



Rabbits and livestock grazing alter the structure and composition of mid-storey plants in a wooded dryland

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ABSTRACT

Woody plants are critical for supporting wildlife and maintaining ecosystem structure and function in drylands. Grazing has the potential to alter woody plant community structure by affecting the size and survival of shrubs and saplings. We assessed the role of recent and historic grazing by livestock, and recent grazing by kangaroos and rabbits, on woody plant structure and composition. We measured the density and species occurrence of saplings and shrubs within three plant communities across 0.5 M km² of eastern Australia and used generalised linear mixed models to examine how grazing, soil texture and the basal area of mature trees altered the structure and composition of mid-storey woody plants. Due to co-evolution, we expected a stronger negative effect of grazing on shrub and sapling density and species occurrence by introduced herbivores than native herbivores and that shorter individuals would be more susceptible to recent grazing activity. We found that the density and occurrence of shrubs and saplings generally responded more negatively to introduced herbivores irrespective of their height. Sapling density was strongly reduced by recent rabbit and livestock grazing but increased in density at sites with greater kangaroo and historic livestock grazing. Recent livestock grazing also reduced the occurrence of sapling species. There were no strong effects of any grazing on shrub density, but rabbit grazing strongly reduced shrub species occurrence, with few strong responses among individual species. Our data provide strong evidence that recent grazing by livestock and rabbits can reduce sapling density and alter woody plant occurrence. This has the potential to induce long-term changes in ecosystem structure by limiting shrub and sapling establishment which could lead to aging and contracting woody plant populations.

1. Introduction

Processes that limit woody plant recruitment have the capacity to induce long-term changes in vegetation structure and composition (Sankaran et al., 2013; Eldridge et al., 2011). Processes may occur rapidly (e.g. deforestation and fire events) or very slowly, with impacts only evident many years after disturbance (e.g. altered climate, fire or grazing regimes; Hiernaux et al., 2009; Cohn et al., 2011) and have the ability to create ‘demographic bottlenecks’ (Sankaran et al., 2013) within the woody plant population. There are several global change drivers that affect rates of woody plant recruitment and mortality and in turn alter structure and spatial arrangement of different sized individuals (i.e. structural diversity), such as biotic invasions, nitrogen deposition and land use intensification such as vegetation clearance and overgrazing. Of these, grazing is arguably one the most important

global drivers of structural changes in woody plant communities as it can produce changes that occur over a range of timescales.

Grazing, particularly by livestock and other introduced herbivores, can alter multiple life stages of woody plants, not only through herbivory, but also by inflicting a range of behavioural and physiological impacts on the ecosystem for example by trampling and disturbing the soil (Trimble and Mendel, 1995) and altering soil nutrients such as nitrogen and phosphorus (Eldridge and Delgado-Baquerizo, 2017). When it removes seedlings and young adults (saplings), grazing can have disproportionately large effects on population structure, spatial arrangement (Berdugo et al., 2018) and the composition of woody plant assemblages (Travers et al., 2018) by altering plant-plant interactions (Flores and Jurado, 2003). Woody plants are important components of many vegetation communities, but are particularly important in drylands (Sankaran et al., 2005) where the structure diversity is closely

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linked to ecosystem function. In these systems woody plants moderate key ecosystem functions such as nutrient cycling, carbon sequestration and soil hydrology (Eldridge and Delgado-Baquerizo, 2017), change habitat and foraging resources for wildlife (Stanton et al., 2018), and affect the long-term persistence and regenerative capacity of plant species (Walck et al., 2011). Drylands make up about 40% of the global land area, and of this, two-thirds is grazed by livestock (Clay, 2004). Understanding how grazing alters woody plants in drylands is therefore critical for ecosystem management.

The relative role that vertebrate herbivores and their grazing-related impacts play in driving changes in woody plant structure and composition varies widely among communities. Shifts in community composition may be induced solely by herbivores (e.g. browsing by elephants and impala in semi-arid savannas; Midgley et al., 2010) or require a combination of grazing and other drivers such as increasing temperatures (e.g. tree-line changes; Trembl et al., 2016) to affect changes in woody plant structure. Some studies have shown that managed grazing by cattle (Osem et al., 2015; Schoenbaum et al., 2018) or horses (Menard et al., 2002) can be a useful conservation tool for managing woody plants. In many cases, however, unmanaged grazing can have unintended consequences, such as the expansion of woody plants into grasslands (woody encroachment; Eldridge et al., 2011). While such consequences may not necessarily reduce total ecosystem diversity or functionality (Eldridge and Soliveres, 2014), grazing-induced shifts in woody plant structure can have detrimental impacts on a range of biota such as rodents (Tabeni et al., 2007) and other small mammals (Eccard et al., 2000), birds (Val et al., 2018) beetles (Liu et al., 2012) and reptiles (Germano and Hungerford, 1981). Understanding, therefore, how specific herbivores can produce broad-scale shifts in woody plant structure and composition is critical for effective land management. Relatively few studies, however, have assessed the top-down regulation of woody species structure by grazing related impacts of multiple herbivores at varying densities (but see Endress et al., 2016).

