

Introduced and native herbivores have different effects on plant composition in low productivity ecosystems

Samantha K. Travers¹  | David J. Eldridge² | Josh Dorrrough³ | James Val⁴ | Ian Oliver^{5,6}

¹Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia

²Office of Environment and Heritage, c/- Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia

³Office of Environment and Heritage, Merimbula, NSW, Australia

⁴Office of Environment and Heritage, Buronga, NSW, Australia

⁵Office of Environment and Heritage, Gosford, NSW, Australia

⁶School of Environmental and Rural Sciences, University of New England, Armidale, NSW, Australia

Correspondence

Samantha K. Travers, Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia. Email: s.travers@unsw.edu.au

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Abstract

Questions: Understanding how livestock grazing alters plant composition in low productivity environments is critical to managing livestock sustainably alongside native and introduced wild herbivore populations. We asked four questions: (1) does recent livestock and rabbit grazing reduce some plant attributes more strongly than others; (2) does grazing by introduced herbivores (i.e. livestock and rabbits) affect plants more strongly than native herbivores (i.e. kangaroos); (3) do the effects of recent livestock grazing differ from the legacy effects of livestock grazing; and (4) does the probability of occurrence of exotic plants increase with increasing net primary productivity (NPP)?

Location: South-eastern Australia.

Methods: We measured the recent grazing activity of co-occurring livestock (cattle, sheep, goats), rabbits and kangaroos by counting faecal pellets; historic grazing activity by measuring livestock tracks; and derived NPP from satellite imagery. We used a hierarchical GLMM to simultaneously model the presence or absence (i.e. probability of occurrence) of all plant species as a function of their attributes (growth form, lifespan and origin) to assess their average response to recent grazing, historic grazing and productivity in a broad-scale regional study.

Results: Recent and historic livestock grazing, rabbit grazing and increasing NPP reduced the average probability of occurrence of plant species, although responses varied among plant attributes. Both recent and historic livestock grazing strongly reduced the average probability of occurrence of native species, and forbs and geophytes, but differed in their relative effects on other growth forms. Recent livestock grazing, rabbit grazing and NPP had similar effects, strongly reducing native species and forbs, geophytes, shrubs and sub-shrubs. The overall effects of recent kangaroo grazing were relatively weak, with no clear trends for any given plant attribute.

Conclusion: Our results highlight the complex nature of grazing by introduced herbivores compared with native herbivores on different plant attributes. Land managers need to be aware that domestic European livestock, rabbits and other free-ranging introduced livestock such as goats have detrimental impacts on native plant communities. Our results also show that kangaroo grazing has a relatively benign effect on plant occurrence.

KEYWORDS

cattle, forb, grass, grazing, kangaroo, livestock, NPP, occupancy model, plant traits, rabbit, sheep, shrub

1 | INTRODUCTION

Interactions between land-use intensification and climate are predicted to exacerbate global climate changes in terrestrial ecosystems (Maestre, Eldridge, & Soliveres, 2016). Grazing by free-ranging and fenced livestock is one of the most widespread land uses globally (Diaz et al., 2007). Livestock grazing sustains the livelihoods of millions of people worldwide but is also a substantial cause of land degradation (Steinfeld et al., 2006). Overgrazing has profound effects on ecosystem structure, composition and functions (Eldridge, Poore, Ruiz-Colmenero, Letnic, & Soliveres, 2016), and the resulting degradation is most pronounced in low productivity environments (drylands), which support about 40% of Earth's human population (Prävälje, 2016). Understanding the effects of grazing in low productivity environments is critical if we are to manage livestock sustainably alongside wild herbivores, in a future world where the climate is drier and more variable (Prävälje, 2016).

The effects of grazing by wild and domestic herbivores on plant communities are complex, particularly in low productivity environments (Lezama et al., 2014; Milchunas, Sala, & Lauenroth, 1988). The impacts of herbivores are driven largely by the type of herbivore, their preferences within and among species and the frequency, intensity and timing of their herbivory (Kimuyu, Sensenig, Riginos, Veblen, & Young, 2014; Riginos & Grace, 2008). As ecosystems evolve with a particular suite of herbivores and a definitive range of grazing intensities, any changes in herbivore activity in terms of either the type of herbivore or, independently, the intensity of herbivory, can influence vegetation composition. Consequently, native herbivore activity may adversely affect native vegetation if there are large shifts in their density or grazing intensity. The degree to which herbivores can affect plant communities is influenced by a number of factors, including plant responses to herbivory through tolerance or avoidance strategies, evolutionary history of the site, and site productivity (Proulx & Mazumder, 1998). For example, prolonged heavy grazing by livestock under low productivity can alter the relative cover of dominant growth forms and change plant community composition. This could occur through herbivores selecting for shorter rather than taller plants, or preferentially grazing on more palatable perennial plants, leading to a dominance of less palatable annual plants (Lavorel, McIntyre, Landsberg, & Forbes, 1997; Milchunas et al., 1988). This may occur slowly as gradual nutrient enrichment from grazing livestock alters soil nutrients, leading to compositional effects in the vegetation (Dorrough, McIntyre, & Scroggie, 2011). The strategies that different plants use to respond to grazing by particular herbivores are strongly driven by their evolutionary exposure to herbivory (Briske, 1996). However, few studies have considered the specific effects of co-occurring herbivores on different types of plants.

