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RESEARCH ARTICLE

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Livestock activity increases exotic plant richness, but wildlife increases native richness, with stronger effects under low productivity

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Abstract

1. Grazing by domestic livestock is one of the most widespread land uses world-wide, particularly in rangelands, where it co-occurs with grazing by wild herbivores. Grazing effects on plant diversity are likely to depend on intensity of grazing, herbivore type, co-evolution with plants and prevailing environmental conditions.
2. We collected data on climate, plant productivity, soil properties, grazing intensity and herbivore type, and we measured their effects on plant species richness from 451 sites across 0.4 M km^2 of semi-arid rangelands in eastern Australia. We used structural equation modelling to examine the direct and indirect effects of increasing grazing intensity by different herbivores (cattle, sheep, kangaroos, rabbits) on native and exotic plant species richness across all sites, and in subsets focusing on three woodland communities spanning a gradient in productivity.
3. Direct effects of grazing by all herbivores were strongest under low productivity but waned with increasing productivity. Increases in the intensity of recent and historic livestock grazing corresponded with greater exotic plant richness under low productivity and less native plant richness under both low and moderate productivity. Rabbit effects were greatest under moderate productivity. Overall, the effects of kangaroos were benign. Grazing indirectly affected native and exotic plant richness by increasing soil phosphorus and reducing soil health (i.e. nutrient cycling).
4. *Synthesis and applications*. Our study shows that livestock grazing increases exotic species richness but reduces native richness, while kangaroo grazing increases native richness in environments with low productivity. The results provide clear messages for land managers and policy makers: (1) the coexistence of livestock grazing and plant diversity is only possible within more productive environments and (2) grazing under low or moderate productivity will impact upon native and exotic plant richness.

KEYWORDS

Australia, grazing, herbivory, kangaroo, livestock, plant richness, productive environments, rabbit, semi-arid woodland, structural equation modelling

1 | INTRODUCTION

Grazing by domestic livestock might be used to manage plant communities for uses other than the production of food and fibre (e.g. Pykälä, 2005). Livestock grazing can alter plant structure and soil cover to maximize habitat value for birds (e.g. plains wanderer; Baker-Gabb, Antos, & Brown, 2016) and mammals (e.g. elk in the western United States; Frisina & Morin, 1991), and could reduce the risk of wildfires (Williamson, Murphy, & Bowman, 2014). Grazing has been invoked as a potential mechanism to maintain species richness under high levels of productivity because it reduces the biomass of plants that suppress subordinate species (Borer et al., 2014; Lunt, Eldridge, Morgan, & Witt, 2007). However, livestock grazing can also reduce the richness of many taxa (including plants, animals and non-vascular plants) due to the direct effect of disturbance and alteration of vegetation and soil structure. It can also alter community composition, benefitting less palatable plants, and drive declines in ecosystem functioning due to trampling and changes in resource heterogeneity (Eldridge, Poore, Ruiz-Colmenero, Letnic, & Soliveres, 2016; Fleischner, 1994; Steinfeld et al., 2006).

The effects of grazing on plant richness are varied (Cingolani, Noy-Meir, & Díaz, 2005), and in many systems, we still lack a comprehensive understanding of the mechanisms that control the effects of grazing on plant diversity across large regional scales. The effects of herbivores on plant richness are likely to vary with: (1) the intensity of grazing (grazing pressure, stocking rate; Eldridge et al., 2016), (2) the history of co-evolution between plants and herbivores (Lunt et al., 2007), (3) herbivore type (e.g. livestock versus native herbivores; Kimuyu, Sensenig, Riginos, Veblen, & Young, 2014), (4) community productivity (e.g. Lezama et al., 2014), and (5) environmental conditions such as climate, soil type or fertility, which influence plant community structure indirectly through mechanisms such as the capacity of the soil to hold water (e.g. Dodd, Lauenroth, Burke, & Chapman, 2002; Lezama et al., 2014; Senft et al., 1987). The relative importance of these different drivers of grazing effects is still poorly understood. In addition, grazing effects are not only direct but can also be indirectly mediated by changes in resource availability or physical properties of surface soils (Schrama et al., 2013). Furthermore, any effects of grazing are likely to be compounded by the interactions between domestic herbivores and the wild (e.g. rabbits, goats, deer) or native (e.g. kangaroos in Australia) herbivores that inhabit extensive areas grazed by livestock (Bagchi & Ritchie, 2010).

In Australia, grazing by wild herbivores (goats and rabbits) has been identified as a threatening process under the Environment Protection and Biodiversity Conservation Act 1999 (EA, 1999). Feral goats and rabbits cause significant habitat degradation and reduce pastoral productivity and habitat of native fauna and flora (e.g. Tiver & Andrew, 1997). Densities of kangaroos, the predominant native mammalian herbivore in Australia, has increased markedly in the 200 years since European settlement due to greater access to livestock watering points, removal of top predators, and changes in vegetation structure and composition (Letnic & Crowther, 2013). Kangaroo grazing can be intense, leading to reductions in plant cover and changes in vegetation composition (Noble & Tongway, 1986). However, although kangaroo populations are relatively high, their effects on ecosystems are poorly known. Kangaroos might be expected to have less effect on plant communities than domestic livestock because they graze less intensively, are unconstrained by fencing and therefore more selective, and unlike European livestock, have co-evolved with the existing vegetation. The extent to which effects attributed to livestock are in fact caused by wildlife such as kangaroos is an important management issue.

