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RESEARCH ARTICLE

Microsite and grazing intensity drive infiltration in a semiarid woodland

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Abstract

Human activities such as vegetation removal and overgrazing that result in changes in land cover have substantial impacts on ecosystem processes, including the infiltration of water. Different land cover types (microsites) vary in their capacity to conduct water, but the extent to which infiltration is affected by different herbivores or microsites is largely unknown. We examined the effects of grazing and microsite on infiltration in two extensive woodland communities in semiarid eastern Australia that vary in current condition. Poor condition sites had lower steady-state infiltration under ponding than either average or good condition sites, and this effect was consistent across the two communities. Ponded infiltration and sorptivity beneath grasses, shrubs or trees were about twice that on bare soil, and this corresponded to greater indices of macroporosity. Structural equation modelling showed that shrubs, trees, and grasses had strong positive effects on sorptivity and steady-state infiltration under ponding, whereas grazing had generally negative effects. The suppressive effects of grazing on soil hydrological processes were mainly due to cattle grazing. The positive effects of grasses, shrubs, and trees on hydrology were twice as strong as the negative effects of grazing. Our results also suggest that prolonged overgrazing that leads to reductions in grass cover is likely to have a synergistic reduction in hydrological function in these woodlands by reducing the cover of highly conductive patches and by reducing the extent of macropores.

KEYWORDS

disk permeameter, grazing, infiltration, livestock, macropores, semiarid woodland

1 | INTRODUCTION

Human activities have led to dramatic changes in land cover and land use, with flow on effects to ecosystem properties and processes, and the livelihoods of its human inhabitants. The impacts of land cover change are likely to be most pronounced in arid and semiarid environments (drylands) that are already severely degraded and predicted to increase in size by up to 23% by the end of this century (Pravalie, 2016). Drylands also support about 40% of Earth's human population, many in the developing world (Pravalie, 2016). Understanding how they respond to land cover and land use change therefore is a critical knowledge need if governments are to formulate policies and develop strategies to improve management and prevent further degradation.

Vegetation clearance and overgrazing by European livestock have been identified as two major drivers of land use and land cover change

in drylands (Maestre et al., 2016). In eastern Australia, much of the native vegetation has been substantially altered by a combination of vegetation clearing and overgrazing in the 200 years since European settlement. Extensive removal of vegetation, primarily for agriculture, has converted large areas of the original extensive cover of eucalypt woodlands into a series of small fragmented remnants with only a relatively small percentage of the original unmodified woodlands remaining (Prober & Thiele, 1995). Tree loss has been associated with almost every aspect of land degradation in Australia (Bird et al., 1992), with degradation of remnants indicated by the rapid decline and death of trees, lack of recruitment, loss of understorey species, soil erosion, and invasion by unpalatable, often exotic plant species (Yates & Hobbs, 1997). Although some extensive patches of woodland still persist on the margins of the subhumid zones, many are substantially degraded, in poor health, and often dominated by old even-sized trees with little evidence of recruitment (Yates & Hobbs, 1997).

Overgrazing, the second major driver of woodland degradation, can lead to short-term shifts in the composition of plant communities and longer term, more insidious effects on woodlands by degrading surface soils (Eldridge, Delgado-Baquerizo, Travers, Val, & Oliver, 2016; Lunt, Eldridge, Morgan & Witt 2007; Zhang, Eldridge, & Delgado-Baquerizo, 2016). Livestock trampling, for example, compacts the soil surface, reduces its structural complexity, and alters nutrient pools and hydrological processes (Eldridge, Soliveres, Bowker, & Val, 2013). More localised effects include increases in runoff and erosion (Smith et al., 2007). Grazing-induced changes in hydrological function in woodlands can have cascading effects on ecosystem properties and processes and lead to long-term reductions in pastoral production and resilience (Fernandez, Gil, & Distel, 2009). Grazing has been shown to influence hydrological function in northern Australian rangelands (Frazer and Stone, 2006), and a comprehensive assessment of livestock effects indicates substantial reductions in ecosystem function, including changes in soil function, by overgrazing (Eldridge, Poore, Ruiz-Colmenero, Letnic, & Soliveres, 2016).

Australia's semiarid woodlands are highly structured into three broad microsite types that have markedly different hydrological signatures: (a) woody (tree and shrub) patches, (b) intervening interspaces dominated by herbaceous plants, biocrusts (biological soil crusts), and bare soil, and (c) patches of perennial grasses interspersed throughout the interspaces (Eldridge & Freudenberger, 2005). These three microsites differ markedly in their capacity to capture and store rainfall (DeFries & Eshleman, 2004; Eldridge & Freudenberger, 2005), and are maintained by strong source-sink processes driven by the redistribution of runoff water (Chartier, Rostagno, & Pazos, 2011; Gómez, Olivas, Moreno, Sannwald, & Rodríguez, 2015). Overgrazing, which can eliminate perennial grasses (Hodgkinson, Terpstra, & Muller, 1995), and removal of trees and shrubs lead to major changes in woodland hydrology. However, the relative effects of both processes are poorly known. Although much is known about the effects of tree removal on hydrological processes at the regional scale (e.g., Zhang, Walker, & Dawes, 1999), relatively little is known about how more subtle processes of grazing might influence infiltration. Grazing has been shown to remove perennial grasses and reduce the capacity of woodland soils to conduct water by destroying macropores (Eldridge & Koen, 2003). Perennial grasses may represent the only structural vegetation elements in the semiarid woodlands, where trees have been removed, and may provide, therefore, the only opportunity to trap runoff and enhance infiltration.