In this study we disentangle the effects of different co-occurring herbivores and NPP on plant occurrence in a large-scale, regional study in semi-arid south-eastern Australia. Australia has a relatively short history of grazing by domestic livestock (~230 years), but a rich evolutionary history (~50 M year) of grazing by unique native herbivores (kangaroos, *Macropus* spp.). Australian vegetation has evolved with soft-footed, forb- and grass- grazing herbivores, and their populations, and hence grazing intensity, has fluctuated with “boom and bust” productivity cycles (Dawson, 2002). In the 230 years since European settlement, hard-hooved domestic livestock have been grazing and browsing extensive areas of Australia at grazing intensities that are unsustainable. This has resulted in substantial soil degradation, soil nutrient enrichment, alterations to nutrient pools and shifts in vegetation composition and structure (Dorrough, Ash, & McIntyre, 2004; Dorrough et al., 2011; Vesk, Leishman, & Westoby, 2004), particularly in low productivity environments (Tongway, Sparrow, & Friedel, 2003). These changes have occurred against a backdrop of major shifts in wild herbivore densities. Increases in the density and distribution of livestock watering points have allowed kangaroos to proliferate, leading to changes in vegetation composition (Tiver & Andrew, 1997). Similarly, the invasion of the European rabbit (*Oryctolagus cuniculus*) has had substantial impacts on shrub recruitment and groundstorey composition and cover, with increasing rabbit densities associated with increases in the cover and biomass of exotic European forbs (Leigh, Wood, Holgate, Slee, & Stanger, 1989). Feral goats (*Caprus hircus*), deer, water buffalo, camels and other introduced herbivores have also presented problems at local and regional scales (Tiver & Andrew, 1997).

We present a novel study assessing the independent effects of co-occurring herbivores on plant composition by modelling the occurrence of individual plant species using a single hierarchical model (Gelfand et al., 2003; Jamil, Ozinga, Kleyer, & ter Braak, 2013; Pollock, Morris, & Vesk, 2012). We assessed the relative effects of recent and historic livestock grazing by cattle (*Bos taurus*), sheep (*Ovis aries*) and goats (*Capra hircus*), recent grazing by rabbits (i.e. introduced herbivores) and kangaroos (i.e. native herbivores) and NPP, and examined how species responses varied based on fundamental plant attributes (i.e. origin, life span and growth form). To our knowledge, no previous studies have considered the effects of different types of herbivore on different suites of plants. Our study aimed to assess how different herbivores affect different types of plant. Specifically, we aimed to investigate whether recent livestock and rabbit grazing would modify differentially the probability of occurrence of native, exotic, perennial and annual plants (Dorrough et al., 2004; Lange & Graham, 1983; Lunt, Eldridge, Morgan, & Witt, 2007; Vesk et al., 2004) and whether livestock and rabbits had a relatively differential effect than native herbivores (Tiver & Andrew, 1997). Our model also allowed us

to compare the effects of recent livestock grazing with the legacy effects of livestock grazing (i.e. historic grazing), and to understand how these four measures of grazing affect specific plant growth forms. We also included NPP in our model as we expected that the probability of occurrence of exotic plants would increase, and annual plants decline, with increasing NPP. This is because low productivity sites favour annual plants over perennials, particularly where rainfall is highly variable (Westoby, 1979/80), and higher productivity sites often have soils with more nitrogen, favouring exotic plants (Prober, Thiele, Lunt, & Koen, 2005).

2 | METHODS

2.1 | Study area

Our study was conducted at 451 sites across 500,000 km² of south-eastern Australia and was designed to assess the impacts of grazing in three broad semi-arid woodland communities dominated by Black box (*Eucalyptus largiflorens*), White Cypress pine (*Callitris glaucophylla*) or River red gum (*Eucalyptus camaldulensis*). This area is semi-arid with average rainfall varying from 385 to 460 mm/year, and mean temperature of about 18°C.

The Cypress pine community occurs on land forms ranging from source-bordering dunes on floodplains to rocky hills. The soils have gradational profiles consisting of Quaternary colluvium and aeolian deposits, and are generally low in C, N and P. The understorey in these communities varies according to soil type and disturbance (fire, grazing) history. The Black box community occurs on upper level floodplains of inland rivers, lakes and swamps that receive infrequent flooding (10–40 years; Smith & Smith, 2014). Their soils have a deep uniform profile and are relatively high in silt and clay (Eldridge, Koen, & Harrison, 2007). The understorey can be extremely variable, depending on grazing history, rainfall and latitude (Keith, 2004). The River red gum community occurs as riverine forests adjacent to the lower terraces of major river systems that receive natural floodwaters every 8–15 years, which enhance the regeneration of *E. camaldulensis*. Their underlying soils are deep uniform clays with relatively high nutrient levels.