In this study, we analysed the effects of different herbivore types (native, feral and domestic grazers) on plant (exotic and native) richness and soil attributes at 451 sites differing in productivity. The objectives of our study were (1) to examine the effects of recent and historic grazing by managed (cattle, sheep) livestock on plant richness, (2) to compare this effect with that of grazing by free-ranging herbivores, kangaroos (*Macropus* spp.) and feral goats and European rabbits (*Oryctolagus cuniculus*), and (3) to evaluate changes in the effect of different herbivores when they co-occur and across a gradient of productivity. We had four hypotheses (see details in Figure 1, Table 1): (1) We expected to detect strong negative effects of livestock on native plant richness (Hypothesis 1) but few effects of kangaroos (Hypothesis 2), because unlike kangaroos, livestock are constrained in paddocks and have not co-evolved with native plants. However, notwithstanding any broad regional effects under Hypothesis 1, we expected marked declines in species richness with grazing under low productivity (e.g. Cingolani et al., 2005; Lezama et al., 2014; Proulx & Mazumder, 1998; but see Eldridge et al., 2016) but an enhancement or maintenance of plant richness under higher productivity (Hypothesis 3). Finally, we expected that grazing would affect richness by altering soils in two ways: (1) by reducing the capacity of the soil to cycle nutrients, enhance infiltration or resist erosion, with differential effects on native and exotic species, and (2) by altering soil phosphorus (P) levels (Hypothesis 4). High levels of soil P in drylands are associated with the redistribution of P-rich sediments due to erosion (Delgado-Baquerizo et al., 2013) or livestock movement (Duncan, Dorrough, White, & Moxham, 2008). We expected, therefore, that grazing would enhance soil P, thereby indirectly affecting plant richness.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study spanned ~900 km of longitude at 451 sites across a large area (0.4 M km^2) of eastern Australia. The sites were selected to capture three markedly different semi-arid woodland communities. These communities are used extensively for livestock grazing, but large areas have been dedicated for conservation (national parks, nature reserves) and smaller areas to native forestry. Across this gradient, the climate is semi-arid, with slightly more rainfall during the six warmer months in the central section and during the cooler months in the south and south-west. Rainfall varies from 385 to 460 mm/year, but average temperatures are relatively constant (*c*. 18°C) across the gradient (Table 2). Soil textures range from sandy clay-loams in cypress pine to silty loams in blackbox and red gum communities.

Our sites were selected based on the overstorey dominance of three focal tree species: white cypress pine (*Callitris glaucophylla*), blackbox (*Eucalyptus largiflorens*) and river red gum (*Eucalyptus camaldulensis*). At the least productive end of the gradient (based on NPP data from MODIS imagery: 0.64 g C m^{-2} $days^{-1}$) are sites located within the blackbox community (Table 2), which is generally found on higher level floodplains that receive floodwater very infrequently (10–40 years; Smith & Smith, 2014). The soils have uniform and deep profiles and contain relatively high levels of silt (56%) and clay (19.3%, Eldridge, Koen, & Harrison, 2007, Table 2). At the most productive end of the gradient (NPP: 1.03 g C m^{-2} $days^{-1}$) are sites dominated by river red gum; inland riverine forests located on the lower terraces of major western river systems (Murray, Murrumbidgee and Lachlan Rivers). These systems receive supplementary moisture from floodwaters every 8 to 15 years, have very deep, relatively uniform soil profiles, and have the highest levels of fine sediments (silt and clay) and soil nutrients along the gradient (Table 2). The soils are relatively resistant to disturbances due to relatively frequent inundation by floodwaters. At intermediate positions in the gradient (NPP: 0.75 g C m^{-2} $days^{-1}$) are the cypress pine sites, which occurred on level to slightly undulating plains where moisture is derived entirely from rainfall. The soils have gradational soil profiles derived from Quaternary colluvium and aeolian material, with low levels of carbon, nitrogen and phosphorus restricted to the uppermost soil layers.

2.2 | Site establishment

Distance from permanent water is a useful surrogate of grazing intensity (Fensham & Fairfax, 2008). To select sites, we randomly assigned each of the 451 sites (151 for cypress, 150 for blackbox and 150 for red gum) to a specific distance from water, which ranged from 200 to >2000 m. Sites were inspected to ensure that they were more than 250 m from any major road (except for sites along road verges). Sites were selected from long-term grazing exclosures, low intensity and long ungrazed conservation reserves, road verges subjected to intermittent grazing, and woodlands with long histories of more intense grazing to sample across a full spectrum of recent (last 2–3 years) and historic (up to 20 years) grazing intensities.

2.3 | Site assessment and grazing intensity

Each site comprised a 200-m long transect and was measured only once. Transects were established parallel to the nearest livestock watering point, which was generally an earthen dam, to ensure a similar distance to the water of all points in the transect. Along this transect, we positioned five 25 m^2 (5 m × 5 m) quadrats (hereafter large quadrats) every 50 m, within which we centrally located a smaller (0.5 m × 0.5 m) quadrat (hereafter small quadrats). Within the large quadrats, we recorded the cover and abundance, by species, of all vascular plants. We also assessed the cover of groundstorey plants and shrubs at 100 points, located every 2 m along the 200 m transect using a point-intercept method.

To assess recent grazing intensity, we identified and counted the dung of all herbivores within the large (cattle, sheep/goat, kangaroo) and small (kangaroo, rabbit, sheep/goat) quadrats. Dung counts are used widely to estimate herbivore abundance (Johnson & Jarman, 1987). 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. At 10 sites, we counted, collected, dried and weighed the dung from 10 large quadrats to obtain a relationship between dung counts and their dry mass for each herbivore type. This relationship was then used to calculate the total oven-dried mass of dung per hectare per herbivore as our measure of recent grazing intensity. Where dung from the same herbivore was assessed in both the large and small quadrats, we derived an average mass per hectare based on both quadrats for that herbivore type. We were unable to discriminate between sheep, goat and in very few cases deer (*Cervus* spp.) dung, or between European rabbit and European hare (*Lepus europaeus*) dung. 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 & Landsberg, 2004).