Woody plant recruitment is essential for maintaining a structurally diverse plant community. However, recruitment into adult size classes is often slow and episodic (Bond and Keeley, 2005), and punctuated by long periods of very low or nil recruitment. The relationships between mature trees and their mid- and under-storey protégé species (*sensu* nurse-protégé interactions Flores and Jurado, 2003) can range from competitive to facilitatory, and may vary depending on environmental conditions and life history stage. For example, mature trees can ameliorate harsh abiotic conditions for mid- and under-storey vegetation and enhance their resources such as water, by hydraulic lift (Dawson, 1993), yet also compete with them for resources at later life stages (Perea et al., 2016). Although the composition of the woody community plays a substantial role in determining these plant-plant interactions, there is growing evidence that the woody structure of communities (i.e. the mix of canopy trees and mid-storey woody plants) is driven by rainfall and soil texture, which determine available soil moisture (Sala et al., 1997), but also by grazing and fire (Bond and Keeley, 2005). Within Australia's semi-arid woodlands, few tree and shrub seeds persist in the soil seedbank (Callister and Westbrooke, 2017), providing a major limitation to tree and shrub recruitment when combined with soils that have low soil moisture storage potential. Woody plant recruitment over much of Australia's drylands is limited almost exclusively to periods of above-average rainfall (Nano and Pavey, 2013). In these systems, low grazing pressure is also critical for successful woody plant recruitment and establishment, with strong evidence indicating that heavy grazing by livestock (Callister et al., 2018), rabbits (Zimmer et al., 2017) and native herbivores (Bond and Keeley, 2005) can substantially reduce or even eliminate (Cohn et al., 2013) the successful recruitment of woody plants.

Here we assess the broad impacts of grazing, by different co-occurring herbivores, on the structure (density of short and tall shrubs and saplings) and composition (probability of species occurrence) of mid-

storey woody plants. Woody plants were assessed based on their growth form, with juvenile trees (diameter at breast height [DBH] < 5 cm; Cohn et al., 2011) classified as 'saplings', and shrubs of all life stages classified as 'shrubs'. To find consistent trends in the impacts of specific herbivores, we sampled a large number of sites (451) across a large area (0.5 M km²) to offset the nuances of specific site-level differences that can alter recruitment (e.g. resource availability, plant-plant interactions, seed dispersion, pollination). To assess grazing-related impacts, we used measurements of dung to assesses recent grazing by introduced livestock, including sheep (*Ovis aries*), goats (*Capra hircus*) and cattle (*Bos taurus*), introduced free ranging herbivores (i.e. European rabbits [*Oryctolagus cuniculus*] and European hares [*Lepus europaeus*]) and native free-ranging herbivores (i.e. kangaroos [*Macropus* spp.]); and used stock tracks to assess historic grazing by livestock. Our models also accounted for the fact that variation in soil texture and existing mature trees are known to affect mid-storey woody plant structure and composition. We used these models to test three hypotheses. Firstly, we hypothesized that native herbivores would have relatively lower impact than introduced herbivores on the native shrubs and saplings due to co-evolution. We therefore predicted that recent grazing by livestock and rabbits would reduce shrub and sapling density and species occurrence more than recent grazing by native herbivores. Kangaroos have a strong dietary preference for grasses (Tiver and Andrew, 1997) and there is limited evidence that they reduce woody plant recruitment in drylands (but see Gordon et al., 2017). Secondly, we hypothesized that younger woody plants would be more susceptible to the impacts of herbivory and trampling than older individuals (Sun and Liddle, 1993). We therefore expected that the density of relatively shorter, and presumably younger, saplings and shrubs would be more susceptible than taller saplings and shrubs to physical damage by trampling as well as herbivory. Finally, we tested the hypothesis that facilitation by mature trees occurs more frequently in resource-limited environments (Flores and Jurado, 2003). We therefore predicted that the relationships between sapling or shrub density and mature tree cover would be positive on coarse-textured soils where soil moisture is limited. We tested these hypotheses using data collected from three extensive plant communities with a broad distribution across semi-arid Australia, and which vary in their underlying landforms, soil properties and dominant species structure.

2. Methods

2.1. Study area

We surveyed 451 semi-arid woodland sites across a large area (0.5 M km²) of eastern Australia. The climate in this region is Mediterranean, with slightly more rainfall during the cooler months. Average rainfall (385–460 mm yr⁻¹) and average annual temperatures (~18 °C) varied little across the region. Our sites were selected to capture three broad vegetation communities dominated by either White Cypress pine (*Callitris glaucophylla* F. Muell.), Black box (*Eucalyptus largiflorens* F. Muell.), or River red gum (*Eucalyptus camaldulensis* Dehnh.). The Cypress pine communities occur on a range of landforms including alluvial sand hills and rocky hills, dry slopes and peneplains. The underlying soils are gradational, consisting of Quaternary colluvium and aeolian deposits and are low in carbon, nitrogen and phosphorus and are covered by dense biocrusts in undisturbed areas (Thompson et al., 2006). The mid- and under-storey in these communities is generally driven by soil type and disturbance history (i.e. fire, grazing). The Black box dominated communities occur on the drier heavy alluvial clays surrounding inland rivers, lakes and swamps that receive infrequent floodwater (10–40 years; Smith and Smith, 2014). Their soils have a deep uniform profile and are relatively high in silt and clay. The mid- and under-storey composition can be quite variable and is generally driven by grazing history, rainfall and flood frequency (Keith, 2004). River red gum communities generally occur along the

tributaries and lower terraces of the major river systems. Their underlying soils are uniform and deep with relatively high levels of clay and soil nutrients. Flood frequency and grazing appears to control the composition of mid- and under-storey species and the success of regeneration of *Eucalyptus camaldulensis*, with rainfall induced floodwaters every 8–15 years and occasional regulated "environmental flows" in the interim.

