Rabbit impacts on ground layer plant communities in arid rangelands

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Kangaroo exclosure conserving purplewood wattle at Bush Heritage Australia - Boolcoomatta Reserve, November 2019.

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Abstract

In Australia, rabbits have gained a legendary reputation as destructive pest that has contributed to extensive land and vegetation degradation. While legends persist, less is known, objectively, of the impact rabbit grazing has had on rangeland ground layer vegetation. In this study we quantified plant species by density or percent cover to assess whether present day rabbit grazing, with interaction with naturally present kangaroo grazing, results in alternate plant communities. We also compared species diversity, richness and the abundance of species grouped by growth form (forb, grass, shrub, sub-shrub) and life history. Four sites were sampled across Boolcoomatta Reserve (SA), Mungo National Park (NSW) and Yathong Nature Reserve (NSW), located across semi-arid to arid climates at which permanent herbivore exclusion fences had been at work for between 13 and 20 years. We found kangaroo grazing had neutral to beneficial effects on the ground layer flora assemblage, facilitating *Callitris* recruitment, removing the pasture weed *Marrubium vulgare*, reducing the dominance of competitive grasses and shifting plant communities in the absence of rabbit grazing. Rabbits were associated with the presence of *Marrubium vulgare*, inhibited *Callitris glaucophylla* recruitment and in isolation from livestock, are likely to be maintaining Australian rangelands in a degraded state. We find that in the absence of livestock, rangeland flora composition may change across semi-arid and arid regions with rabbit control or elimination and these changes can be facilitated under kangaroo grazing.

Introduction

Over the past century, rabbits have gained a legendary reputation as a landscape altering pest whose impacts have permanently degraded the condition of Australian rangelands (Jernelöv 2017; Peacock 1908; Strive and Cox 2019). Released for game at Barwon Park, Victoria in 1859, rabbit numbers exploded and rabbits quickly established new territory reaching south-west Queensland in less than 40 years and the west Australian coast by 1910 (Jernelöv 2017; Rolls 1969). Rabbits gained notoriety for damaging pasture and competing with livestock, causing economic losses among graziers as a result of starved livestock, pasture degradation and soil loss (Alves *et al.* 2022; Fleming *et al.* 2002; Rolls 1969; Strive and Cox 2019). Some degraded pastures, once abundant with "common herbs and grasses" (Peacock 1908, p48) were transformed into fields of unpalatable daisies and were accompanied with thousands of dead, ring-barked shrubs and trees (Peacock 1908).

Until the 1950s, accounts of rangeland changes by rabbits had largely been anecdotal (Gooding 1955; Peacock 1908; Rolls 1969). Consistent with anecdote, contemporary studies using rabbit exclusion have found the presence of rabbits inhibits tree and shrub recruitment (Lange and Graham 1983; Mutze *et al.* 2016b; Sinclair 2005; Travers *et al.* 2019; Zimmer *et al.* 2017). While woody species have received experimental attention, there are few studies on the impact of rabbits on rangeland ground layer plant communities that incorporate grasses, forbs and small shrubs.

In a simple two year rabbit exclosure experiment examining the effects of rabbit grazing, in a semi-arid mallee community, Cochrane (1966) reported higher species richness of ground layer plants and shrubs in an exclosure after rabbits had been removed. Due to the study's small scale and lack of replication, the results reported have limited power and at best suggest further investigation into rabbit grazing impacts on ground layer plants is warranted.

Notable studies on the impact of rabbit exclusion on rangeland ground layer plant communities include Foran *et al.* (1985) and Leigh *et al.* (1989). Both studies used newly established rabbit exclosures in semi-arid to arid Australian rangeland with Foran *et al.* (1985) reporting plant community responses over two years and Leigh *et al.* (1989) over six years. While Foran *et al.* (1985) reported no changes in ground layer plant species composition over the study period, the short period of the study meant effects of flood or drought on the recruitment and loss of possibly unaccounted for dormant species, due to rabbit grazing, were not measured (Foran *et al.* 1985). Leigh *et al.* (1989) measured vegetation changes over a period of time that included wet and dry years and found that rabbit exclusion resulted in higher grass vegetation biomass and higher species

richness however their study did not give detailed species quantities. Anecdotally, however, Leigh *et al.* (1989) reported no apparent changes in plant communities after 10 years.