Perennial grasses conduct large quantities of water (Castellano & Valone, 2007; Chartier et al., 2011; Eldridge et al., 2013), but differences in their relative effectiveness compared to trees and shrubs will depend on disturbance history, soil condition, plant and litter cover, and the extent of biologically produced pores (macropores or biopores) in the soil. Here, we examined the effects of (a) quantitative site condition (based on disturbance history), (b) quantitative grazing intensity, and (c) microsite (patch) type on infiltration in two woodland communities that occur over large areas of semiarid eastern Australia and that have been subjected to varying levels of disturbance since European settlement. We first compared the early (sorptivity) and late (steady-state infiltration [SSI]) stages of infiltration under four microsites (trees, shrubs, perennial grasses, and bare soil) at sites allocated to three

levels of grazing-induced disturbance from healthy functional to severely degraded and dysfunctional sites. We predicted that woody patches would have greater infiltration across the gradient but that there would be strong interactions between microsite and site condition; specifically, that woodland sites in good condition would have higher infiltration across all four microsites. This should occur because well-managed sites would have soils that are dominated by macropores, which largely drive the infiltration process. We then examined the effects of grazing intensity by domestic livestock (sheep or goats and cattle) and free-ranging herbivores (kangaroos and rabbits) on infiltration using structural equation modelling. We predicted that infiltration would be greater under woody patches than grasses or bare soils but that increased grazing intensity would reduce infiltration by reducing plant cover and changing surface soil morphology. This would occur because grazing would be expected to reduce plant size and therefore litter production and habitat for soil microarthropods such as termites that are important for conducting water through macropores.

2 | METHODS

2.1 | Study sites and design

The study was undertaken at 36 sites across two woodland communities, black box (*Eucalyptus largiflorens*) and cypress pine (*Callitris glaucophylla*) that occur over extensive areas of eastern Australia. The sites were located between Cobar in northern New South Wales and Tocomwal in southern New South Wales across an area used extensively for livestock grazing but with smaller areas devoted to conservation and forestry. Across this area the climate is Mediterranean and semiarid (aridity index = 0.26 to 0.39; see below), with slightly greater rainfall in the east-central areas during the six warmer months, and in the south and southwest during the six cooler months. Average rainfall (385 to 460 mm yr⁻¹) and average temperatures (~18 °C) varied little across the sites.

For each community, we examined 18 individual sites scattered widely across the distribution of the community; six in the northern region, six in the centre, and six in the south. Sites in each region spanned a grazing disturbance gradient (see below). Each region had six sites, with two replicates of each disturbance state (i.e., condition classes), undisturbed (good condition), moderately disturbed (average condition), and highly disturbed (poor condition; $n = 36$).

2.2 | Quantitative determination of degradation status and grazing intensity

Sites were assigned to one of the three condition classes, based largely on grazing management history derived from data from a large regional survey of 300 sites within these two communities. The assignment was based on values of biocrust, litter and groundstorey plant cover, soil carbon, soil surface health and morphology, and the extent of livestock and wild herbivore (kangaroos, *Macropus spp.*; European rabbits, *Oryctolagus cuniculus*) grazing (Appendix S1). For example, undisturbed (high condition) sites had an extensive cover of biocrusts, extensive litter cover, a plant

community dominated by native species with a good mixture of annuals and perennials, abundant large grass butts, little evidence of erosion, high scores of the stability index (see Appendix S2), and little evidence of recent (dung counts) or historic (stock tracks) livestock grazing. Highly disturbed sites were characterised by opposite levels of these attributes, and moderately disturbed sites intermediate between the two.

At each of the 36 sites, we established a 100 m transect, perpendicular to the main watering point, along which we positioned three large quadrats (5 m × 5 m) at 0, 50, and 100 m. Within these plots, we centrally located a smaller (0.5 m × 0.5 m) quadrat. To assess grazing intensity, we counted the dung of sheep or goats, kangaroos, and rabbits in the small quadrats, and sheep or goats, rabbits, kangaroos and cattle dung in the large quadrats. Dung and pellet counts have been used widely to estimate the abundance of large herbivores, including kangaroos (Johnson & Jarman, 1987; Marques et al., 2001). For cattle, we counted dung events rather than individual fragments, that is, we considered a number of small fragments to have originated from one dung event if the fragments were within an area of a few metres. We used algorithms, developed previously for the study area (see Eldridge, Delgado-Baquerizo, et al., 2016) to calculate the total oven-dried mass of dung per hectare per herbivore based on the number of pellets recorded in the field. This total oven-dried mass of dung was used as our measure of recent grazing intensity for each herbivore (Eldridge, Poore, et al., 2016). Where dung of a particular herbivore occurred in both small and large quadrats, the values were averaged. Our measure of historic livestock grazing was calculated as the total cross-sectional area of livestock tracks crossing the 100-m transect at each site.

