
Grazing	-0.37	-0.58	-0.44	-0.48	0.20
Shrub height	0.37	-	0.41	-	0.21
Litter cover	-	-	-	-	-
Biocrust cover	-	-0.23	-	-	0.20
Macropores	-	-	-	-	-

els experienced in this site were unlikely to reduce litter levels required to support subterranean termite populations. Indeed, in other studies we have found that increased grazing leads to reduced levels of litter cover but this depends on the type of grazing herbivore and site productivity (Eldridge, Delgado-Baquerizo, Travers, Val, & Oliver, 2017).

Conclusions

Our results indicate that the presence of shrubs can partly compensate for the negative effects of heavy livestock grazing on infiltration processes, and this effect is greater for larger shrubs. In the context of traditional management practices in semi-arid rangelands such as broadscale shrub removal to increase pastoral production, pastoralists should be cognizant of the fact that there are production benefits of retaining

areas of shrubs to sustain functional hydrological processes. Larger plants had a greater positive impact on hydrology. Thus the retention of larger shrubs and reduction in livestock grazing would likely have multiple ecosystem benefits such as greater biodiversity of a range of taxa including arthropod fauna (Blaum et al., 2009; Fabricius, Burger, & Hockey, 2003; Hering et al., 2018), leading to multiple positive feedbacks, including improved soil health. Greater infiltration capacity, supported by a more patchy vegetation pattern, reduces water runoff and erosion, counteracting degradation processes such as gully erosion. As larger shrubs enhance the mass of litter on the soil and the density of surface macropores, we would expect larger plants to become focal points for hydrology, biodiversity and ultimately, sites of sustained productivity and diversity of understorey plants. In light of predicted future climate scenarios involving lower more variable rainfall, a greater density of large-sized shrubs would likely buffer the

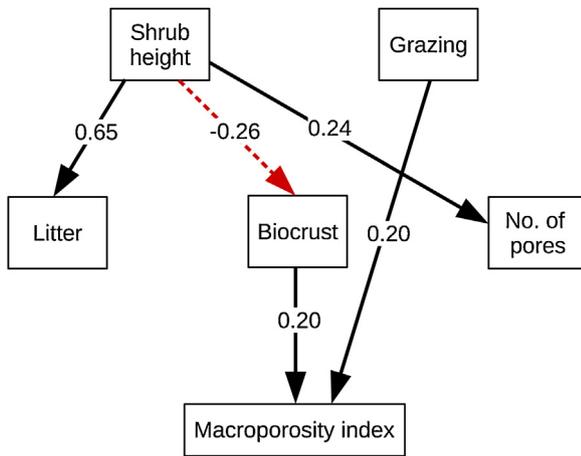


Fig. 5. Structural equation model for the macroporosity index. The value and sign of the standardized path coefficients indicate the strength of the effects among variables. Negative relationships are shown as broken red arrows and positive relationships are represented by solid black arrows. Non-significant pathways are not shown. The proportion of variance in the macroporosity index explained by the variables in the model is 0.14. Model fit: $\chi^2 = 0.48$, $df = 3$, $P = 0.92$, $NFI = 0.997$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

effects of a drier hotter climate compared with cleared rangelands.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.baae.2019.06.003>.

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