2.2. Field survey

For each community, we located 150 sites (151 in Cypress pine) to sample a range of distances from permanent water, land tenures and grazing histories (further details in [Eldridge et al., 2017](#)). Each site comprised a 200 m long belt transect running perpendicular to the nearest permanent water point, (e.g. earthen dam, tank, permanent water bodies, etc.). The belt transects varied in width from 1 m to 10 m, depending on stand density. Along the transect we identified all tree and shrub species and measured the density of mature trees (DBH \geq 5 cm; [Cohn et al., 2011](#)) in four DBH classes (5–10 cm, 10–20 cm, 20–30 cm and $>$ 30 cm) and saplings (0.5–3 m tall) and the density of shrubs ($>$ 0.5 m tall). Shrubs and saplings were tallied in two height classes 0.5–1.3 m (Short) and 1.3–3 m (Tall), as we expected shorter individuals to be more susceptible to trampling damage from recent livestock grazing. We used the mature tree DBH data from mature trees to approximate basal stem area ($\text{m}^2 \text{ha}^{-1}$) for each site, and calculated sapling and shrub density per hectare from the area surveyed.

We assessed grazing intensity using dung (faecal pellet) surveys. Dung counts are often used to estimate large herbivore abundance. In arid and semi-arid ecosystems, dung counts are useful for estimating short to medium term grazing pressure as dung often has a surface residence time of several years ([Bahamonde et al., 2017](#)). Along this transect we positioned five 25 m² quadrats (5 m x 5 m, 'large quadrat') every 50 m, within which we centrally located a smaller 0.5 m x 0.5 m quadrat ('small quadrat'). We assessed cattle (*Bos taurus*) dung within the large quadrat and kangaroo, rabbit and hare, sheep and goat dung within the small and large quadrats. Small quadrats made it easier to search for, and count, individual pellets, but were not large enough to be representative of dung within a site, whereas counts of kangaroo, rabbit/hare, sheep/goat dung in the large quadrat were approximations. For cattle, we counted dung events rather than individual fragments and we counted individual pellets for the other herbivores. Samples of dung were collected from every site to calculate the oven dried mass of dung per hectare of each herbivore from each quadrat. Data were then averaged over all quadrats for each herbivore (i.e. five large quadrats for cattle or five small + five large quadrats for the remaining herbivores) to give an average mass per hectare for each type of herbivore, for each site. The mass of sheep and cattle dung was then summed to give a measure of recent livestock grazing. To assess historic grazing intensity, we measured the width and depth of all livestock tracks crossing the 200 m transect to derive a total cross-sectional area of livestock tracks for each site ([Pringle and Landsberg, 2004](#); Figure A). Livestock tracks develop in these systems through repetitive trampling by large-bodied, hard-hooved animals that have not co-evolved with these ecosystems. Stock tracks persist within the landscape for many decades as the soil compaction and damage to biological soil crusts takes many years to recover ([Trimble and Mendel, 1995](#)). Rabbits and kangaroos, however, do not leave such persistent marks within the landscape, and therefore their historic grazing impacts could not be inferred.

2.3. Statistical methods

We analysed the density (plants per hectare) of all saplings and shrubs in two separate generalised linear mixed models. As our data were strongly right skewed, and zero inflated with a long tail for both tree and shrub data, we used a negative binomial error structure in our

models. To reduce variation and improve model fit, the density data were capped at 3000 and 10 000 individuals per hectare for shrubs and trees, respectively. Models were designed to assess the additive fixed effects of height class, grazing (recent livestock, historic livestock, kangaroo and rabbit), soil texture (% sand) and mature tree basal stem area ($\text{m}^2 \text{ha}^{-1}$), plus two-way interactions between each measure of grazing and height class, and an interaction between basal stem area and soil texture. This was necessary because we expected a stronger relationship between basal stem area and sapling and shrub density with increasing sand content. There was no spatial autocorrelation among sites and our predictors were not highly correlated (Pearson's correlation $<$ 0.40) and did not exhibit multicollinearity (Variance inflation factor $<$ 2). The random effects structure accounted for the separate communities as random intercepts and allowed the slopes and intercepts of each model term to vary for each height class.

We assessed the probability of species occurring for shrubs and saplings separately; examining the binary presence-absence data for all species across all sites. Species that occurred at two or fewer sites were omitted prior to analyses. These models had a similar design, assessing the additive fixed effects of grazing (recent livestock, historic livestock, kangaroo and rabbit), soil texture (% sand) and mature tree basal stem area ($\text{m}^2 \text{ha}^{-1}$), and an interaction between basal stem area soil texture. Slopes and intercepts for all fixed effects were allowed to vary among species, and intercepts were allowed to vary among communities ([Pollock et al., 2012](#)).

Prior to analyses, all grazing predictors (recent livestock, historic livestock, kangaroo and rabbit) were log ($x+1$) transformed and all model terms standardized (i.e. z-score transformation). Centring values on zero improves the interpretation of the model coefficients and allows the model intercepts to be interpreted as average responses, and the slope terms to be partial dependencies, conditional upon the remaining continuous variables having mean values ([Pollock et al., 2012](#)). Our density models were constructed using a negative binomial distribution within the 'glmmadmb' function from the 'glmmADMB' package ([Fournier et al., 2012](#); [Skaug et al., 2013](#)), and occurrence models using a binomial distribution within the 'glmer' function from the 'lme4' package ([Bates et al., 2015](#)) within R (Version 3.4.4, [R Core Team, 2018](#)). Confidence intervals around the model parameters (fixed and random) for the final models were estimated using parametric bootstrapping (500 simulations). We tested interactions using a moving window approach and explored variation in individual species responses using their Best Linear Unbiased Predictors (BLUPs).