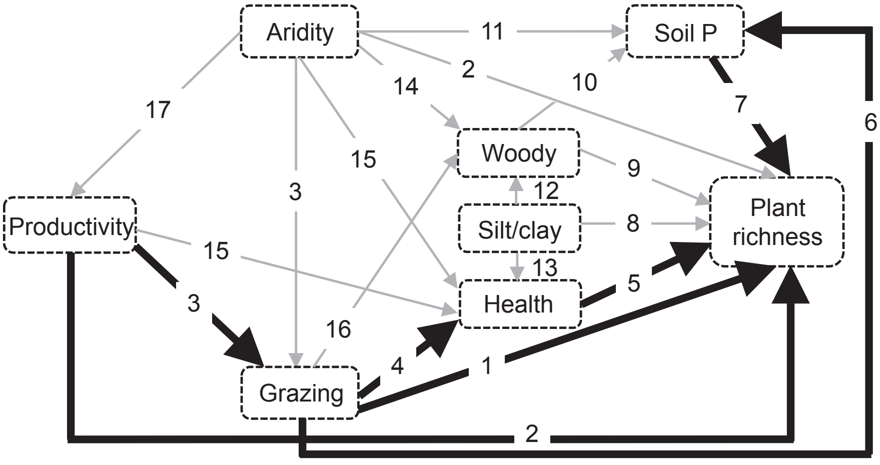


FIGURE 1 Conceptual a priori model for total plant richness for all 451 sites. The variables aridity, productivity, grazing, soil health (health), soil silt + clay content, soil phosphorus (P), and woody (shrub, tree) cover are indicated as broken boxes. Numbers correspond to pathways identified in Table 1. The thick pathways represent direct relationships corresponding to our hypotheses

TABLE 1 Hypothesized mechanisms underlying the grazing–plant–soil a priori model

Path	Hypothesized mechanism
1	(±) Livestock grazing is likely to shift community structure from natives (often grasses) to exotics (generally forbs) with variable effects on richness (Cingolani et al. (2005). Benign effects of kangaroo grazing on native plants, but unknown effects on exotics
2	(?/−) Productivity effects unknown, but lower plant richness, and proportion of native and perennial plants with increased aridity (Thompson & Eldridge, 2005)
3	(+) Declining productivity (more arid) associated with more feral goats and European rabbits; (−) larger property size associated with greater kangaroos grazing. Grazing capacity increases with increasing productivity
4	(−) Herbivore activity reduces biocrust cover (Eldridge, 1998), compacts soils, reduces macroporosity and soil C and N (Eldridge, Soliveres, Bowker, & Val, 2013)
5	(+) Healthy soils support higher levels of native plant richness through greater water holding capacity, increased nitrogen from biocrusts, greater litter cover and enhanced soil surface stability (Eldridge et al., 2013); (?) negative or benign effects for exotic plants
6	(+) Increased deposition of P in livestock dung (Dorrough & Scroggie, 2008)
7	(±) Deposition of P in dung enhances exotic plants (Dorrough & Scroggie, 2008) and may reduce cover of natives (e.g. Lambers et al., 2010)
8	(+) Perennial richness may increase with more clay; (+) ephemeral richness likely to decline with increasing clay content (sensu Inverse Texture Hypothesis; Noy-Meir, 1973)
9	(+) Increasing plant richness/biomass with increasing woody cover under low levels of grazing, but (−) reductions under high grazing levels (Eldridge et al., 2013)
10	(+) Greater concentration of P under woody plants due to organic material deposition (Lambers et al., 2010), P-rich dung deposited by resting herbivores (Dorrough, Moxham, Turner, & Sutter, 2006)
11	(+) Soil P mobilized by increasing aridity via erosion (Delgado-Baquerizo et al., 2013)
12	(−) Cover of native shrubs increases on coarse-textured soils (Noble & Tongway, 1986) but variable woody density depending on plant community type (Keith, 2008)
13	(−) Soil health indices decline with increasing clay content (Tongway, 1995)
14	(+) Native shrub cover on coarse-textured soils increases with increasing aridity (Noble & Tongway, 1995) but likely varies with community type (Keith, 2008), aridity and productivity
15	(+) Greater biocrust cover (Delgado-Baquerizo et al., 2016); (−) less plant cover (Eldridge et al., 2013) with increasing aridity; and vice versa for productivity
16	(+) Greater cover of woody shrubs with increased historic grazing (livestock tracks) but unknown (shrub cover) or nil (tree cover) trends for recent grazing
17	(−) Reduced productivity with increased aridity

2.4 | Net primary productivity and aridity

We calculated net primary productivity for each site using MODIS satellite imagery data (http://neo.sci.gsfc.nasa.gov/) with a spatial resolution of 1 km. These data provide a more realistic measure of long-term site productivity than above-ground biomass, which is seasonally and spatially highly variable. The three vegetation communities represented a gradient in NPP, expressed as a time rate of C production, from low (blackbox: 0.64 g C m^{-2} $days^{-1}$) to medium (cypress pine: 0.75 g C m^{-2} $days^{-1}$) to high (red gum: 1.03 g C m^{-2} $days^{-1}$; Table 2). If our hypothesis that grazing effects differ with productivity levels is upheld (Hypothesis 3), this would justify separate analyses of herbivore effects for the three communities. Despite some overlap in productivity, we retained the community-level analyses for three reasons. First, although all communities are woodlands with similar soils, there are idiosyncratic differences among them that could lead to differential effects of grazing on richness (e.g. soil depth). Second, although all herbivores occurred across the three communities, their relative abundances differed slightly, with rabbit grazing more common in cypress pine and cattle more common in red gum. Finally, there are subtle differences in the way these three woodland systems are managed. Grazing in red gum communities relies on moving livestock after flooding, whereas livestock are retained year-round in the cypress pine community.