2.2 | Site establishment

Within each community we chose 150 sites (151 in Cypress pine) across a spectrum of grazing histories and a range of land tenures (e.g. conservation reserves, forestry reserves, travelling stock reserves, town commons, former commercial grazing properties) at varying distances from permanent water, which we used in an initial desktop selection process for selecting sites (see Eldridge, Delgado-Baquerizo, Travers, Val, & Oliver, 2016). We selected sites to span a range of distances from water that ranged from 50 m to >2 km. Sites were inspected to ensure that they were >250 m from any major road (except for sites along travelling stock reserves). At each site we established a 200-m transect perpendicular to the nearest livestock watering point, which was generally an earthen dam or water tank. Along this

transect we positioned five 25 m² (5 m × 5 m) plots ("large quadrat") every 50 m. Within the large quadrat we nested a smaller 0.25 m² (0.5 m × 0.5 m) quadrat ("small quadrat").

2.3 | Floristic survey

Within each large quadrat we identified all vascular plants, where possible, to species level. Data from the five large quadrats were combined to produce a site-level species list for the 125-m² survey area. All sampling was conducted between Sept 2013 and Mar 2014.

Where plants could not be identified in the field, voucher specimens were collected for later identification. For 68 genera, unknown plants were pooled to the genus level (e.g. *Crassula* spp., *Rytidosperma* spp., *Wahlenbergia* spp.). For two families, Orchidaceae and Rubiaceae, unknown specimens were pooled at the family level. Pooled plant groups were treated as individual "species" for the purposes of our analyses.

2.4 | Plant attributes

We classified each species on the basis of three simple attributes: origin (exotic or -native), life span (annual or perennial [including biennial]) and growth form (tree, shrub, subshrub, grass, forb, geophyte, sedge, vine) using data from the PlantNET database (PlantNET 2016; <http://plantnet.rbg Syd.nsw.gov.au>). We combined plant growth forms into three pairs: grass and sedges; forb and geophytes; sub-shrub and shrub. We expected these paired growth forms would respond similarly.

2.5 | Recent and historic grazing activity and NPP

We identified dung and counted faecal pellets for three groups of herbivores: (1) livestock (cattle, sheep, goats) (2) kangaroos and (3) rabbits and hares (*Lepus europaeus*). For cattle, we counted individual dung events, in the large quadrats only rather than individual pellets (see Eldridge, Delgado-Baquerizo, et al., 2016). The remaining herbivore pellets were counted in the small quadrats and estimated in the large quadrats. Dung and pellet counts are often used to estimate the abundance of large herbivores (Marques et al., 2001) including Eastern Grey Kangaroo (*Macropus fuliginosus*; Johnson & Jarman, 1987). Samples of dung pellets were collected from every site to calculate the average oven-dried mass per hectare for each dung type for every site. We averaged the mass per hectare across all plots for each site, i.e. data were averaged over five large for cattle or ten plots (5 small + 5 large plots) for the remaining herbivores. From these data we developed three measures of recent grazing activity: livestock (sum of cattle, sheep and goats), kangaroos and rabbits (kg/ha). We also measured the width and depths of all livestock tracks crossing the 200-m transect to derive a total cross-sectional area of livestock tracks for each site. The summed cross-sectional area for each transect is our measure of historic livestock grazing activity (cm²).

We chose NPP (g C m⁻² d⁻¹) as it represents a broad measure of how recent climatic conditions have translated to biomass productions

in these systems. We obtained data from MODIS satellite imagery, at 1 km spatial resolution, for each 2-year period prior to our field survey (<https://modis.gsfc.nasa.gov/>). NPP values ranged from 0.22 to 1.72 g C m⁻² d⁻¹ across our sites, and varied little among communities (Cypress Pine 0.75 g C m⁻² d⁻¹; Black box 0.64 g C m⁻² d⁻¹; River red gum 1.02 g C m⁻² d⁻¹).

2.6 | Data preparation

Prior to analysis, NPP and the four grazing predictors (recent livestock, kangaroo and rabbit grazing; historic livestock grazing) were standardized (z-score transformed, i.e. mean subtracted and then divided by the SD). This allowed the model intercept to be interpreted as an average response and the slope terms to be partial dependencies, conditional upon the remaining continuous variables having mean values (Pollock et al., 2012). We removed all occurrences of vines and trees prior to analyses as our intent was to focus on those plants that occurred in the ground layer and that would be directly affected by grazing mammals. We also excluded all species that occurred at fewer than four sites. The species-level data (response) were converted to a binary presence/absence for each species for each site to allow us to model probability of occurrence.