Contemporary rangeland – rabbit impact studies in Australia have taken place in the context of effective biological rabbit control, starting with the release of myxoma virus in 1950 (Strive and Cox 2019). Release of the myxoma virus caused a spectacular crash in Australia's rabbit population which continues to be maintained with the assistance the rabbit haemorrhagic disease, appearing in 1995 (Strive and Cox 2019). As most research on rabbit – vegetation impacts has taken place after widespread chronic rabbit overabundance, contemporary studies can only assess recovery in vegetation that has probably been permanently altered (Leigh *et al.* 1989). As a result, we may not know if changes in vegetation due to the removal of a contemporary, residual rabbit activity represents what might have been prior to rabbit invasion.

In this study, we aimed to measure changes in the floristics of present-day ground layer plant communities in response to rabbit exclusion and kangaroo exclusion, complimenting research by Mills *et al.* (2020). To assess grazing effects, we measured the height of the ground layer and the density and cover of plant species and plant growth forms inside and outside of long-term herbivore exclosures. Vegetation occupying the space from ground level to 1 m in height was included and vegetation communities were located in semi-arid and arid regions of eastern Australia. As our study used exclosures that were constructed after the establishment of rabbit haemorrhagic disease, our results represent changes possible after chronic rabbit grazing. We tested the hypotheses:

1) Rabbit grazing reduces plant species richness compared to rabbit excluded areas while kangaroos have a benign impact.

2) Vegetation grazed by rabbits has differing species assemblages compared to plots grazed by kangaroos or under rabbit exclusion and includes more short-lived and introduced species.

3) Rabbit - vegetation changes at in lower productivity sites will be more pronounced compared to higher productivity sites.

Methods

Location

We surveyed three de-stocked conservation reserves on former century old pastoral land (Finlayson *et al.* 2021; Gojak 1991; Leigh *et al.* 1989; Midgley *et al.* 1998) of increasing aridity in New South Wales and South Australia (Table 1). In the year leading up to the surveys, reserves had received 100 – 200 mm above their average long term rainfalls (Bureau of Meteorology 2023d). Surveys were conducted in February 2022 in Mungo National Park (Mungo) and April 2022 in Boolcoomatta Reserve (Boolcoomatta) and Yathong Nature Reserve (Yathong). Yathong Nature Reserve, established 1971 – 1977 (Leigh *et al.* 1989), contained three exclosure blocks set in a grassy woodland (Specht 1981) featuring scattered *Casuarina pauper* and *Geijera parviflora* trees (belah wilga woodland, Mills *et al.* 2020). Mungo National Park, established 1978 (Midgley *et al.* 1998), contained eight exclosure blocks with four set in grassy *Callitris glaucophylla* woodland on sand dunes and four set in a mixed chenopod and grassy *Maireana pyramidata* (bluebush) shrubland on lakebed sites (Mills *et al.* 2020). Two dune and two lake exclosure sets were built in 2000 with the remainder built in 2008 (Zimmer *et al.* 2017). Boolcoomatta Reserve, established 2006 (Finlayson *et al.* 2021), contained four exclosure blocks featuring mixed chenopod and grassy ground layers. Two were set in *Acacia aneura* (mulga) low woodland (hilltop and gully sites), one set on the flats beside a shallow drainage line with *Alectryon oleifolius* shrubs, and one set on a sand dune growing *Acacia carneorum* shrubs (purplewood, Finlayson *et al.* 2021). Due to the non-replication of vegetation communities at Boolcoomatta, we treated the four exclosure sets as a single community (chenopod shrubland) in analyses.

Table 1: Climate, vegetation and exclosure construction data for Yathong, Mungo and Boolcoomatta Reserve.

		Mean annual					
Conservation reserve	Geographic coordinates	Rainfall (mm)	Min temp. (°C)	Max temp. (°C)	Vegetation community	Exclosure establishment year	Replicate blocks
Yathong	32.63 °S, 145.56 °E	374	10.9	24.4	Belah wilga woodland	2003	3
Mungo	33.56 °S, 143.12 °E	269	11.4	26.4	*Callitris glauc.* woodland	2000 & 2008	4
					Bluebush shrubland		4
Boolcoomatta	31.94 °S, 140.59 °E	206	13.6	24.0	Chenopod shrubland	2010	4

Rainfall and temperature data from nearest weather stations for: Yathong, Hillston Airport 075032, 100 km south, (Bureau of Meteorology 2023a); Mungo, Pooncarie Mail Agency 047029, 50 km west (Bureau of Meteorology 2023b) and

Boolcoomatta, Umberumberka Reservoir 047039, 65 km east (Bureau of Meteorology 2023c; Fleming *et al.* 2002). Exclosure establishment years from Mills et al. (2020)