We also used the FAO Aridity Index (AI) to account for the climatic variation across the study area in our analyses. Aridity was calculated as 1−AI, where AI = precipitation/potential evapotranspiration using FAO's Global Aridity Map (http://ref.data.fao.org/map?entryId=221072ae-2090-48a1-be6f-5a88f061431a). Aridity was negatively related to annual mean precipitation in our database (Spearman's $\rho = -0.95$; $p < .001$; $n = 451$).

2.5 | Measures of soil nutrient cycling, infiltration and resistance to erosion

We used rigorous, field-based protocols to assess the status and morphology of the soil surface within the small quadrats (Tongway, 1995). Within each of the five small quadrats at a site, we measured 13 attributes: surface roughness, crust resistance, crust brokenness,

TABLE 2 Mean (±*SE*) values of a range of biotic and abiotic attributes, plant richness (at two spatial scales) and dung loads for different herbivores across the productivity gradient. Sheep dung includes sheep + goats; rabbit grazing includes rabbits + European hares. Within a row, difference superscripts indicate a significant difference at $p < .05$ (one-way analysis of variance)

	Productivity level					
	Low blackbox		Moderate cypress pine		High red gum	
Attribute	*M*	*SE*	*M*	*SE*	*M*	*SE*
Rainfall (mm/year)	385^{a}	3.2	460^{b}	4.6	441^{b}	3.2
Aridity$^{\#}$	0.26^{a}	0.004	0.32^{b}	0.005	0.39^{c}	0.005
Productivity (g C m^{-2} days^{-1})	0.64^{a}	0.017	0.75^{b}	0.018	1.03^{c}	0.022
Sand (%)	24.0^{a}	0.65	60.0^{b}	0.98	14.4^{c}	0.37
Silt (%)	56.7^{a}	0.88	27.1^{b}	1.01	71.7^{b}	0.49
Clay (%)	19.3^{a}	0.68	12.9^{b}	0.82	13.9^{b}	0.33
Stability index (%)	53.3^{a}	0.42	61.7^{b}	0.60	62.2^{b}	0.38
Infiltration index (%)	21.6^{a}	0.23	21.9^{a}	0.33	23.3^{b}	0.24
Nutrient index (%)	23.7^{a}	0.41	26.3^{b}	0.45	30.9^{c}	0.40
Biocrust cover (%)	6.3^{a}	0.53	18.2^{b}	0.86	0.8^{c}	0.15
Soil total carbon (%)	2.75^{a}	0.10	2.08^{b}	0.06	4.84^{c}	0.11
Soil total nitrogen (%)	0.205^{a}	0.005	0.152^{b}	0.003	0.307^{c}	0.006
Soil available phosphorus (ppm)	51.86^{a}	2.31	14.38^{b}	0.689	61.08^{a}	2.02
Native plant richness (1.25 m^{2})	11.9^{a}	0.31	10.8^{a}	0.40	6.9^{b}	0.23
Native plant richness (125 m^{2})	27.5^{a}	0.65	26.8^{a}	0.88	19.0^{b}	0.51
Exotic plant richness (1.25 m^{2})	3.4^{a}	0.19	4.5^{b}	0.24	4.6^{b}	0.29
Exotic plant richness (125 m^{2})	7.7^{a}	0.37	9.6^{b}	0.36	11.9^{c}	0.53
Cattle dung (kg/ha)	28.8	4.2	142.0	39.1	17.8	4.1
Sheep/goat dung (kg/ha)	3.4	0.7	12.1	3.2	0.2	0.1
Rabbit dung (kg/ha)	2.2	0.4	12.2	2.4	1.0	0.5
Kangaroo dung (kg/ha)	18.9	1.7	52.7	3.4	33.2	2.4

$^{\#}$Aridity = (1—Aridity Index)

crust stability, surface integrity (cover of uneroded surface), cover of deposited material, biocrust cover, plant foliage and basal cover, litter cover, litter origin, and the degree of litter incorporation, and the texture of a sample of soil from the top 5 cm using the hydrometer method (see Appendix S1). An index of soil health was calculated as the arithmetic mean of the standardized (*z*-transformed) values of the 13 surface attributes (Appendix S1). Indices derived from these 13 attributes have been shown to be strongly correlated with ecosystem functions related to soil stability, nutrient cycling and infiltration (Maestre & Puche, 2009). Available phosphorus (P) in the top 5 cm of the soil was calculated according to Colwell (1963).

2.6 | Statistical analyses

We used Structural Equation Modelling (SEM; Grace, 2006) to analyse the effects of different grazing intensities (i.e. the mass of dung from different herbivores and density/size of livestock tracks) on plant richness (the total number of different species within the five large quadrats, separated into exotics or natives) and the explanatory variables tree cover, shrub cover, soil silt + clay content, soil health, soil P, aridity, and productivity. In all models, the effects of recent and historic grazing were combined into a single composite variable ("grazing"). Increases in this composite variable corresponded to increasing grazing intensity. 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). We performed an overall (regional) model with all our sites together, to investigate average effects of different types of herbivores, and then three community-specific (productivity) models to address interactions between herbivory and productivity.