2.7 | Statistical analyses

Rather than model the response of species individually or use distance-based modelling (Warton, Wright, & Wang, 2012), we used a single hierarchical species–environment–trait GLMM, using the presence or absence of all plant species as the response variable (Pollock et al., 2012). This modelling approach allowed us to: (1) assess whether the probability of occurrence of individual species varied in response to grazing and NPP; (2) jointly examine how responses to grazing and NPP varied according to plant attributes; and (3) compare the relative effects of different herbivore types on plant occurrence. These types of hierarchical models allow infrequently occurring species to be incorporated into models (Dorrough & Scroggie, 2008; Oliver, Dorrough, Doherty, & Andrew, 2016) and are being increasingly used to simultaneously model species and trait responses to environmental predictors (e.g. Dorrough & Scroggie, 2008; Jamil et al., 2013; Pollock et al., 2012).

The GLMM was fitted using the “glmer” command within the “lme4” package within R (v 3.1.2; R Foundation for Statistical Computing, Vienna, Austria). Our model consisted of the additive fixed effects of each of the four measures of grazing (recent livestock, kangaroo and rabbit grazing, historic livestock), NPP, plant longevity (annual, perennial), plant origin (native, exotic) and plant growth form (three pairs: grass + sedge; forb + geophyte; sub-shrub + shrub). This component of the model allowed us to estimate the “average” effect of each of these variables across all species. To enable us to examine how the effects of grazing and NPP varied among plant attributes, we also included two-way interactions between each of the plant attributes and each measure of grazing, and each plant attribute and NPP. We included “species” as a random intercept, which allowed us to take

into account how the overall probability of occurrence varied among individual species. However, we expected that the probability of occurrence of each species would also vary with changes in grazing and NPP. In a GLMM this is achieved by incorporating random slopes for each species with respect to each of the grazing and NPP variables (Pollock et al., 2012). We included vegetation community and site as random intercepts in our model to account for correlation among our samples.

As our response data were binary (presence/absence data of each species at each site), we used a binomial error structure. All models used Laplace approximation of the model likelihood. This model allowed us to examine the overall effect (i.e. “average species” response) of each fixed effect for each suite of plants, and the deviation of each species from the overall effects. Confidence intervals (CI) around the model parameters (fixed and random) were estimated using Wald CIs as model complexity and computing limitations prevented the use of bootstrapped CIs. Data were explored by plotting average responses and some individual species conditional models and associated approximated 95% CI for each random slope.

3 | RESULTS

3.1 | Plant composition in each community

Across 451 sites we recorded 819 plant taxa, comprising 611 native and 208 exotic species (Appendices S1 and S2). Native perennial forbs were the most diverse group of species, accounting for 23.4% of the total number of species. Native annual forbs and exotic annual forbs accounted for 17.9% and 13.1% of species, respectively. Native perennial grasses were the next most diverse group, representing 10.3% of all species. Forbs were the most diverse growth form across these communities, and exotic forbs accounted for 17.5% of all species.

3.2 | Effects of grazing on the probability of occurrence of different species

Recent and historic grazing by livestock, and recent grazing by rabbits, reduced the average probability of occurrence of plants overall (Figure 1). The overall effect of recent grazing by livestock was more strongly negative than grazing by rabbits or historic grazing (Figure 1). These three grazing measures also affected different types of plants in different ways (Figure 2). Grazing by livestock and rabbits reduced the average probability of occurrence of native plants more strongly than exotic plants, (Figure 1 [Livestock × Origin, Rabbit × Origin, Historic × Origin], Figure 2a–c). For recent livestock and rabbit grazing, we found grasses and sedges responded differently to other growth forms (Figure 1 [Livestock × Form, Rabbit × Form]), with recent livestock reducing the average probability of occurrence of forbs, geophytes, shrubs and sub-shrubs more strongly than grasses and sedges (Figure 2d). This trend was opposite for rabbit grazing, with the average probability of occurrence of grasses and sedges reduced more strongly than forbs, geophytes, shrubs and sub-shrubs (Figure 2f). Increasing levels of

FIGURE 1 Fixed effect estimates and 95% Wald CI from the binomial GLMM of plant species frequency of occurrence. For categorical effects, the categories shown are relative effects compared with the missing categories (i.e., annual life span, exotic origin and forb + geophyte growth form). P = perennial; N = native; G, S = grass + sedge; S, S = shrub + sub-shrub. Model terms with strong effects have CIs that do not pass through the dashed ($x = 0$) line