Exclosures

Exclosure blocks included a fenced plot that prevented the passage of kangaroos and rabbits (Exclude all), a fenced plot that permitted entry by rabbits and not kangaroos (Exclude kangaroo) and a fenced plot that permitted entry by kangaroos and not rabbits (Exclude rabbit). Fences shared similar construction among conservation reserves where rabbits were excluded by a 4 cm aperture hexagonal netting (chicken wire) formed to a height of 60 - 90 cm and held flat to the ground, leading away from the fence for 60 cm, to prevent tunnelling into the exclosures. Kangaroos were excluded using 15 x 30 cm weld-mesh or similar, formed typically to 180 cm high with the exception of the oldest exclosures at Mungo which were 150 cm high. Fences that excluded both animals combined constructions. Exclosure sizes varied among reserves however all were at least 24 x 24 m. Control plots (20 x 20 m) at Boolcoomatta and Mungo were located with centres 30 m from a randomly selected edge of a fenced plot in similar vegetation. Control transects at Yathong were located in similar vegetation on a randomly selected fence edge starting from 3 m from a fence. Potential sites with anthropogenic disturbance were excluded from selection.

Sample site location

Boolcoomatta and Mungo vegetation were sampled inside 20 x 20 m plots randomly located within exclosures (Figure 1). Plots were divided into quadrants and a 4 x 4 m concentric nested quadrat was centred on random coordinates within each quadrant (Figure 1). Coordinates were produced that positioned the quadrat with at least 1 m clearance from the fence edge. The concentric nested quadrat was used to measure plant species density while random 20 m transects across the plot were used for percent cover and ground layer height measurements (Table 2).

At Yathong, we could not sample the vegetation with the concentric nested quadrat frame due to the dense, knee-high grass being flattened, obstructing the view of the ground and species between. Instead, species were quantified inside four, 2 x 2 m quadrats laid on a random transect starting 3 m from a fence edge and in open grassy ground that gave at least 1m clearance from the dripline of large trees and shrubs. Quadrats were spaced 6 m apart so to fit within width of the 24 x 24 m

exclosures (Figure 1). Plant species were quantified using percent cover and ground layer plot height was measured along random transects within the 2 x 2 m quadrats (Table 2).

Table 2: Measurements taken to quantify individual plant species and growth forms

Reserve	Species	Growth form
Boolcoomatta	Density	% cover
Mungo	Density	% cover
Yathong	% cover	Derived from species % cover