2.3 | Assignment of microsites and measures of soil health

To measure soil hydrology, we used the three positions along the 100-m transect to select replicate microsites. At each of the three transect positions, we selected four different microsites (tree, shrub, perennial grass, and bare soil). Small (0.5 m × 0.5 m) quadrats were placed at each of these microsites. For trees and shrubs, the quadrats were placed towards the centre of the canopy, but for grasses, around individual butts or clumps of grasses. Within these small quadrats, we assessed the cover of all vascular plants by species. These data were used to obtain a value of total plant richness and average plant cover for each microsite per site.

Within the small quadrats, we also assessed the health of the soil surface (*sensu stricto* Tongway, 1995) by measuring 12 surface attributes: surface roughness, crust resistance, crust brokenness, crust stability, surface integrity, cover of deposited material, biocrust cover, plant basal cover, litter cover, litter origin, the degree of litter incorporation, and surface soil texture (Appendix S2). The values of these attributes were used to calculate an index of soil health as the sum of the values of the 12 surface attributes divided by 72, the maximum possible score, and expressed as a percentage (Appendix S2). Indices derived from these 12 attributes have been shown to be strongly correlated with ecosystem functions related to soil stability, nutrient cycling, and infiltration (Maestre & Puche, 2009).

2.4 | Field measurements of soil hydrological properties

At each microsite, we used two disk permeameters, simultaneously, to measure sorptivity and SSI under ponding (+10 mm) and under tension (−40 mm). Disk permeameters were placed within 30 cm of each other or as close as possible for measurements over grass butts. The tension permeameter was placed on a thin bed of sand to provide a uniform contact with the soil surface, and the ponded permeameter on a steel ring above a pond of water about 5 cm deep. For shrubs and trees, the permeameters were placed towards the centre of the canopy. For grass microsites, the above-ground material was clipped and the permeameters placed directly over the grass butt. The permeameters were run for at least 12 min to ensure that they had achieved SSI. This method allowed us to calculate values for both stages of infiltration: sorptivity, the early stage, and SSI, the final stage of infiltration.

Sorptivity is the initial rapid stage of infiltration, which occurs when the soil is initially dry and water flow is dominated by the soil's capillarity properties. This stage usually lasts less than 10 min (White, 1988). SSI, the latter phase of infiltration, occurs once the flow rate is constant and gravitational forces predominant (Eldridge, 1993; White, 1988). The −40 mm tension (negative pressure) was applied to the permeameter under tension. This measures water flow through matrix pores (*syn.* micropores), that is, the interspaces between individual mineral grains and soil particles, which are not biogenic. The ponded permeameter measures flow through both matrix pores and macropores (Perroux & White, 1988). Macropores are biogenic pores formed by plant roots or soil fauna and are generally >0.7 mm in diameter (James, Eldridge, Koen, & Whitford, 2008).

2.5 | Statistical analysis

Our analyses were conducted in two stages. In the first stage, we used linear mixed models analysis of variance in R (Version 0.98.1102, R Core Team, 2016) to assess the effects of three levels of site condition on five hydrological values: four measures of infiltration (sorptivity and SSI under both ponding and tension) and a macroporosity index. The macroporosity index is defined as the ratio of sorptivity at two supply potentials ($\text{sorptivity}_{+10 \text{ mm}}/\text{sorptivity}_{-40 \text{ mm}}$). This index reveals the extent to which macropores contribute to total water flow (White, 1988). It is indicative of conductive and functional soils with high levels of biological activity (Perroux & White, 1988). The five hydrological values were \log_{10} transformed prior to analysis to stabilise the residuals and the results presented as back-transformed means. The first stratum of the analysis of variance model examined community effects (blackbox vs. cypress pine) and the second stratum site condition (good, average, and poor) and its interaction with community. The third stratum examined microsite effects (tree, shrub, grass, and open) and the two- and three-way interactions with site condition and community. Tukey's post hoc Least Significant Difference (LSD) test was used to compare group means. Additional stata examined random effects such as region, that is, whether the sites were in the north, central, or southern parts of the community.