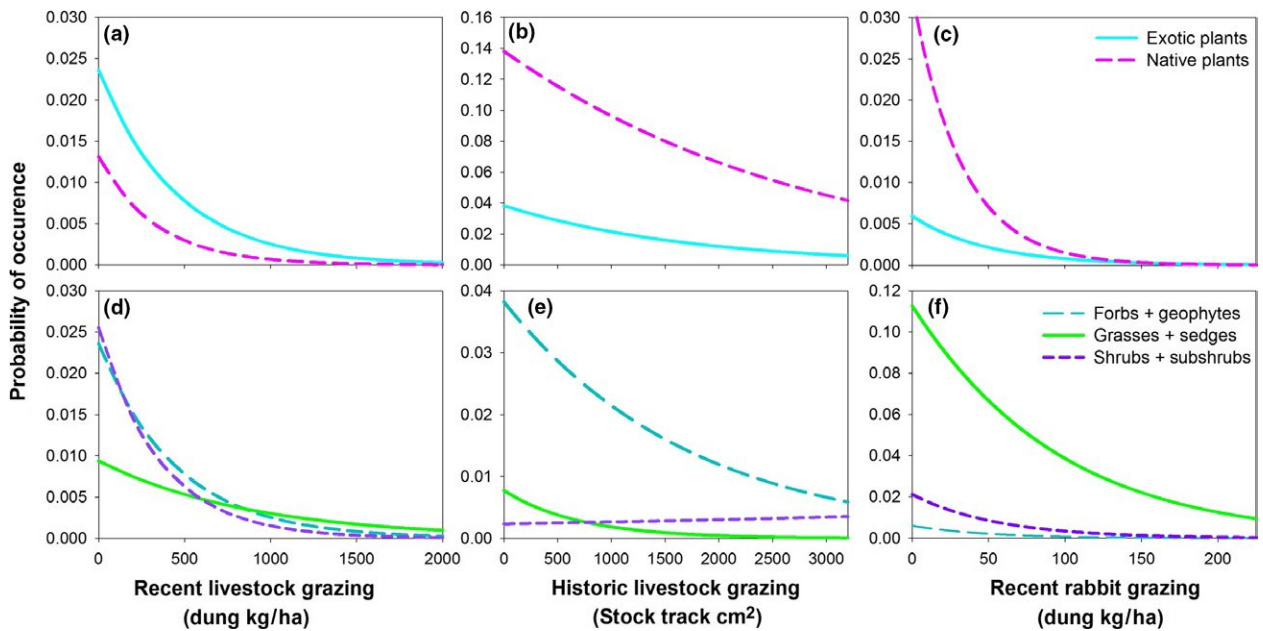
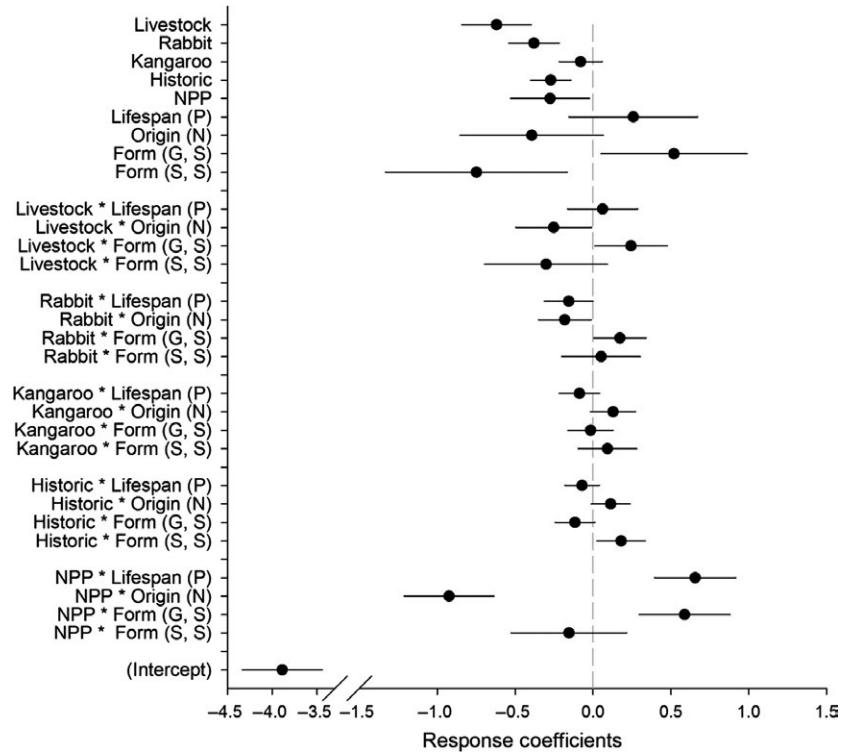


FIGURE 2 Effect of recent livestock grazing (i.e. sheep and cattle dung: kg/ha), historic livestock grazing (livestock tracks: cm²/200 m) and recent rabbit grazing (dung: kg/ha) on the average probability of occurrence for native and exotic plant species (a–c) and plant growth forms (d–f; forbs + geophytes, grasses + sedges and shrubs + sub shrubs)

historic grazing tended to increase the average probability of occurrence of shrubs and sub-shrubs but reduced the average probability of occurrence of grasses, sedges, forbs and geophytes (Figure 2e). There were no strong differences between annual and perennial plants in response to these three measures of grazing, but there was weak evidence that rabbit grazing reduced the average probability of occurrence of perennial plants more than annuals (Figure 1).