3. Results

3.1. Shrub and sapling density

The density of short and tall shrubs and saplings was far greater and more variable in the Cypress pine community than in the other communities (Fig. 1a). The density of saplings was clearly greater than shrubs in all communities, with the Cypress pine also containing the greatest density of saplings, followed by the River red gum community (Fig. 1a). Similar trends were found in the species richness data (Fig. 1b), which we describe in more detail below. Shrub density appeared to be unaffected by grazing, soil texture or mature trees, regardless of their height class (Fig. 2a).

Rabbit grazing, and to a lesser extent recent livestock grazing, reduced the density of saplings and this trend was consistent across all communities, regardless of sapling height class (Fig. 2b). Conversely, recent grazing by kangaroos, and to a lesser extent historic livestock, were associated with greater sapling density across all sites, and this effect was independent of sapling size. There was weak evidence that the relationship between sapling density and mature stem basal area became more positive with increasing sand content (Fig. 2b, B), but the main effects of soil texture and mature tree basal area on sapling density showed no clear trends.

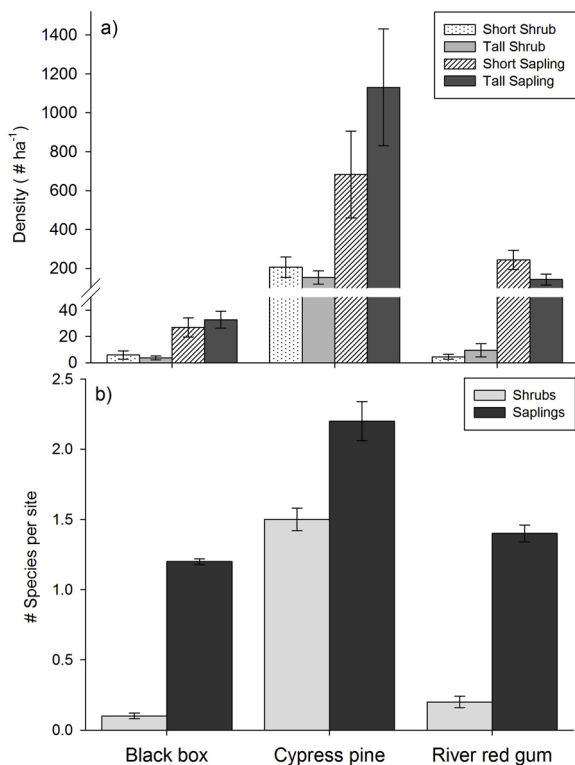


Fig. 1. Average (\pm SE) of (a) density of tall and short shrubs and saplings within each community per hectare and (b) number of species of shrubs and saplings at each site. Values shown are averaged over 151 sites for Cypress pine and 150 sites for both Black box and River red gum.

Estimates of the variance of the random intercept for both shrub and sapling density models revealed variation was greatest among communities (shrub $\sigma^2 = 2.30$; saplings $\sigma^2 = 1.85$; Figs. 1a and 2). The variance of the slopes for short and tall plants was also quite low for all predictors for both shrub and sapling density ($\sigma^2 < 0.03$).

3.2. Species occurrence

Across all sites and all communities, we recorded 42 species of shrubs (including two exotic species) and 27 species of trees (including two exotic species). Of these, 23 shrub (including one exotic species, *Lycium ferocissimum*) and 18 tree (all native) species were found at more than two sites and were included in our species occupancy analyses. On average, the Cypress pine community supported more shrub and

sapling species per site than the River red gum and Black box communities (Fig. 1b).

Only rabbit grazing strongly reduced the occurrence of shrubs, with marginal effects of recent and historic livestock grazing and soil texture, and no effects of kangaroos or mature trees on shrub species occurrence (Fig. 3a). The main effects of shrub species occurrence represent the average response of shrub species, with most measures of grazing, soil texture and mature trees showing relatively high variation among species-specific responses (Fig. 4). Best Linear Unbiased Predictors for rabbit grazing revealed the response of individual species was fairly consistent, with low variation among species ($\sigma^2 = 0.07$; Fig. 4c). Apart from rabbit grazing, there was weak evidence for three trends of shrub occurrence (1) increasing with greater levels of historic grazing, and (2) sandier soils; and (3) shrub occurrence reducing with increases in recent livestock grazing (Fig. 3a). The estimated variances of the random effects showed that the highest variation among species was in response to soil sand content ($\sigma^2 = 0.49$; Fig. 4f), and the lowest variation among species was in response to historic livestock grazing ($\sigma^2 = 0.05$; Fig. 4b).

Few shrub species responded strongly to our measures of grazing (Fig. 4). Across all shrub species, the occurrence of *Eremophila longifolia* was most strongly reduced by rabbit grazing (Fig. 4c) as rabbit grazing had an overall negative effect on shrub occurrence (Fig. 3a). Although our two measures of livestock grazing had weak effects overall due to large variation among species, some individual species responded to these measures more strongly than the remaining species. For example, recent livestock grazing generally reduced species occurrence, yet *Senna artemisioides* subsp. *artemisioides* and *Eremophila sturtii* were not as strongly reduced by recent livestock as the remaining species (Fig. 4a). However historic livestock grazing tended to enhance species occurrence overall, yet *Senna artemisioides* subsp. *artemisioides* and *Acacia dealbata* were not as strongly enhanced by historic grazing as the remaining species (Fig. 4b). *Dodonaea viscosa* subsp. *angustifolia* however, was the species most strongly enhanced by increases in historic livestock grazing (Fig. 4b).