In the second stage, we used structural equation modelling (SEM) to explore relationships among our hydrological variables, our

quantitative assessments of grazing intensity, and tree-shrub-grass microsites (see Appendix S3). SEM tests the plausibility of a causal model, based on a priori information, in explaining the relationships among different variables. In our model, we predicted that grazing intensity would have direct effects on individual measures of hydrology (e.g., SSI under ponding) but also indirect effects via changes in soil health and plant cover. We expected microsite to also exhibit direct effects on specific hydrological measures. We used SEM because it allowed us to partition direct and indirect effects of one variable upon another and to estimate the strengths of these multiple effects. This is particularly important in grazing studies because grazing has both direct effects on soil health, for example, by disturbing surface soils through trampling, and indirectly, through removal of plant material (herbivory) and therefore decomposition processes (Eldridge, Delgado-Baquerizo, et al., 2016).

In our models, we combined the effects of recent and historic grazing into a single composite variable ("grazing"). Increases in this composite variable corresponded to increasing total grazing pressure. The use of composite variables does not alter the underlying SEM models but collapses the effects of multiple, conceptually related variables into a single-combined effect, aiding the interpretation of model results (Grace, 2006). The four microsites were treated as categorical variables with two levels (0 or 1). This approach allowed us to compare the effect of a particular microsite (e.g., tree) on infiltration compared with the average of the remaining microsites (e.g., bare areas + grasses + shrubs). We used bare areas as a procedural control, so this microsite was not explicitly considered in our models. We also included an aridity index in our models because it has been shown to be a useful tool to account for spatial variability in sites (Delgado-Baquerizo et al., 2013) and, rather than use regional location (north, central, and south) or latitude, it provides insights into possible effects of rainfall and evapotranspiration on the hydrology. Aridity was calculated as $1 - AI$, where $AI = \text{precipitation} / \text{potential evapotranspiration}$ from Worldclim interpolations (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005).

To improve normality, we standardized the values for soil health, plant cover, aridity, and grazing (z -transformed) prior to analyses. 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. The infiltration and nutrient model with the

strongest measures of fit (e.g., low χ^2 , high GFI, and high NFI) was interpreted as showing the best fit to our data (see Appendix S4). All SEM analysis was conducted using AMOS Software Version 20. The stability of these models was evaluated as described in Reisner, Grace, Pyke, and Doescher (2013).

3 | RESULTS

3.1 | Soil hydrology in relation to condition, microsite, and vegetation community

Values of the five hydrological variables did not differ between the blackbox and cypress pine communities. However, we detected significant differences among the three condition classes, with poor sites having significantly less SSI under ponding (20.4 ± 0.25 ; mean \pm standard error, SE) than either average (29.5 ± 0.23) or good (36.0 ± 0.21) sites ($F_{2,8} = 7.16, p = .017$; Table 1). This condition effect was consistent across the two communities (Appendix S4).

We detected significant differences among microsites for all hydrological variables except SSI under tension (Figure 1, Appendix S4). When averaged across communities and condition classes, ponded values of SSI and sorptivity on bare soil were about half that of the other three microsites (infiltration: $F_{3,90} = 20.48, p < .001$; Sorptivity: $F_{3,90} = 18.00, p < .001$). There was a slight decline in sorptivity under tension from bare to tree microsites ($F_{3,90} = 4.305, p = .007$). We failed to detect any significant microsite by condition interactions ($p > .32$, Appendix S4), indicating that, for all hydrological variables, microsite effects were consistent across the three levels of condition.

There was a consistent increase in the macroporosity index from open sites (10.8 ± 1.03 ; mean \pm SE) to grasses (18.3 ± 2.03), shrubs (25.0 ± 2.68) or trees (23.9 ± 3.52 ; Figure 2). However, microsite effects varied between the two communities for our other measures of infiltration. For example, there was significantly more ponded infiltration and ponded sorptivity under shrubs and trees in cypress pine than in blackbox (community by microsite interaction: $F_{3,90} = 6.15$ and $3.72, p < .001$ and $.014$ for infiltration and sorptivity, respectively; Figure 3) but no differences in open microsites (Figure 3b and 3d). Under tension, community differences were only apparent under shrubs and trees (community by microsite interaction: $F_{3,90} < 4.98, p < .029$), again with larger values in cypress pine. There were no significant three-way interactions.

TABLE 1 Mean (\pm SE) values for the five measures of hydrology for the three condition class (poor, average, and good condition) sites. Different superscripts indicate a significant difference at $p < .05$

Hydrological attribute	Site condition					
	Poor		Average		Good	
	Mean	SE	Mean	SE	Mean	SE
Sorptivity (+10 mm)	124.43 ^a	14.85	157.89 ^a	15.96	175.73 ^a	14.72
Sorptivity (-40 mm)	7.26 ^a	0.64	8.19 ^a	0.68	8.74 ^a	1.15
Steady-state infiltration (+10 mm)	20.40 ^a	5.16	29.45 ^b	3.81	35.95 ^c	4.15
Steady-state infiltration (-40 mm)	1.47 ^a	0.15	1.66 ^a	0.17	1.80 ^a	0.31
Macropore index	17.14 ^a	4.80	19.28 ^a	11.85	19.31 ^a	17.29