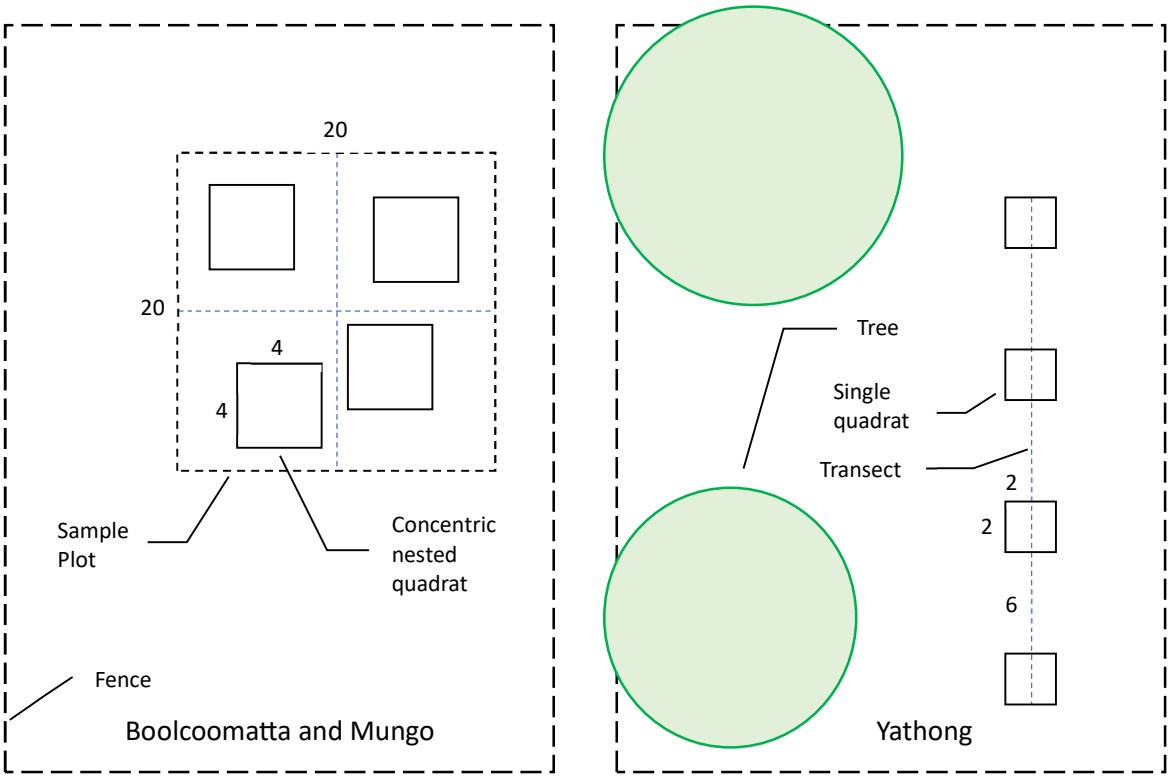


Figure 1: Sampling arrangement inside exclosure and control plots at reserves visited. Sample plots at Boolcoomatta were randomly placed within the constraints of the exclosure fence. Plots were divided into quadrants and concentric nested quadrats randomly placed within the constraints of the quadrants. Sample plots at Yathong used transects randomly placed within the constraints of the exclosure fence and drip line of large trees and shrubs. Numbers are edge measurements in metres. Drawing not to scale.

Survey methodology:

The density of individual plant species, horizontal coverage of plants, classified by growth form, and the height of vegetation were measured. Growth form was chosen as a method to group species by morphology with similar responses to disturbance (Lavorel *et al.* 1997). Growth forms used to

classify plants species included shrubs, subshrub, tufted grasses, forbs, (Table 3) and were based on descriptions in National herbarium of New South Wales (2022), Cunningham *et al.* (1992), entries in Austraits (Falster *et al.* 2021).

Table 3: Descriptions of growth forms categorising plant species identified in plots

Growth form	Description	Example
Forb	Non-woody herbaceous species	*Asteraceous spp. Lepidium spp.*
Grass	Tufted grass	*Enneapogon avenaceus, Austrostipa scabra*
Shrub	Woody shrub species with a nominal height greater than 30 cm and up to 1 m tall	*Maireana pyramidata, Nitraria billardierei*
Subshrub	Woody shrubs or woody herbaceous species with a nominal height of 30 cm or less	*Sclerolaena patenticuspis, Sida intricata*

Horizontal ground coverage of plants (dead and alive plants combined) was measured using 100 regular points spread over five 20 m random transects within the 20 m plots (2 m transects within 2 m plots at Yathong) to estimate cover at 1% resolution (Figure 2c & 2d, ground cover extent of 4 m^2 out of the 400m^2 plots and 0.04 m^2 out of the 4 m^2 plots). For each transect point, the presence of the highest stratum of plant growth form, bare ground, litter was recorded. Percent cover was estimated for each growth form using equation (1):

Equation 1

$$\%\ cover\ = \frac{counts\ for\ growth\ form}{total\ plot\ counts} \times\ 100$$