In contrast, grazing by kangaroos had relatively weak and uncertain effects on the average probability of occurrence of plant species (Figure 1). Increasing grazing pressure by kangaroos neither increased nor reduced the average probability of occurrence of species overall, and had no strong effects on plants, based on their origin, life span or growth form (Figure 1). There was, however, a weak increasing effect of kangaroo grazing on the occurrence of native plants (Figure 1).

3.3 | Effects of NPP on the probability of occurrence of different species

The average probability of occurrence of plant species declined with increasing NPP, but these effects differed among different suites of plants (Figures 1 and 3) and individual species (Appendices S2 and S3). The average probability of occurrence of annual plants declined while perennial plants increased with increasing NPP (Figures 1 and 3a). Similarly, the average probability of occurrence of native plants declined more than exotics with increasing NPP (Figures 1 and 3b). Increasing NPP also tended to reduce the probability of occurrence of forbs, geophytes, shrubs and sub-shrubs but, unlike rabbit and live-stock grazing, increased the probability of occurrence of grasses and sedges (Figures 1 and 3c).

From the random terms in our model, variation was higher among species ($\sigma^2 = 1.670$) than among communities ($\sigma^2 = 0.182$) or sites within communities ($\sigma^2 = 0.601$). This is somewhat expected due to the large differences in the frequency of occurrence among species. This species variation is further supported by the conditional models of Best Linear Unbiased Predictors (BLUPs) of the random slopes for

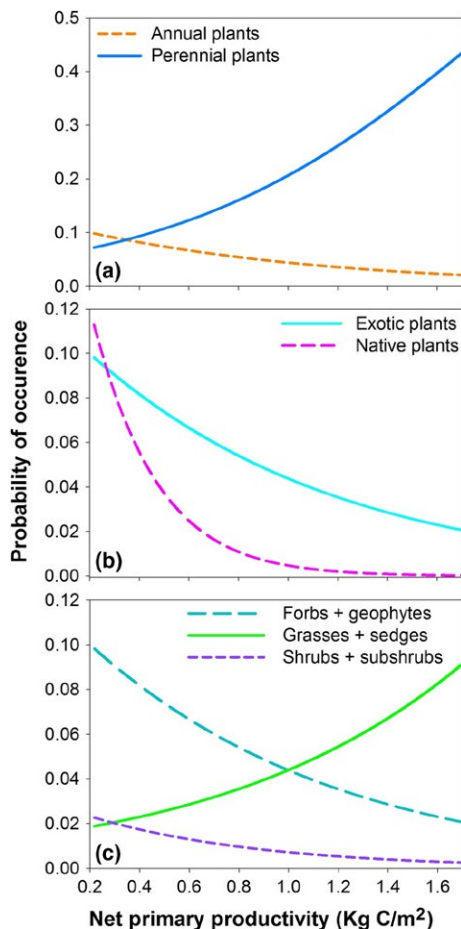


FIGURE 3 Effects of net primary productivity on the average probability of occurrence for (a) annual and perennial plants species, (b) native and exotic plants and (c) plant growth forms (forbs + geophytes, grasses + sedges and shrubs + sub-shrubs)

each species (Appendices S2 and S3). Variation among species was largest in response to NPP ($\sigma^2 = 1.01$) and recent domestic grazing ($\sigma^2 = 0.661$), with similar variation between rabbits ($\sigma^2 = 0.456$) and kangaroos ($\sigma^2 = 0.455$), and the lowest variation for historic grazing ($\sigma^2 = 0.338$; Appendix S3).

4 | DISCUSSION

Our novel, large-scale study was able to independently assess the impacts of co-occurring herbivores on specific suites of plants and distinguish between the recent and historic impacts of grazing. The effects of grazing on plant community composition were herbivore-specific, with introduced herbivores (livestock, rabbits) reducing the probability of occurrence of all plants overall, and native herbivores (kangaroos) having little impact. Both recent and historic livestock grazing reduced native plants, as expected, but they differed in the severity of their impacts on different plant growth forms. Increasing kangaroo grazing did not reduce grasses, as might be expected, given that kangaroos predominantly forage on grasses (Dawson, 2002), and we found relatively benign impacts of kangaroos. Overall, our study highlights the dichotomy between livestock/rabbit and kangaroo grazing, and therefore the complex nature of grazing by introduced and native herbivores on plant community composition in a relatively low productivity landscape with a relatively short exposure to grazing by livestock.