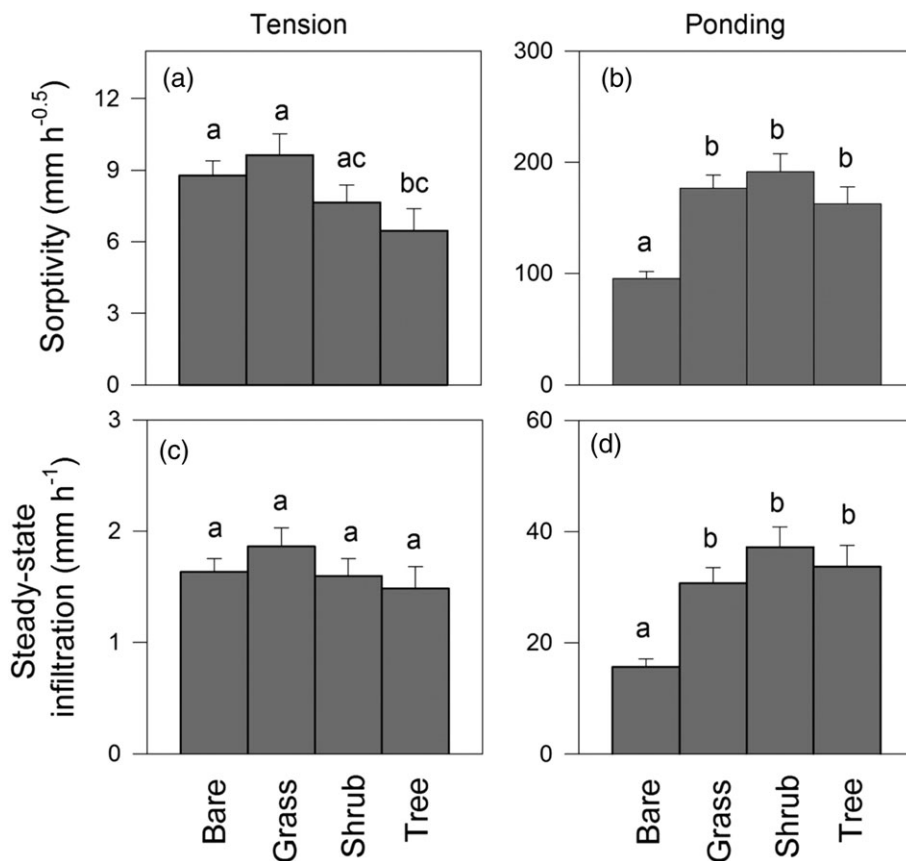


FIGURE 1 Back-transformed means (\pm SE, $n = 54$) for sorptivity ($\text{mm h}^{-0.5}$) and steady-state infiltration (mm h^{-1}) under -40 mm tension and under $+10$ mm of ponding for the four microsites averaged across condition class and plant community. Different letters with a panel indicate a significant difference in the measure of hydrology among different microsites

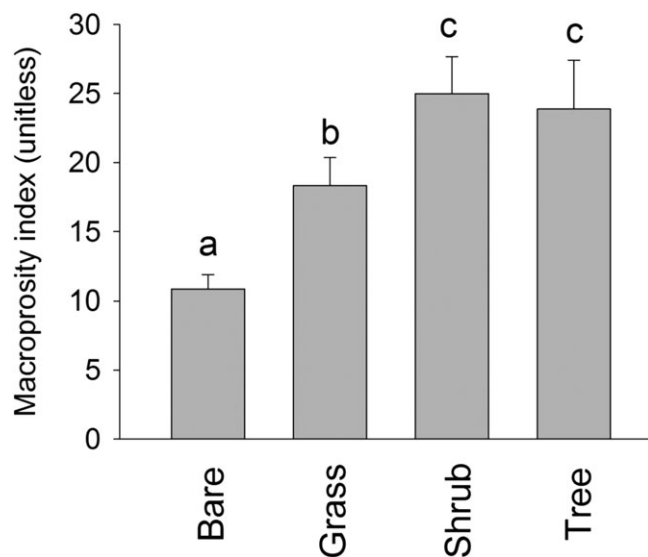


FIGURE 2 Back-transformed mean (\pm SE) values of the macroproposity index for the four microsites. Different letters indicate significant differences at $p < .05$

3.2 | Quantitative models of hydrology

Our SEM showed that shrubs, trees and grasses had strong positive effects on sorptivity and steady-state infiltration under ponding, and the macroproposity index (Figure 4, Table 2). Grazing

had direct negative effects on all measures of hydrology, except the macroproposity index (Table 2) and some indirect effects, on ponded sorptivity and steady state infiltration, mediated by increases in plant cover (Figure 4). The magnitude of standardised total effects (the sum of all direct and indirect effect that one attribute has on another) indicates that the suppressive effects of grazing on hydrology were mainly associated with cattle grazing.