Our models considered effects of individual herbivores and some meaningful interactions. The composite variable considered the combined effects of grazing by cattle, sheep/goats, kangaroos, rabbits and historic grazing, and four specific interactions: cattle × kangaroo, cattle × rabbits, sheep/goats × kangaroos and sheep/goats × rabbits. We did not consider rabbit × kangaroo or sheep/goat × cattle interactions due to multicollinearity issues and also because these were the two least expected interactions as few land managers in the area run mixed herds of sheep and cattle, and kangaroos and rabbits tend to graze different parts of the landscape, so would tend not to interact. All four interactions were included in the regional native richness model, but only two interactions (cattle × rabbits, sheep/goats × kangaroo) were retained in the regional exotic richness model to avoid multicollinearity, as they were highly correlated with other predictors. For the separate productivity models, all four interactions were included for low productivity, and but only two for both moderate (cattle × rabbit, sheep × rabbit) and high (cattle × rabbit, cattle × kangaroo) productivity in order to prevent multicollinearity.

We used a two-step process, first developing a regional model for 451 sites with productivity, aridity, grazing, soil health, silt/clay, soil P, shrub cover and tree cover in relation to native and exotic plant richness. We then developed separate models for each productivity class, based on the results of the first step, which indicated a productivity effect on plant richness. Our a priori model (Figure 1) predicted a number of direct and indirect effects of grazing and productivity on plant richness via its effects on soil health, soil P and woody plants (tree and shrub cover).

In order to test whether the different responses were due to changes in productivity or other inherent characteristics of the three communities, we ran linear models to examine the effect of community type on native and exotic plant richness, separately, extracted the residuals from this model, and use the residuals as our dependent variable in the SEM, effectively taking out any community effect from our models but still allowing us account for differences in productivity.

Before fitting empirical data to our a priori models, we examined the univariate correlations among all variables and standardized our predictors (grazing data, woody cover, soil health, silt/clay content) to improve normality. All the relationships were linear and, therefore, we did not model quadratic relationships. The a priori model (Figure 1) was compared with the variance–covariance matrix to assess the overall goodness-of-fit, using the χ^2 statistic. The goodness-of-fit test estimates how well our data are reflected by the a priori structure. Thus, high probability values indicate that these models are highly plausible causal structures underlying the observed correlations. Analyses were performed using the AMOS 22 (IBM, Chicago, IL, USA) software. The model with the strongest measures of fit (e.g. low χ^2, high Goodness-of-Fit Index [GFI] and high Normal Fit Index [NFI] or low root mean square error of approximation [RMSEA]) was interpreted as showing the best fit to our data (Appendix S2). The strength and sign of relationships among the variables is represented by path coefficients, which are analogous to partial correlation coefficients (Grace, 2006).

3 | RESULTS

Overall, richness of native plants was two to three times greater in communities of low (blackbox) or moderate (cypress pine) than high (red gum) productivity (ANOVA: $F_{2,448} = 40.67$, $p < .001$). Exotic plant richness showed the opposite response, being lower in the low productivity community ($F_{2,448} = 11.55$, $p < .001$, Table 2).

3.1 | Productivity and grazing effects on plant richness

For the regional model, native plant richness declined strongly with increasing productivity (Figure 2), but there were only weak effects for exotic richness (Figure 3; Appendix S3). The standardized total effects (STE) indicate that all measures of recent and historic grazing were associated with reductions in native plant richness, with effects strongest for recent grazing by cattle and rabbits. Kangaroo grazing, however, was associated with increases in native total plant richness (Figure 2). There were no direct grazing effects on exotic plant richness (Figure 3). Sheep grazing tended to exacerbate the negative effects of rabbits on native plant richness, and dampened the positive effect of kangaroos on exotic plant richness (Appendix S4). When we re-ran the SEMs using the residuals extracted from the linear models, the standardized path coefficient between productivity and native plant richness declined only slightly (−0.50 to −0.40), but there was still a strong effect on native richness. In the exotic richness model, removing the community effect had very little influence on the productivity-exotic richness model (−0.06 to −0.14).

3.2 | Community-level effects

The average negative grazing effect on species richness observed in our regional model changed when considering the different productivity levels characterizing each community. Grazing had a positive effect on native and exotic species under low productivity and no effect under high productivity (Figure 4a,c; Appendix S5). A strong negative effect was observed within the moderate productivity community, but only for native plant richness (Figure 4b). Differences in response to grazing were also attributable to different herbivores. Under low productivity, kangaroo grazing was associated with increased native plant richness (STE = 0.22) and historic livestock grazing with reduced native plant richness (STE = −0.22). Recent grazing by both cattle (STE = 0.27) and kangaroos (STE = 0.21) was associated with increased exotic plant richness (Appendix S6). For moderate productivity, recent grazing by both cattle (STE = −0.28) and rabbits (STE = −0.36) was associated with reduced native plant richness, but kangaroo grazing with increased exotic plant richness (STE = 0.31; Appendix S6). The explanatory power of the three community models, measured as model R^2, varied greatly, from 0.20 (exotic richness; low productivity) to 0.52 (native richness; high productivity, Figure 4a–c). The three community models were a reasonable fit to the data (GFI > 0.981, RMSEA < 0.020, $p_{\mathrm{RMSEA}} > 0.166$). Sensitivity analyses using the residuals of all variables after controlling for the effect of "community type" were consistent with the results presented here, revealing that the dependency of grazing effects on productivity were not confounded by other factors characterizing the different communities.