Saplings occurred less frequently as recent livestock grazing increased (Fig. 3b). This effect was quite strong across all species with very low variation among individual species responses ($\sigma^2 = 0.06$). There were also two marginal trends. Firstly, increasing rabbit grazing reduces sapling occurrence (Fig. 3b) and this response was also relatively consistent across individual species (i.e. low variability; $\sigma^2 = 0.07$; Figure C). Secondly, the relationship between sapling occurrence and mature stem basal area became more positive as soils became sandier (Fig. 3b).

From the random intercepts of our model community had a stronger effect on shrub occurrence than sapling occurrence, with slightly

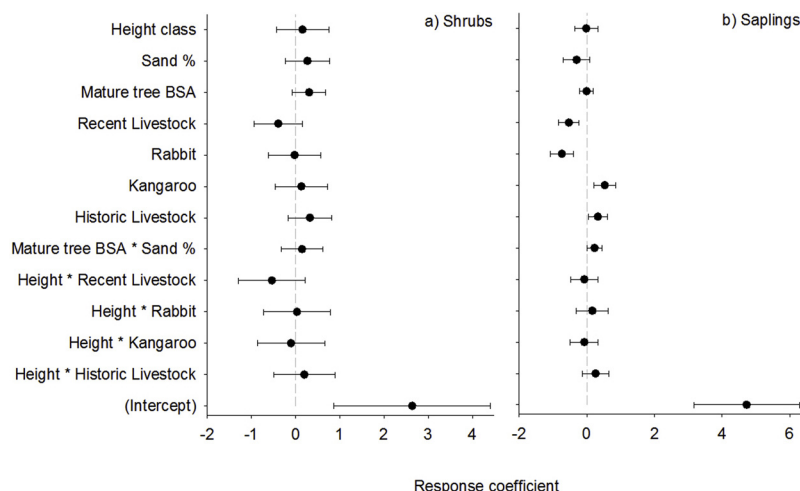


Fig. 2. Response coefficients (model slopes) and their bootstrapped confidence intervals (CI) for the explanatory variables and model intercept of two separate models: (a) shrub and (b) sapling density (response variables). Significance is determined when confidence intervals do not intersect the $x = 0$ (vertical dashed line). The sign of each coefficient directly represents whether the model slope is positive or negative. The absolute value of each coefficient is interpreted as its relative strength when compared with the remaining explanatory variables within that same model. We discuss marginal effects in the text as weak trends where the CI values would round to zero at one decimal point (i.e. the mature tree BSA * sand % interaction in subplot b). BSA = Basal stem area of mature trees.

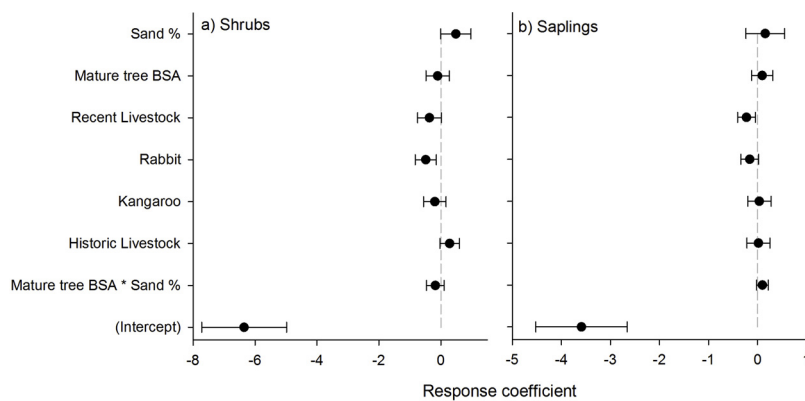


Fig. 3. Response coefficients (model slopes) and their bootstrapped confidence intervals (CI) for the explanatory variables and model intercept of two separate models: (a) shrub and (b) sapling species occurrence model (response variables). Significance is determined when confidence intervals do not intersect the $x = 0$ (vertical dashed line). The sign of each coefficient directly represents whether the model slope is positive or negative. The absolute value of each coefficient is interpreted as its relative strength when compared with the remaining explanatory variables within that same model. We discuss marginal effects in text as weak trends where the CI values would round to zero at one decimal point (i.e. recent and historic livestock, sand % in subplot a; rabbit and mature tree BSA * sand % in subplot b). The supporting random components of these models are provided in Fig. 4 for shrubs, and Figure C for saplings. BSA = Basal stem area of mature trees.