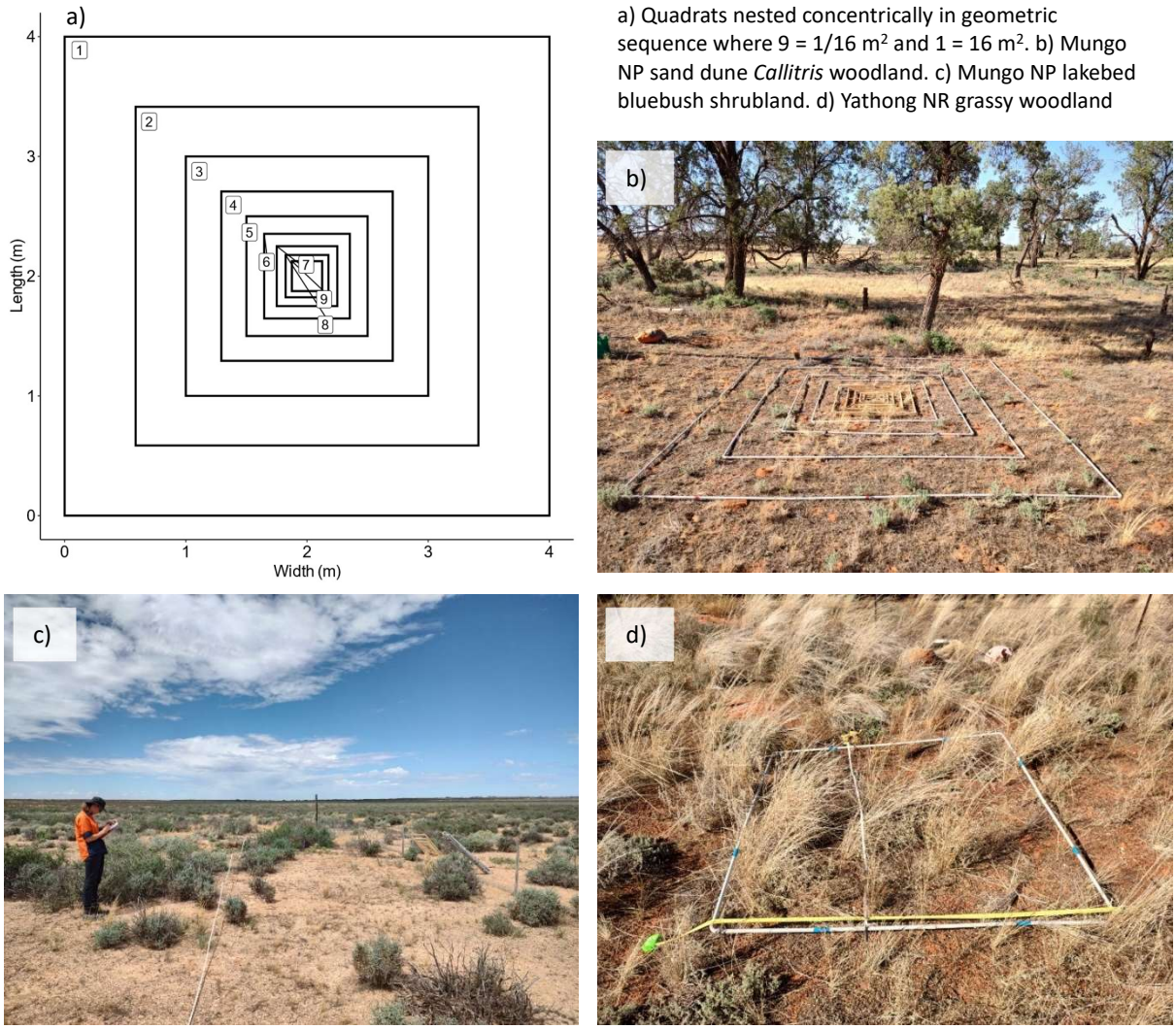
Plot height was measured at 10 random points spread over the same five 20 m (2 m) random transects. At each point, a ruler was used measure the height, above ground level, of the highest intersecting vegetative material.

As a way of efficiently quantifying sparse vegetation (in this study, less than 1% cover) in a repeatable way, concentric nested quadrats were used (Figure 2a & 2b, Morrison *et al.* 1995; Outhred 1984) to estimate the density of individuals of each species. Quadrats used nine nested, square, concentric quadrats placed on the vegetation with sizes ranging in geometric progression from 16 m^{-2} to 16 m^2. Quadrats were numbered from smallest to largest, nine to one. By searching the quadrats from

smallest to largest, species were given an importance score (Morrison *et al.* 1995; Outhred 1984) where a species was scored once by its presence in the smallest quadrat. These scores give an estimate for density of individuals in a species which was derived using the equation (2):

Equation 2

$$species\ density = 2^{(importance\ score\quad)}$$



a) Quadrats nested concentrically in geometric sequence where 9 = 1/16 m^2 and 1 = 16 m^2. b) Mungo NP sand dune *Callitris* woodland. c) Mungo NP lakebed bluebush shrubland. d) Yathong NR grassy woodland

Figure 2: Sampling methods: Concentric nested quadrat: a) design and b) in situ (Boolcoomatta Reserve and Mungo NP). Point samples along transects inside: c) 20 x 20 m plot (Boolcoomatta Reserve and Mungo NP) and d) 2 x 2 m (Yathong NR).