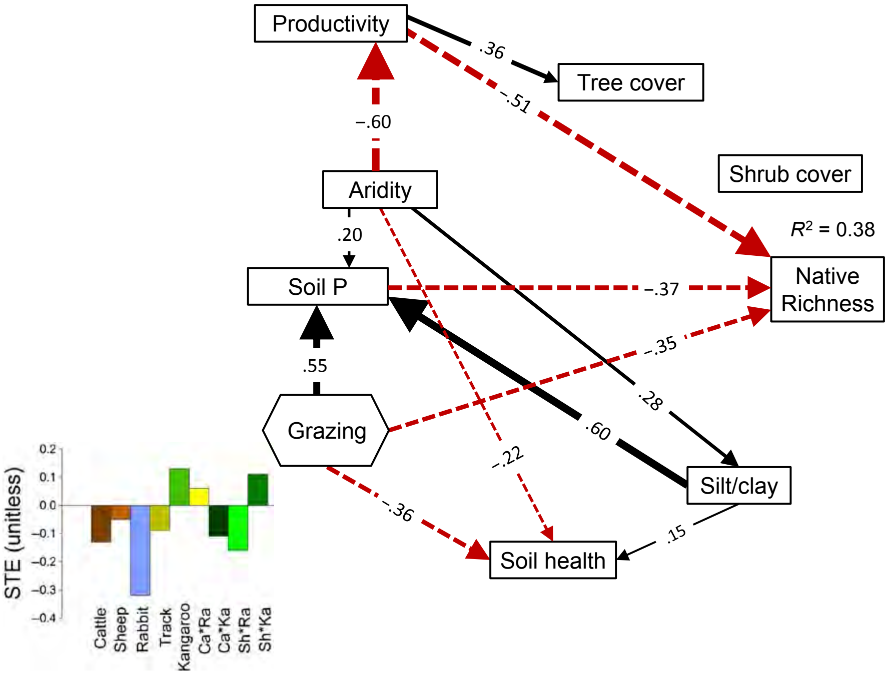
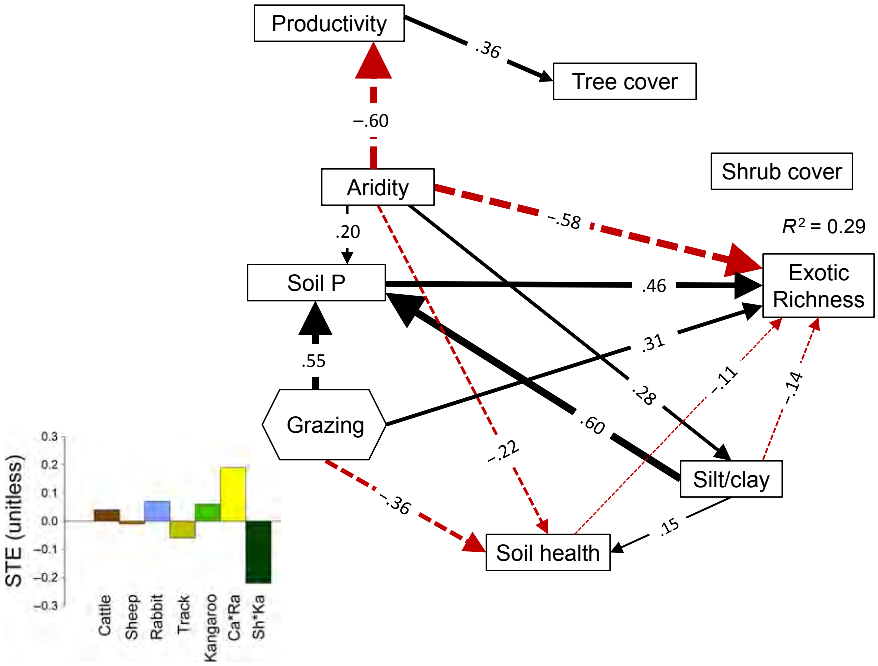


FIGURE 2 Regional structural equation model depicting the effects of productivity, soil phosphorus (soil P), grazing, silt and clay content, tree and shrub cover, soil health and aridity on native plan t richness across all sites along the productivity gradient. The width of arrows is proportional to the size of 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. Non-significant pathways have been omitted for clarity (χ^2 = 24.31, *df* = 17, *p* = .111, NFI = 0.993, GFI = 0.994, Bollen-Stine = 0.614). The histograms indicate the standardized total effects (STE); the sum of direct and indirect effects of our five measures of grazing on plant richness. Ca, cattle; Sh, sheep; Ra, rabbit; Ka, kangaroo [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 3 Regional structural equation model depicting the effects of productivity, soil phosphorus (soil P), grazing, silt and clay content, tree and shrub cover, soil health and aridity on exotic plant richness across all sites along the productivity gradient. The width of arrows is proportional to the size of 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. Non-significant pathways have been omitted for clarity (χ^2 = 18.14, *df* = 14, *p* = .20, NFI = 0.990, GFI = 0.995, Bollen-Stine = 0.62). The histograms indicate the standardized total effects (STE); the sum of direct and indirect effects of our five measures of grazing on plant richness. Ca, cattle; Sh, sheep; Ra, rabbit; Ka, kangaroo [Colour figure can be viewed at wileyonlinelibrary.com]



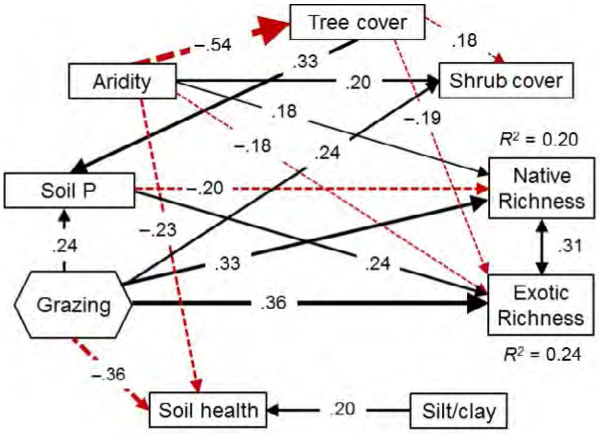
3.3 | Indirect effects of grazing on plant diversity via soil properties

Recent livestock and rabbit grazing suppressed the richness of native plants by enhancing soil P levels in all communities (Figure 4a,b). Under moderate productivity, there was a weak indirect negative effect of grazing on native plant richness, mediated by reductions in soil health. Grazing under moderate productivity also enhanced exotic richness indirectly via the suppression of native richness or shrub cover.