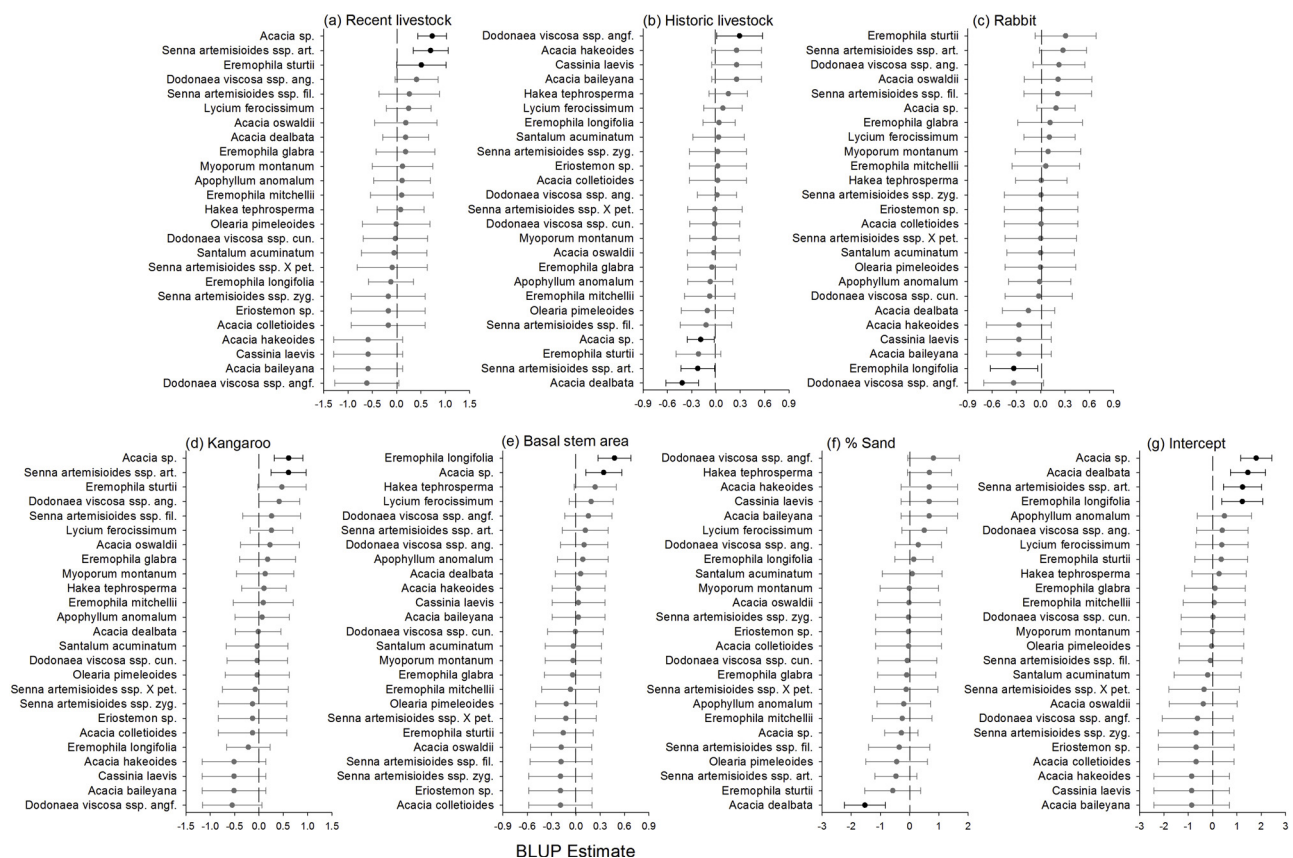


Fig. 4. Best Linear Unbiased Predictions (BLUP) of the random effects for each shrub species (Y axis) for all model components: (a) recent livestock grazing, (b) historic livestock grazing, (c) kangaroo grazing, (d) rabbit grazing, (e) mature tree basal stem area, (f) soil sand content (sand %), (g) intercept. Data presented here supports this model's fixed effects (Fig. 3a), with $x = 0$ (dashed lines) representing the average response across all species for each model component (Fig. 3a). Significant deviations of an individual species from the average species response are determined when the confidence interval does not intersect $x = 0$. Unknown species of *Acacia* which were only identified to genus were all included as "*Acacia* spp.". The following sub-species (ssp.) names were abbreviated: *angustifolia* (angf.), *angustissima* (ang.), *artemisioides* (art.), *cuneata* (cun.), *filifolia* (fil.), *petiolaris* (pet.), *zygophylla* (zyg.).

greater variation in shrub occurrence among communities ($\sigma^2 = 1.10$) than among species ($\sigma^2 = 1.02$). However, for saplings, the variation in occurrence among species ($\sigma^2 = 1.98$) was much stronger than among communities ($\sigma^2 = 0.32$). Although grazing clearly altered sapling density, there were no strong responses of any sapling species in response to any measure of grazing, with large variation in the responses of individual species (Figure C 1–7).

4. Discussion

Grazing effects on mid-storey woody plants differed substantially between saplings and shrubs, with evidence that grazing by introduced

herbivores (rabbits and livestock) alters dryland woodland structure. Our study was designed to assess the relative effects of grazing, mature trees and soil texture on mid-storey structure and composition in semiarid woodlands. Sapling density was affected by all measures of grazing, but sapling height did not appear to affect their susceptibility to grazing. However, only increases in recent livestock grazing reduced the occurrence of sapling species. Effects on shrub density were more variable, with no clear effects of grazing, soil texture or mature tree cover, regardless of shrub height. Although the response of individual shrub species was highly variable, individual shrub species were less likely to occur as rabbit grazing increased. We also found some weak evidence that shrub species occur more frequently with increasing

levels of historic livestock grazing and soil sand content but their occurrence declines with increasing recent livestock grazing. Understanding what drives woody mid-storey density and composition in woodlands is important for managing fuel loads, habitat, regeneration and soil function (Eldridge et al., 2011; Stanton et al., 2018). Overall, we found that the factors driving shrub and sapling density and composition were often species-specific, and such grazing-related impacts have the potential to have long lasting, legacy effects on tree stand density in woodlands.