Quantifying vegetation productivity

Measuring vegetation attributes remotely is a convenient method for gauging vegetation condition over a broad area (Asrar *et al.* 1984) however these methods have their limitations. Vegetation net primary productivity (NPP), the output of new biomass in a plot, over a period of time (Moore *et al.* 2018; Xu *et al.* 2012), can be linked to the leaf area index of a plot (area of leaf surface/area of bare ground), measured by the normalised difference vegetation index (NDVI) or related fraction cover (Schloss *et al.* 1999). Similarly, biomass in a plot may be measured by field measurements or light detection and ranging (LiDAR). Both measures give a linear prediction of the productive capacity of plot in a space from bare ground up to a leaf area index (LAI) of one (Asrar *et al.* 1984; Carlson and Ripley 1997) or up to a closed canopy (Moore *et al.* 2018). Beyond these values, the relationship becomes asymptotic or reverses where canopy shading of sub-storey plants and canopy self-shading limit productivity (Fotis and Curtis 2017).

While NDVI data has a long collection history, at a single point in time, NDVI is insensitive to differences in vegetation types of equal greenness, such a crop next to a forest (Montandon and Small 2008). In vegetation of low cover, NDVI values are confounded by soil reflectance resulting in overestimation of green cover (Montandon and Small 2008). As a result of these limitations, NDVI type data are more suited in modelling landscape productivity at coarse scales over multi-year periods (Schloss *et al.* 1999).

Satellite or airborne LiDAR can accurately measure the height profile of a vegetation plot (Drake *et al.* 2002; Muir *et al.* 2018) from which percentile height and mean plot height metrics can be produced. In temperate, boreal forests, woodlands and grasslands, field measured above ground biomass is strongly correlated with LiDAR derived mean plot heights (Lefsky *et al.* 2002; Proulx 2021) while median plot height provides a strong predictor of tropical forest above ground biomass (Drake *et al.* 2002).

Relating the annual rate of net primary production of a community to biomass, however, requires some care. Data from Whittaker and Likens (1973) suggests a linear relationship between global NPP to ecosystem biomass however more recent studies suggest this relationship breaks down in tropical forests systems. A linear increase in the productive capacity in grassland in response to average plant height has been demonstrated (Brown and Cahill 2019) and similarly where biomass increases from woodland to semi closed forest communities (Keeling and Phillips 2007; Moore *et al.* 2018). Moore

et al. (2018) show NPP of evergreen tropical forest is no greater than in tropical semi-deciduous forest and at least as much as tropical dry forest, despite evergreen tropical forest having the highest biomass. In a study of multiple datasets Keeling and Phillips (2007) find increases in the NPP of tropical forests is not associated with increases in forest biomass. Based on these studies, the NPP vs biomass relationship breaks down under tropical conditions, similar to the NPP vs LAI relationship, however there is potential to use the association in dry to temperate ecosystems.

In this study, we used LiDAR data to measure the mean height of the surrounding vegetation community, as a proxy for vegetation productivity at each block. The mean height of a plot increases as both the height and gaps between canopy plants decrease as annual growing conditions improve from arid to temperate, in mature vegetation (Specht 1981). Mean vegetation height was derived from the Australia wide remotely sensed 2009 Vegetation Height and Structure dataset (30 m resolution, Scarth 2023). At each block location, the vegetation height values from the 25th, 50th, 75th and 95th percentile rasters were extracted from a square of 9 pixels, centred over each control plot. The mean height for each pixel was approximated by adding the probability weighted percentile height values. The mean of each 90 x 90m pixel block was calculated to give the mean vegetation height at the block location.

Spotlight survey

Herbivore density was quantified following methods in Mills *et al.* (2020). We surveyed over two – three nights on different routes, of up to 12 km, within reserves passing through the vegetation communities studied. Herbivores were spotted and counted from a vehicle moving between 10 – 20kmh^{-1}, using a 50 W equivalent LED spotlight. Kangaroos within 100 m of the vehicle were included while the distance searched for rabbits was 60 m due to difficulty spotting rabbits beyond this distance. This produced a 200 m belt transect kangaroos and 120 m belt transect for rabbits from which herbivore density was derived.

Statistical analysis of ground sample data

Data were wrangled, plotted and analysed in R, version 4.2.2 (R Core Team 2022). Data were wrangled and plots generated using the 'tidyverse' series of packages (Wickham *et al.* 2019). Univariate data were analysed using the 'glmmTMB' package (Brooks *et al.* 2017), 'parameters'

package (Lüdecke *et al.* 2020) in conjunction with 'lme4' (Bates *et al.* 2015) and 'parallel' (R Core Team 2022); and 'performance' package (Lüdecke *et al.* 2021). Community indices including Shannon's diversity (Shannon 1948) and species richness were generated using 'vegan' (Oksanen *et al.* 2022) and multivariate community analysis used 'mvabund' (Wang *et al.* 2022). Herbivore density data and across vegetation community comparisons were fitted with a generalised linear model while all vegetation data were fitted using generalised linear mixed models taking on the form (Equation 3):