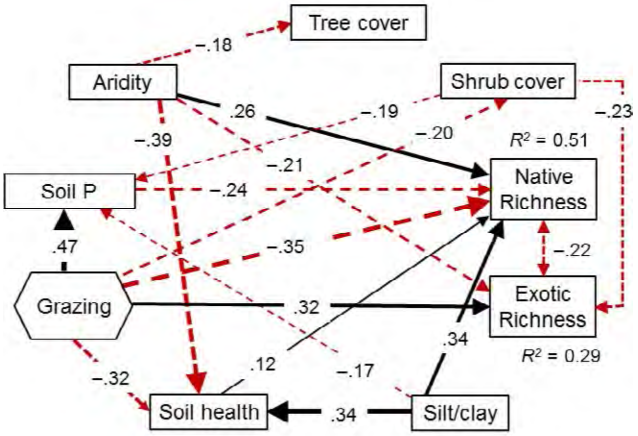
4 | DISCUSSION

Consistent with our hypotheses, across all productivity levels, recent and historic livestock grazing reduced native plant richness, whereas grazing by kangaroos had mostly benign or neutral effects. Further, grazing effects were more pronounced under lower productivity and waned under higher productivity. Finally, we found some support for an indirect effect of grazing on richness via changes in soil health and soil P, but only under moderate productivity. Taken

(a) Low



(b) Moderate



(c) High

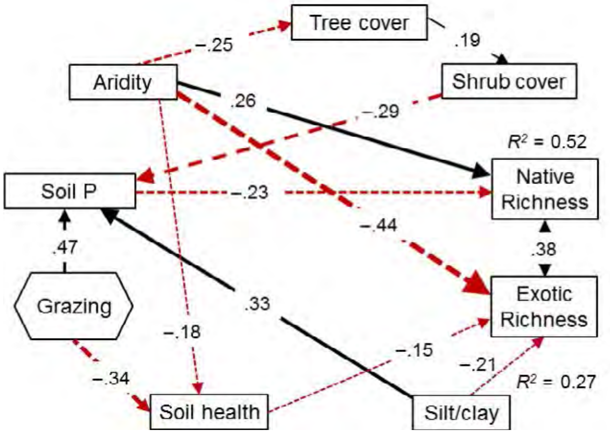


FIGURE 4 Structural equation model depicting the effects of grazing, silt and clay content, soil phosphorus (P), tree and shrub cover, soil health and aridity on native and exotic plant richness for (a) low (blackbox), (b) moderate (cypress pine) and (c) high (red gum) productivity communities. The width 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 given adjacent to each pathway. Non-significant pathways have been omitted for clarity. Double ended arrows indicate correlations. Low productivity: $\chi^2 = 25.34$, $df = 37$, $p = .927$, GFI = 0.981, RMSEA = 0.001, Bollen-Stine = 0.90. Moderate productivity: $\chi^2 = 19.109$, $df = 18$, $p = .385$, GFI = 0.984, RMSEA = 0.020, Bollen-Stine = 0.166. High productivity: $\chi^2 = 21.7$, $df = 28$, $p = .791$, GFI = 0.986, RMSEA = 0.001, Bollen-Stine = 0.370). [Colour figure can be viewed at wileyonlinelibrary.com]

together, our results provide compelling evidence that herbivore type and grazing intensity affect the richness of groundstorey vegetation, but that these effects depend on site productivity. Our study provides a clear message for land managers and policy makers: (1) the coexistence of livestock grazing and plant diversity is only possible within more productive environments, and (2) grazing under low or moderate productivity will impact upon native and exotic plant richness.

4.1 | Grazing effects on plant diversity along productivity gradients

That grazing effects on plant species richness were more pronounced under low productivity and waned with increasing productivity is consistent with the results of extensive meta-analyses (e.g. Milchunas & Lauenroth, 1993; Olff & Ritchie, 1998; Proulx & Mazumder, 1998) and recent empirical studies of change in diversity and composition across large productivity gradients in Europe and the United States (Bakker, Ritchie, Olff, Milchunas, & Knops, 2006; Lezama et al., 2014). However, a recent meta-analysis of grazing effects across continental Australia revealed little change in plant richness with rainfall, perhaps because of the different complement of herbivores and the coarseness of the grazing assessment used in that study (Eldridge et al., 2016). Our current results can be explained by the constrained regrowth of grazed plants caused by resource limitation under low productivity (Olff & Ritchie, 1998; Proulx & Mazumder, 1998). Thus, grazing could act as an environmental filter, based on differential tolerance of species to herbivory or soil-induced disturbance. The effect would be to reduce plant vigour and potential to resprout due to low levels of available nutrients, thereby reducing the total community species pool.