4 | DISCUSSION

We examined the effects of microsite, levels of site degradation and increasing grazing intensity by different herbivores on water infiltration in two semiarid woodlands. We found that infiltration rates were greater under trees and shrubs than in the unvegetated interspaces and that microsite effects were generally stronger for total (ponded) infiltration when both macropores and matrix pores were allowed to conduct water. Greater levels of site degradation and higher intensity of grazing, predominantly by cattle, reduced all of our hydrological measures, but the effects of grazing were subordinate to microsite effects. Our results suggest that land use management actions that results in the removal of woody vegetation, particularly trees and shrubs, are likely to have a greater effect on site-level hydrology than changes in grazing intensity. However, our results also suggest that prolonged overgrazing, which leads to

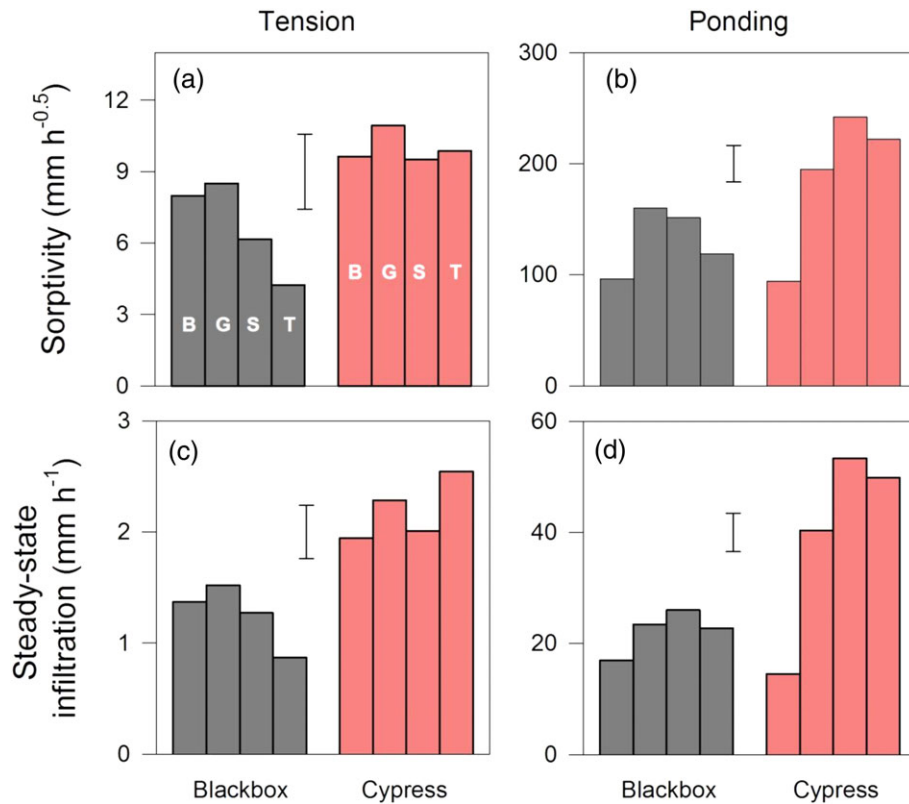


FIGURE 3 Back-transformed means (\pm SE, $n = 54$) for (a) sorptivity ($\text{mm h}^{-0.5}$) and (c) steady-state infiltration (mm h^{-1}) under -40 mm tension and (b) sorptivity and (d) steady-state infiltration under $+10$ mm of ponding for the four microsites in the blackbox and cypress pine communities. B = bare ground, G = grass, S = shrub, T = tree. Bars indicate the 5% LSD for community by microsite interaction