Equation 3

$$y \sim plot + (1 \mid block)$$

where:

y = the response variable

plot = fixed effect for herbivore exclusion treatment (control, exclude all, exclude kangaroo, exclude rabbit). Analyses including vegetation community included this term as a fixed effect.

block = random effect for exclosure blocks fitted as a *y* intercept

Herbivore density, species density, ground cover and ground layer height data were fitted under the Tweedie family of distributions (Jørgensen 1987), with variance powers adjusted automatically. Community indices fitted Gaussian distributions and community composition data was analysed using 'manyany' function (mvabund) under a Tweedie distribution (Jørgensen 1987). 'Manyany', which uses multiple generalised linear mixed models, was used over traditional distance techniques as this method accounts for mean-variance relationships in the data and has a higher sensitivity to differences in assemblage (Warton *et al.* 2012). P – values for community analyses were adjusted using the Holm method (Holm 1979) to reduce the probability of type I error resulting from multiple comparisons among plots. Community data were plotted using copula ordination along latent variable axes generated from the 'manyany' models (Popovic *et al.* 2019). In all cases, no data were transformed and residual plots for each model were checked to ensure homoscedasticity before models were used.

Significance testing of the generalised linear mixed models was carried out using parametric bootstraps to give credible p-values (Faraway 2016; Zuur *et al.* 2007). Significance testing of the

multivariate models used PIT-trap resampling a method similar to a parametric bootstrap (Warton *et al.* 2017). All resampling techniques used 1000 iterations. Statistically significant results were those with probability values equal to or less than 0.05. Associated credible intervals (CI) for the model slope coefficients are listed. Post-hoc pairwise analysis of bootstrapped model components was made using 'emmeans' package (Lenth 2023) providing Bayesian probability of direction (pd) for model slope coefficients. A pd value of 0.975 or more is equivalent to a two-sided significance probability of 0.05 or less and suggest a significant difference among treatments compared (Makowski *et al.* 2019).

Results

Across vegetation communities

Mean vegetation height, used as a proxy for vegetation productivity ranked the Mungo bluebush shrubland as least productive (2.96 m) followed by the Boolcoomatta chenopod shrubland (3.54 m), Yathong belah wilga woodland (3.62 m) and Mungo *Callitris glaucophylla* woodland (4.76 m). Overall species diversity was not significantly different among the Mungo sites and Boolcoomatta (Figure 9, $P > 0.05$) however species diversity at Yathong was significantly lower than at Mungo or Boolcoomatta (Yathong – Mungo bluebush, $t = -3.806$, $P = 0.015$; Yathong – Boolcoomatta, $t = -4.341$, $P = 0.007$; Yathong – Mungo *Callitris*, $t = -5.501$, $P = 0.001$). Overall species richness was not significantly different among Mungo sites and Boolcoomatta (Figure 9, $P > 0.05$). Overall species richness at Yathong was significantly lower than at Mungo or Boolcoomatta (Yathong – Mungo bluebush, $t = 2.956$, $P = 0.003$; Yathong – Boolcoomatta, $t = 2.581$, $P = 0.007$; Yathong – Mungo *Callitris*, $t = 4.457$, $P < 0.001$).

Among notable vegetation attributes, Mungo bluebush shrubland had higher shrub cover compared to Yathong woodland (Figure 11, Mungo bluebush – Yathong, $t = 6.564$, $P < 0.001$) however there were no significant differences in shrub cover compared to Boolcoomatta and Mungo Callitris woodand (Mungo bluebush – Boolcoomatta, $t = 2.201$, $P = 0.195$; Mungo bluebush – Mungo *Callitris*; $t = 3.042$, $P = 0.056$). Grass covers at Yathong compared to the Mungo *Callitris* or Mungo bluebush communities were not significantly different (Yathong woodland - Mungo *Callitris*, $t = 1.298$, $P = 0.586$, Yathong woodland – Mungo bluebush, $t = -2.239$, $P = 0.184$) however Boolcoomatta showed significantly lower grass cover than Yathong (Yathong woodland – Boolcoomatta, $t = 4.249$, $P < 0.001$).