4.2 | Indirect effects of grazing on plant richness via soil properties

Livestock-induced increases in exotic plant richness under low and moderate productivity could be due to direct grazing-related factors or indirectly, via changes in soil P. Direct effects probably relate to relaxation of competitive exclusion of smaller, ephemeral taxa, which in the absence of herbivory, would be out-competed by dominant, generally moderate nutritional grasses with high cover and biomass (Damhoureyeh & Hartnett, 2002). This phenomenon has been observed in tall tussock grassland in eastern Australia where grazing causes a shift from high biomass grasses such as *Themeda* spp. to shorter, native or exotic grasses and forbs (Prober & Lunt, 2008). Equally plausible is the notion of an indirect effect of grazing via changes in soil nutrients such as nitrogen in dung and urine or soil

P. Low levels of soil P are known to initiate and maintain native plant community richness on nutrient-poor soils (e.g. Lambers, Brundrett, Raven, & Hopper, 2010), and addition of high levels of phosphates, a bi-product of grazing, will maintain the cover of exotic, often annual plants at the expense of natives (Dorrough & Scroggie, 2008; Prober & Lunt, 2008).

Grazing altered plant richness indirectly by reducing soil health and enhancing soil P, but only under moderate productivity, thus partially supporting our fourth hypothesis. Rabbits effects under moderate productivity (STE = 0.44; Appendix S6) were likely due to the extensive soil disturbance associated with the construction of their communal burrows, resulting in exposure of P-rich subsoil (Eldridge & Koen, 2008). The lack of a response under high productivity probably relates to the fact that soil P was already high, perhaps due to a legacy effect of historic grazing, and/or the fact that native richness was already low and dominated by taxa tolerant of high P levels. Under moderate and high productivity, the indirect effects of livestock activity on richness via increased P were relatively strong, highlighting the importance of trampling and resource redistribution on species richness compared with the direct effects of herbivore activity on species richness through herbivory and plant disturbance.

4.3 | Grazing effects vary among herbivores

Our results provide strong support for herbivore-specific effects on plant richness. Recent and historic livestock grazing had the largest effects by reducing native richness or enhancing exotic richness. Rabbits also reduced native richness, but only under moderate productivity, where they were most abundant. Even at reportedly high densities, kangaroo effects were either benign or had no effects.

Relatively high kangaroo dung counts at all but two of the 451 sites, and above-ground biomass 2–5 times above threshold levels for kangaroos (*c*. 200 kg/ha Caughley, Shepherd, & Short, 1987), provide strong evidence that kangaroo densities were high across the sites. Despite this, kangaroo grazing was associated with increased native plant richness, but only under low productivity (Appendix S6). Kangaroos also had a positive effect on exotic plant richness under low and moderate productivity, possibly by reducing competition from native grasses, which they prefer (Edwards, Croft, & Dawson, 1996; Landsberg & Stol, 1996), thereby relaxing the suppression of exotic forbs. The dietary overlap between livestock and kangaroos is considerable, particularly during dry seasons (Landsberg & Stol, 1996), and in this study, when kangaroos co-occurred with sheep, exotic plant richness declined substantially, most likely because sheep targeted palatable herbaceous forbs, reducing overall richness. Sheep also exacerbated the negative effects of rabbits on native plant richness. Sheep are generalists (Dawson & Ellis, 1994), whereas rabbits tend to avoid longer, older vegetation in favour of green, often actively growing vegetation (Tiver & Andrew, 1997). Thus, sheep grazing, by removing larger plants, would allow rabbits to graze smaller native forbs, reducing native richness (Leigh et al., 1987). Indeed, the spread of rabbits across Australia is thought to have been assisted by an expanding pastoral industry, with sheep and rabbits making the vegetation more suitable for rabbits (Leigh et al., 1987). Importantly, we only found these interactions to be relevant under low productivity, probably because vegetation is more resilient to these combined herbivory effects under higher levels of resources.

Differences among herbivores may also be related to the indirect effects of trampling or differences in the way herbivores are managed. Cattle hooves exert more than twice the pressure on surface soils than sheep (Noble & Tongway, 1986) or kangaroos (Bennett, 1999) and are, therefore, likely to have a greater effect on soil compaction, disruption of surface crusts and therefore soil-mediated effects on plant richness than kangaroos (or rabbits). Kangaroos can be highly selective because they can move relatively freely in search of green grass (Caughley et al., 1987), unlike livestock that are generally confined to large paddocks year-round and where competition for plants is high.

5 | CONCLUSIONS

Our study shows that the effects of grazing differ with herbivore type and intensity, position within a productivity gradient, aridity, and to a lesser extent, plant origin (native or exotic). These nuances should be taken into account when deciding whether or not to include or exclude livestock grazing as a land management strategy. The effects of grazing on richness are, therefore, likely to be both herbivore- and vegetation community-specific, but also dependent on whether the management context is geared towards maintaining native biodiversity (native richness) or weed control (exotic richness). Our results suggest that there will be clear winners and clear losers, with negative effects of grazing under low to moderate productivity, but indistinct or benign effects under high productivity. Our models also suggest that increasing aridity, a consequence of changing climate in eastern Australia, will generally enhance native richness at the expense of exotics. Our models do not provide a clear mechanism for this, but they appear to be unrelated to changes in densities of different herbivores. Finally, given global concern over the effects of livestock grazing on ecosystem functions and services, a one-size-fits-all approach to grazing management is not supported by a rigorous examination of our data.

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AUTHORS' CONTRIBUTIONS

D.J.E., J.V., I.O. and S.K.T. conceived and designed the study and D.J.E., J.V. and S.K.T. collected the data; D.J.E., M.D.B. and S.S. analysed the data; D.J.E. led the writing of the manuscript, and all authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data on plant richness and grazing are deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.851d0 (Eldridge et al., 2017).

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