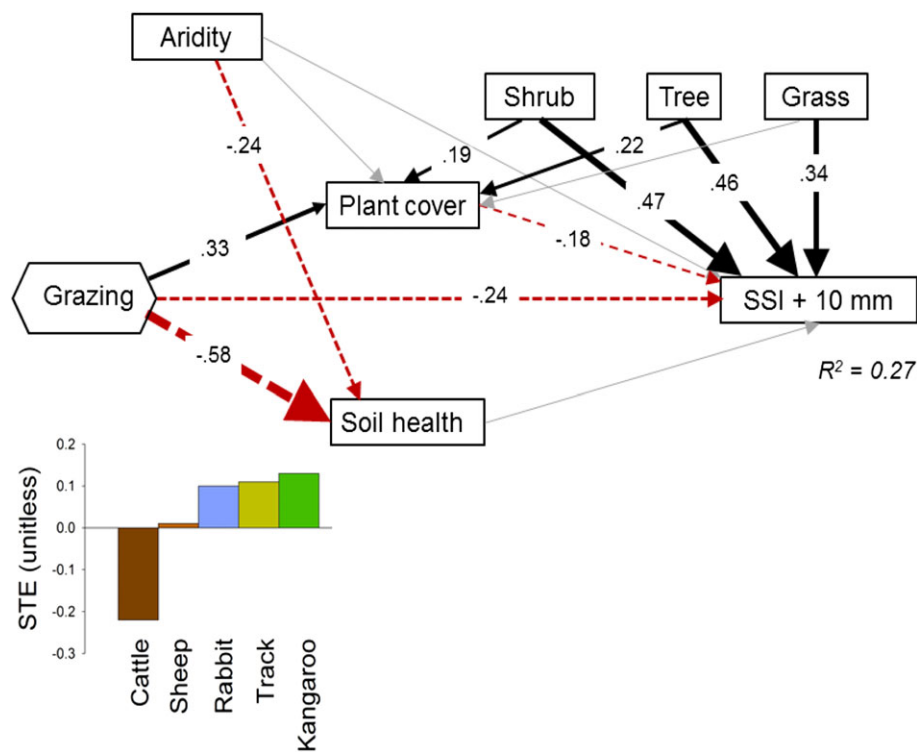


FIGURE 4 Structural equation model depicting the effects of aridity, plant cover, grazing, soil health, shrub, and tree and grass cover on steady-state infiltration (SSI) under ponding. The width of arrows is proportional to the path coefficient, with continuous (positive) and dashed (negative) lines indicating the sign of the relationships. The strength of the path coefficient is superimposed upon each pathway. Nonsignificant pathways are shown in light grey. Model parameters: $\chi^2 = 0.24$, $df = 18$, $p = 1.00$, $NFI = 0.999$, $GFI = 1.00$, $Bollen-Stine = 0.614$. The histograms indicate the standardised total effects (STE); the sum of direct and indirect effects of our five measures of grazing on plant richness. The R^2 value indicates the proportion of total variance in infiltration explained by aridity, plant cover, grazing, soil health, shrub, and tree and grass cover

TABLE 2 Standardised path coefficients, analogous to partial correlation coefficients, for the five hydrological variables, and below, standardised total effects, the sum of direct and indirect effects of different grazing variables on the five hydrological measures; - indicates nonsignificant path coefficient

Attribute	Sorptivity		Steady-state infiltration		Macroporosity index
	Ponding	Tension	Ponding	Tension	
Grazing	-0.23	-0.48	-0.24	-0.45	-
Aridity	-0.18	-	-	-	-
Tree	0.40	-	0.46	-	0.44
Shrub	0.50	-	0.47	-	0.34
Grass	0.40	-	0.34	-	0.23
Soil health	-	-	-	-	-
Plant cover	-0.15	-	-0.18	-	-
Standardised total effects					
Cattle	-0.24	-0.48	-0.22	-0.45	0.14
Sheep	0.02	0.11	0.01	0.14	-0.11
Rabbits	0.05	-0.10	0.13	-0.03	0.10
Tracks	0.08	0.19	0.11	0.17	-0.10
Kangaroos	0.09	0.07	0.10	0.06	-0.04

reductions in grass cover, is likely to have a synergistic reduction in hydrological function in these woodlands by reducing the cover of highly conductive patches and by reducing the extent of macropores.

4.1 | Grasses and woody patches drive infiltration processes

Consistent with global studies from shrublands and woodlands (e.g. Bhark & Small, 2003; Eldridge, Beecham, & Grace, 2015; Eldridge, Wang, & Ruiz-Colmenero, 2015; Gómez et al., 2015; Madsen, Chandler, & Belnap, 2008), we demonstrated substantially greater sorptivity and infiltration under the canopies of long-lived vegetation patches such as shrubs, trees, and perennial grasses than in the interspaces. When water flow was measured under tension thus preventing macropores from conducting water, total infiltration did not vary between open and vegetated microsites. The magnitude of the macroporosity index for soil beneath grasses, shrubs, and trees (range 10–24) suggests that observed differences in hydrology among these microsites were largely due to the presence of macropores; large biologically produced pores that are the principal channels for conducting water. Macropores are most strongly developed beneath perennial vegetation due to the greater density of plant roots, litter and soil faunal activity. Stem-flow deposition of material excreted by invertebrates and birds using woody plant canopies (Belsky et al., 1989) and the shedding of large volumes of litter from trees and shrubs enhance soil carbon and nitrogen pools beneath the canopies (Dean, Milton, & Jeltsch, 1999; Eldridge & Rath, 2002). These favourable abiotic conditions beneath woody canopies support greater densities of termites (Noble, Mueller, Whitford, & Pfizner, 2009) and soil invertebrates (Chilcott, Reid, & King, 1997) that construct biopores, leading to positive feedbacks on soil physical and chemical properties,

increasing infiltration (Eldridge & Freudenberger, 2005; Hu, Li, Li, & Liu, 2015; Pueyo, Moret-Fernandez, Saiz, Bueno, & Alados, 2013; Tobella et al., 2014).