4.1 | Livestock effects on vegetation

Recent and historic livestock grazing reduced the probability of occurrence of native plants overall, consistent with the results of mensurative studies from eastern Australia (Eldridge, Poore, et al., 2016; Fensham, Silcock, & Firn, 2014; Mutze, Cooke, & Jennings, 2016). We found no substantial impacts of recent or historic livestock grazing, however, on perennial species. Both recent and historic grazing reduced native plants more strongly than exotics (e.g. Dorrrough et al., 2004), possibly because most of the exotic plants are more tolerant to grazing by ungulates (Kimball & Schiffman, 2003). In general, increasing livestock grazing at sites of relatively higher productivity with a relatively short history of livestock grazing tends to increase exotic plants whereas grazing under low productivity tends to reduce all plants, irrespective of their origin (Cingolani, Noy-Meir, & Diaz, 2005; Dorrrough et al., 2004; Milchunas et al., 1988). Additionally, Australia's native plants are poorly adapted to grazing under managed pastoralism (Lunt et al., 2007), with grazing by domestic livestock and other introduced herbivores listed as a key threatening process for numerous rare and threatened plant species (Briggs & Leigh, 1996). Although we did not separate the effects of grazing by productivity level, our sites cover a relatively narrow range of productivity ($0.22\text{--}1.72\text{ g C m}^{-2}\text{ d}^{-1}$) and fall towards the lower end of the productivity spectrum, as would be expected for semi-arid woodlands.

Despite the many studies of livestock grazing effects on different plant growth forms (Lavorel et al., 1997), few have explicitly

compared recent and historic livestock effects (though see Kay et al., 2017). Our results showed that recent livestock grazing suppressed the probability of occurrence of grasses and sedges to a lesser extent than other growth forms, but historic livestock grazing had the strongest suppressive effect on grasses and sedges, and even weakly increased the probability of occurrence of shrubs and sub-shrubs. The effects of grazing on grasses and sedges may be linked to broad-scale conditions such as climate. On highly productive soils, at least, rainfall frequency (Westoby, 1979/80) and soil texture (Fensham et al., 2014; Lewis, Clarke, Reid, & Whalley, 2008) have been shown to moderate the effects of livestock grazing on the cover of grasses and sedges. The response of plant growth forms to recent livestock grazing is complex because growth form encompasses a wide range of life histories and plant traits that have variable responses to grazing (Diaz et al., 2007; McIntyre & Martin, 2001; Westoby, 1979/80). For example, forbs and grasses vary substantially in height, shape and palatability. The lower suppressive effect of recent grazing on sedges and grasses may be due to differences in palatability among species within these growth forms. For example, for native perennial grasses, we found that highly palatable (e.g. *Paspalidium jubiflorum*) or threatened (e.g. *Amphibromus fluitans*, *A. pithogastrus*) species responded more negatively to recent livestock grazing than less palatable species such as *Enteropogon acicularis* or *Aristida* spp. Nevertheless, we still found both recent and historic grazing had the strongest suppressive effects on forbs and geophytes. The notion of a stronger grazing effect on forbs than other growth forms has been demonstrated previously in resource-limited ecosystems (e.g. Dorrough et al., 2004; Pettit, Froend, & Ladd, 1995), but is not supported by global syntheses (Diaz et al., 2007). The high proportion of forb species we found across our study sites may indicate that the understorey of these woodlands has already changed dramatically as a result of more than 200 years of European pastoral practices (Lunt et al., 2007). The increase in forbs, particularly exotic forbs, is likely due to changes in soil P, which generally suppresses the growth of native Australian plants (Dorrough et al., 2011). Despite this, we still found that rabbit and livestock grazing did reduce the occurrence of forbs and geophytes.

For historic livestock grazing, we found weaker suppressive effects on the occurrence of shrub species that are prone to woody encroachment (such as *Dodonaea viscosa* subsp. *spathulata*, *Senna artemisioides* subsp. *filifolia*, *Eremophila longifolia* and *E. sturtii*; Noble, 1997) and which respond more positively to historic grazing than other shrub species. This could happen through, for example, the competitive release of unpalatable plants via selective consumption of competitors (i.e. palatable perennial grasses), or soil disturbance from hard-hooved animals that allow exotic or woody species to proliferate (Noble, 1997). In some cases, landscapes once dominated by palatable shrubs and forbs (e.g. the chenopod shrublands) have been transformed into derived grassland (Benson, Ashby, & Porteners, 1997), and in other areas, grasslands and open woodlands have been replaced by dense shrublands (woody encroachment; Eldridge, Soliveres, Bowker, & Val, 2013) in response to heavy grazing by domestic livestock.

4.2 | Different effects of exotic and native wild herbivores on vegetation composition

The impacts of grazing by wild herbivores differed markedly between introduced and native herbivores. Grazing by introduced rabbits (and hares) substantially reduced the probability of occurrence for plants overall. Furthermore, the effects of rabbit grazing were similar to those of recent livestock grazing, with no strong effects on plants based on plant life span, but a stronger reduction of natives than exotics, and a weaker reduction in sedges and grasses than other growth forms. The most pronounced and widely reported effect of rabbits on vegetation is via browsing (e.g. Mutze et al., 2016), this can, in turn, reduce recruitment and therefore alter population dynamics (e.g. Allcock & Hik, 2004). In our study it is possible that many more perennial species were removed as seedlings by rabbits, as even low rabbit densities can eliminate entire cohorts of germinants within weeks (Lange & Graham, 1983). We found that those plant species that responded most positively to rabbit grazing tended to be exotic annual forbs such as Patterson's curse (*Echium plantagineum*), Capeweed (*Arctotheca calendula*) and grasses such as Arabian grass (*Schismus barbatus*), Red Brome (*Bromus rubens*) and *Aira* species that are typically associated with overgrazed sites.