4.1. Grazing affects tree sapling density and shrub occurrence

Grazing-related impacts on woody plant recruitment and establishment have been recorded for many herbivores, including domestic livestock (Eldridge et al., 2011), feral herbivores such as deer (Charro et al., 2018), and free-ranging herbivores that occur in high densities (Sandom et al., 2014) or whose populations fluctuate widely in response to changing seasonal conditions such as rabbits (Dawson and Ellis, 1994), rodents (Smit and Verwijmeren, 2011) and kangaroos (Gordon et al., 2017). We found that grazing altered the density of tree saplings, and these effects were strongly herbivore specific. The detrimental effects on sapling density were caused by recent grazing by introduced herbivores, rabbits and livestock, supporting our hypotheses of native herbivores being less detrimental than introduced herbivores by supporting our predictions for sapling density, but not for shrub density. There was also no evidence that shorter shrubs or saplings were more strongly reduced than larger individuals, suggesting increased herbivory or trampling impacts may not be an issue for plants 0.5–1.3 m tall. Recent grazing by European livestock and rabbits reduced sapling density, whereas sites with a greater density of kangaroos had a greater density of saplings. This is consistent with results from previous studies showing greater kangaroo grazing in the most intact, structurally diverse patches of vegetation with high forage availability (Lavery et al., 2018; Travers et al., 2018). Kangaroos are highly nomadic and selective, and their activity corresponds with periods when plant growth and tissue nutrient concentrations are high. The higher densities of kangaroos associated with areas of dense saplings likely reflects a greater range of plant species available for grazing (Caughley et al., 1987) and potentially, the availability of refugia against predators (Gordon et al., 2017).

Unlike kangaroos, rabbit grazing strongly reduced the density of saplings, clearly reduced the occurrence of shrubs overall, and showed marginal trends for also reducing sapling occurrence, consistent with the large body of literature on their impacts on ecosystems (Noble, 1997; Dawson and Ellis, 1994; Mutze et al., 2016). Across all shrub species we found that rabbit grazing reduced the occurrence of all species, but most strongly suppressed the occurrence of *Eremophila longifolia*, and had the weakest effects on *Eremophila sturtii*, *Dodonaea viscosa* and *Senna artemisioides*, consistent with results elsewhere (Fig. 4c; Tiver and Andrew, 1997). Our data also provide weak, marginal evidence for rabbit grazing reducing sapling occurrence, supporting previous work showing that rabbits reduce *Callitris glaucophylla* recruitment most strongly in low rainfall areas (Cohn et al., 2013). Clear spikes in successful recruitment events exist in stands of *Callitris* species, with far larger numbers of individuals from the late 1800s, prior to rabbit infestations, and again in the 1950s, when the Myxoma virus was released for rabbit control (Noble, 1997). Rabbits tend to consume more roots, barks and twigs of shrubs and saplings, particularly under intense drought conditions when ephemeral herbage is limited (Lange and Graham, 1983). This is known to kill shrubs and small trees and can have long-term impacts on the system by altering plant-plant interactions, altering the proportion of palatable species within the system, and altering shrub foliage, an important drought reserve for larger herbivores (i.e. sheep and kangaroos; Short, 1985). Similarly, in a study from drylands in central South Australia, Mutze et al. (2016) found that even low densities of rabbits (0.5 rabbits ha⁻¹)

completely removed highly palatable juvenile woody plants (plants 0.3–1 m, 5–20 mm stem diameter), and this effect extended to moderately palatable juvenile species at moderate rabbit densities (2 rabbits ha⁻¹). As shrubs and trees regenerate relatively slowly, rabbit grazing therefore has the potential to alter long term system productivity (Dawson and Ellis, 1994). The complete elimination of woody recruits by rabbits can potentially cause legacy effects by creating 'demographic bottlenecks', severely altering ecosystem structure and composition, and can result in the loss of important habitat features, and further reduce future recruitment events. Over time this often leads to aging and contracting woody plant populations (Auld, 1993).

Sites that showed evidence of greater recent grazing activity by livestock had reduced the density and occurrence of saplings, but a strong legacy effect of livestock grazing (i.e. increases in historic livestock grazing) enhanced sapling density. Similar trends were found for shrub density and occurrence, but these effects were weak and variable. Contrasting temporal effects of grazing have been observed with medium-sized woody plants such as *Eremophila* spp. and *Dodonaea* spp. whereby short-term, high intensity effects of livestock (cattle and goats) can reduce shrub density (Tiver and Andrew, 1997), but long-term impacts result in increases in woody cover and density due to the removal of competition from perennial grasses (Sinclair, 2005). Shrub species are, however, highly variable in their responses, with a range of tolerant to relatively grazing-susceptible species (e.g. *Atriplex vesicaria*; Eldridge et al., 1990) leading to no conclusive effects on shrub density, a result supported by our shrub occurrence model. For example, recent rabbit and livestock grazing reduced the occurrence of shrubs overall, though some species tended to be less susceptible to these grazing-related impacts than others (e.g. *Senna artemisioides*, *Dodonaea viscosa* and *Eremophila sturtii*; Eldridge et al., 2013; Robson, 1995) however these results were not significant. In contrast, we found that other species, such as *Acacia dealbata* were more sensitive to the negative effects of historic livestock grazing, likely due to relatively high levels of nitrogen in their leaves, which increases their palatability to livestock (Bengaly et al., 2007). We found no evidence that grazing altered sapling or shrub density based on their height against our predictions for our second hypothesis. This may simply be due to the fact that defining individuals as greater or less than 1.3 m tall failed to capture any potential impacts on smaller and presumably younger plants, which we expected to be more likely to be palatable, and thus more susceptible to grazing (Mutze et al., 2016). It is also important to note that we were unable to assess many species using our occurrence models because they were relatively uncommon across our sites.