4.2 | Herbivore effects on hydrology

Grazing had a direct suppressive effect on rates of infiltration and these effects were stronger under tension when macropores were prevented from conducting water (Table 2). Further, cattle were identified as the main herbivores responsible for this reduction in hydrology. Reductions in soil porosity by livestock trampling can occur due to reductions in the size, extent, and connectivity of macropores (Mead & Chan, 1992). We failed, however, to detect an effect of increased grazing intensity on the macroporosity index, suggesting that the primary mechanism behind a direct effect of grazing on hydrology was not via the destruction of macropores. The most parsimonious explanation is that grazing-induced trampling increases soil compaction, which is consistent with the stronger negative effect of grazing on water flow under tension, that is, when macropores are prevented from conducting water (Table 2). The strong impact of cattle grazing on infiltration likely results from differences in body mass and hoof pressure and therefore soil compaction. Cattle hooves exert twice the static pressure on the soil as those of sheep, and three times that of kangaroos (Graetz & Tongway, 1986). Cattle have been shown to reduce surface roughness and biocrust cover, attributes that are highly correlated with infiltration (Eldridge, Poore, et al., 2016). Thus, trampling by cattle, particularly on wet soils, would compact surface soils and reduce infiltration (Greenwood & McKenzie, 2001), probably by reducing the continuity of pores to the surface but without actually eliminating macropores. Rabbits and kangaroos, unlike cattle, had the opposite effect on infiltration, with slight overall positive effects on SSI under ponding (Table 2). An effect of kangaroos on infiltration has not, to our knowledge, been reported previously.

Soil compaction due to livestock trampling has been demonstrated at animal resting sites under the canopies of trees and shrubs (Hiernaux, Bielders, Valentin, Bationo, & Fernandez-Rivera, 1999). Similarly, long-term livestock removal has been shown to reduce soil compaction and increase rates of water infiltration (Castellano & Valone, 2007). Additional evidence that the effects of cattle grazing are unrelated to collapse of macropores comes from our infiltration results for open areas at the degraded sites. Although these sites had sparse levels of perennial vegetation and were heavily grazed by livestock, they still had macropore indices of ~10, consistent with information from well managed sites on loamy-textured Haplargid and Durargid soils in nearby national parks (Eldridge, Beecham, et al., 2015). They were also an order of magnitude greater than overgrazed semiarid woodlands on similar soils close to the study area (indices ~1–2; Eldridge & Koen, 2003; Greene, 1992). Index values of about 10 suggest that macropores at these sites are relatively resistant to destruction by livestock and that infiltration capacity is more resilient than that in the drier woodland sites. Hydrological function, therefore, may be easier to maintain, given that soil macropores were still relatively abundant, even on the most degraded sites.

Our structural equation model also showed that grazing indirectly reduced infiltration by enhancing the suppressive effect of plant cover

on infiltration (Figure 4). While this might at first sound counterintuitive, and is contrary to our hypothesis, it is consistent with the observation that grazing increases the cover of annual, high biomass exotic forbs such as *Echium plantagineum* (Eldridge, Delgado-Baquerizo, et al., 2016). Large exotic forbs have predominantly fibrous roots, are unlikely to create many macropores, and do not conduct substantial volumes of water into the subsoil (Eldridge & Koen, 2003). Our SEM also indicated that grazing reduced soil health, consistent with a large number of studies globally (e.g. Belsky & Blumenthal, 1997; Eldridge et al., 2011; Eldridge, Delgado-Baquerizo, et al., 2016; Fleischner, 1994; Jones, 2000). However, we did not detect any significant links between soil health and infiltration in the models, which is surprising, given that our index of soil health comprised numerous attributes such as litter cover and incorporation, surface roughness and soil texture that would be expected to be strongly aligned with infiltration capacity (Tongway, 1995).

4.3 | Concluding remarks

We acknowledge that there are substantial limitations in up-scaling our point-scale measures to assess site-level estimates of infiltration. For example, subtle differences in soil texture or surface microtopography could account for some of the differences among sites and microsites, even though our microsites were distributed widely across the sites. Notwithstanding these shortcomings, if we upscale our results to the site level by accounting for the relative contribution of the four microsites, it is clear that site-level infiltration rates decline substantially with declines in site condition, with good condition sites (61.5 mm hr^{-1}) having substantially greater rates of infiltration than either average (41.5 mm hr^{-1}) or poor (29.9 mm hr^{-1}) sites. Direct quantification of how runoff and rainfall are partitioned across the study area would need to be determined before we could conclude that landscape-level water balance differs across the sites.

Overall, the negative effects of grazing were substantially less than the positive effects of different perennial plant patches, largely because grazing did not appear to reduce macroporosity sufficiently to result in substantial reductions in hydrology. It is clear from our work, however, that removal of shrubs, grasses or trees, or the increase in the cover of bare soil, will result in substantial changes in the volume of water infiltrating into the soil. Thus, management practices that alter the relative proportion of the different microsites within these woodlands will have substantial impacts on hydrology. In many of these woodlands, the removal of shrubs and trees is an ongoing management practice aimed at increasing pastoral production (Eldridge & Soliveres, 2014). It is clear that the hydrological impacts of these practices will be large, and given the primacy of woody vegetation in these semiarid systems, it is likely that there will be flow-on effects to soil nutrients (Eldridge, Wang, et al., 2015), animal habitat and plant–plant interactions such as facilitation and competition (Soliveres et al., 2014).

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