Unlike rabbits, we recorded relatively few effects of kangaroo grazing even though recent kangaroo grazing activity occurred at all but two of the 451 sites. Kangaroo grazing neither increased nor reduced overall plant occurrence. Kangaroos had no effect on plants differing in origin, life span or growth form. The relatively low impact of kangaroos is likely due to their high mobility, allowing them to access species-rich patches of vegetation, unlike livestock that are constrained within paddocks (Montague-Drake & Croft, 2004). Thus the weak positive effects of kangaroos on native vegetation are more likely associational, suggesting that kangaroos are associated with species-rich patches rather than directly increasing the frequency of occurrence of particular plant species.

4.3 | Net primary productivity affects vegetation composition

Lower productivity sites in our study tended to be dominated by native and annual plants. In general, environments that have low productivity and unpredictable rainfall select for native annual plants over perennials and exotics (Westoby, 1979/80). When we consider the combined effects of grazing and productivity, native annual plants often dominate in low productivity landscapes that have a short evolutionary history of grazing (Milchunas et al., 1988). Small shifts in productivity and livestock grazing generally select for the same plant traits in systems that are generally considered to have low productivity: short, unpalatable, rosette-forming plants with low specific leaf area (Dorrough et al., 2004; McIntyre, Lavorel, & Tremont, 1995; Tóth et al., 2016). However, they typically select for the opposite traits under high productivity, mesic systems, due to competition for canopy space (Milchunas et al., 1988). We found that the effects of increasing productivity mirrored those of recent grazing by livestock and rabbits,

i.e. reducing the probability of occurrence of forbs, geophytes, shrubs and sub-shrubs more strongly than grasses and sedges. This is also consistent with the notion that more arid and less productive systems favour geophytes and shrubs with extensive root systems (Westoby, 1979/80).

4.4 | Management implications and conclusions

Our results indicate that plant responses vary among different herbivores in these semi-arid woodlands. We found that increases in recent livestock, rabbit grazing and NPP had similar effects on vegetation composition by reducing the probability of plant occurrence, and this was not simply due to sites with relatively higher NPP supporting more livestock or rabbits. In these systems, productivity still played an important role in determining the composition of species and their traits (Cingolani et al., 2005; Milchunas et al., 1988). This suggests to us that vegetational shifts driven by a changing climate could induce the sorts of changes we experienced here with productivity. From our results, it seems clear that there may be detrimental, perhaps even synergistic, reductions in native plant species, particularly forbs and geophytes, and general shifts in plant composition at sites where recent livestock, rabbit grazing or NPP increase. These effects could be further exacerbated if the site has a history of heavy livestock grazing.

Although managed livestock grazing has been used successfully for restoring biodiversity in dry grasslands in Europe and Northern America (Pekin, Wisdom, Parks, Endress, & Naylor, 2016; Tóth et al., 2016), its success is likely due to the fact that livestock in these environments have assumed the functional roles of native herbivores that are also browsing or grazing ungulates. For example, cattle have been used to restore degraded grasslands in the river basins of Finland (Pykälä, 2000). In Australia, calls to use domestic livestock grazing to manage for conservation have rarely considered differences among herbivores or different types of plant (but see Fensham et al., 2014; Lunt et al., 2007). In Australian woodlands, which have had a rich history of browsing by Pleistocene megafauna, there is no evidence to suggest that the domestic livestock are suitable analogues of former native herbivores, largely because neither they, nor any functionally similar animal, have co-evolved with Australia's native plants.

Our results reinforce the need for land managers to manage all introduced herbivores, particularly domestic livestock, rabbits and other free-ranging livestock such as goats and deer. This is particularly important at sites where rabbits and livestock co-occur, or where livestock and/or rabbits occur at sites that have experienced relatively high levels of historic livestock grazing. It is also important to consider site productivity, as this can also have substantial effects on plant composition. It is critical that grazing refuges be established to lessen the landscape-level loss of grazing-sensitive suites of plants. At a broader scale, we suggest an appropriate strategy is to minimize grazing by rabbits and both wild and contained livestock in order to prevent further decline of grazing-sensitive species and the functions and services that they provide.

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ORCID

Samantha K. Travers  <http://orcid.org/0000-0002-6252-1667>

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Appendix S1 Summary of species counts by growth form, life span, origin and community

Appendix S2 Table of best linear unbiased predictors for each species

Appendix S3 Best linear unbiased predictors plotted by growth form and life span

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