The temporal inconsistencies between recent and historic livestock grazing are also difficult to reconcile, with recent livestock grazing reducing sapling density and occurrence, yet sites with evidence of greater levels of past livestock grazing had greater sapling density on average. The underlying mechanisms could relate to a large number of possibilities, ranging from enhanced soil nutrients, to competitive release of woody plants leading to greater plant densities over long periods (Veblen et al., 2015). Our proxy of historic livestock grazing, stock tracks, are limited by their ability to differentiate between extensive and intensive grazing histories. Stock track prevalence in the landscape is also heavily dependent on soil properties and flood events (Trimble and Mendel, 1995).

4.2. The impact of mature trees on sapling density is mediated by soil texture

Under low grazing pressure, recruitment success in woodlands is often high beneath large trees in low density stands (Bond and Keeley, 2005). We found weak evidence that the increasing basal stem area of mature trees was associated with increased sapling density and occurrence, but only on coarser-textured (sandy) soils. Thus, on finer-textured soils, mature trees did not appear to strongly affect the density of saplings. This provides weak support for our predictions for our third

hypothesis, for saplings only. These observations may be due to mature trees increasing soil moisture levels on coarser-textured soils. Soil moisture is a critical driver of plant–plant interactions in drylands and is strongly related to soil texture (Schwinning and Sala, 2004). For example, water drains more rapidly from coarser-textured than finer-textured soils, so saplings would likely benefit from the close association with mature trees by being able to access subsoil moisture enhanced by hydraulic lift (Dawson, 1993). However, positive effects of increasing moisture may diminish due to the competitive effects of woody canopies at later growth stages. There is evidence that mature trees both reduce (Holmgren et al., 1997) and promote (Barnes and Archer, 1999) shrubs and sapling growth beneath their canopies depending on the balance of facilitation and competition. Another possible explanation is that seed dispersal and safe germination sites may differ between *Callitris glaucophylla* and *Eucalyptus* spp. seeds. *Callitris* seeds are larger than *Eucalyptus* seeds and may germinate close to mature trees, whereas *Eucalyptus* seeds are more readily transported, and floodplain and wetland species of *Eucalyptus* often germinate in inundated areas (Petit and Froend, 2001). Cohn et al. (2011, 2012) found that mature trees did not facilitate saplings across a semi-arid rainfall gradient in communities where *Callitris* spp. and *Eucalyptus* spp. co-occurred as the dominant canopy species. However, these studies did not consider shifts in soil texture, which are likely to be a strong driver of understory woody relationships given the primacy of soil moisture in drylands.

Climate is a strong driver of woody plant demography in drylands as recruitment and mortality events are often strongly associated with periods of above- and below-average rainfall (Schwinning and Sala, 2004). Ultimately, the number of saplings and the number and type of shrubs that establish may relate more to a combination of factors that reduce herbivory, competition and desiccation in early life stages rather than the overall success of regeneration (Callister et al., 2018; Tiver and Andrew, 1997). Among our three communities, triggers of recruitment events may also vary. Eucalypt recruitment is most often triggered by fire, but in some cases by soil disturbance or over-bank flooding events (Jensen et al., 2008) whereas *Callitris* is fire sensitive (Cohn et al., 2011) and its recruitment is driven largely by episodic rainfall events and depends on land use and stand density. *Callitris* species also appear to tolerate intra-specific competition, with trees often occurring in dense mono-specific stands, up to 620,000 trees per hectare (Horne, 1990) for many decades. Such dense recruitment does, however, reduce their growth rate and seed production (Cohn et al., 2012).

4.3. Implications and conclusions

Our data add to a growing body of literature demonstrating that recent grazing by livestock and rabbits is likely to further reduce the occurrence of shrubs and the establishment of mature trees by limiting the successful establishment of saplings. Rabbit grazing, in particular, had a strong negative effect on sapling density, supporting the notion that smaller-bodied mammals often have more detrimental impacts on woody plant recruitment than larger herbivores (e.g. Smit and Verwijmeren, 2011).

The effects of even a few failed recruitment events arising from even a single overgrazing event can persist for over a century (Tiver and Andrew, 1997). Grazing can also alter the incidence of sexual reproduction (Xie et al., 2018), the sex ratio of plants in favour of males (Graetz, 1978), competitive or facilitative interactions among species (Charro et al., 2018; Perea et al., 2016), or allow the proliferation of less palatable species. These conditions may be difficult to reverse, so that any sustained lack of woody recruitment can have far reaching legacy effects, such as the failure to provide critical hollow-bearing trees to sustain dwindling populations of hollow-dependent fauna (Saunders et al., 2014). Altered woody plant spatial patterns can also alter fuel loads and connectivity, which are important for shaping fire intensity in flat landscapes (Cohn et al., 2012).

Given predicted increases in drought frequency and severity over the next century in Australia (Eldridge and Beecham, 2018), there are likely to be fewer opportunities for woody plant establishment and accelerated thinning of saplings by introduced herbivores (Fensham et al., 2009). Establishing and maintaining livestock-free areas and managing or eliminating feral animal populations, particularly in low rainfall years, will be required to support successful recruitment events (Tiver and Andrew, 1997). Future land management decisions should consider the consequences of grazing by rabbits and livestock, and potentially the loss of mature habitat trees, as their abilities to alter ecosystem structure has important implications for ecosystem function under a changing climate.

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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.agee.2019.03.003>.

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