There were no significant differences in the densities of rabbits compared to kangaroos across vegetation communities (Figure 3, kangaroo – rabbit, $t = -0.715$, $P = 0.474$). Overall herbivore densities corresponded with overall grass abundance and were lowest at Boolcoomatta compared to the woodland sites (Boolcoomatta – Yathong woodland, $t = -3.971$, $P = 0.018$; Boolcoomatta – Mungo *Callitris*, $t = -5.918$, $P < 0.001$) while herbivore densities at Mungo bluebush were not significantly different (Boolcoomatta – Mungo bluebush, $t = 2.598$, $P = 0.171$).

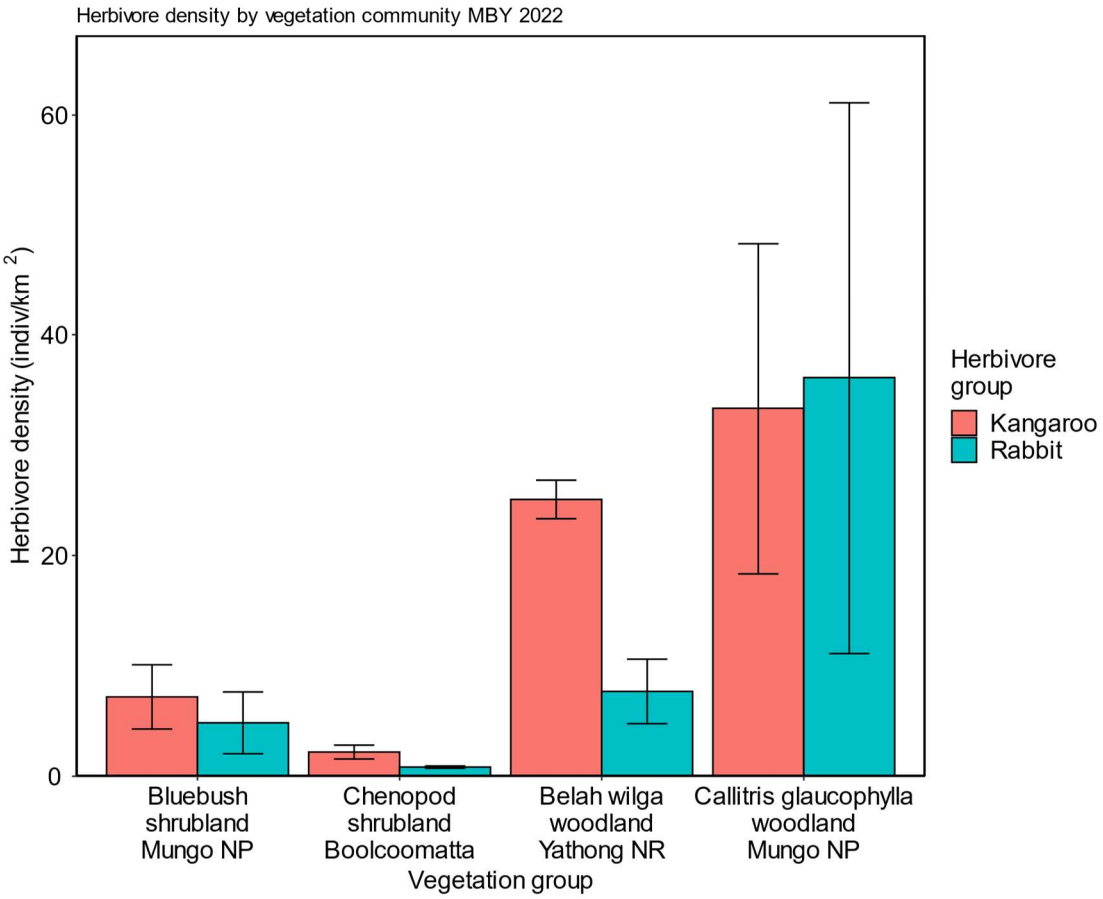


Figure 3: Herbivore densities measured by spotlight surveys in vegetation communities. Vegetation communities arranged from left to right in increasing order of vegetation height as a proxy for productivity.

Site specific herbivore impacts

Mungo bluebush shrubland

There was no significant difference in mean height of plots, species diversity or species richness among herbivore exclusion treatments in the Mungo bluebush shrubland (Figure 9, P > 0.05). Comparing plant community assemblages across herbivore exclusion treatments revealed no significant differences among plot combinations (P > 0.05) except for the openly grazed plots compared to the rabbit only excluded plots (Figure 10, manyany, control – exclude rabbit: test statistic = 805.55, P = 0.006). There were no significant differences among plots in the cover of bare ground, forbs, grasses, shrubs and subshrubs (Figure 11, P > 0.05). The cover of litter was significantly lower inside of rabbit only excluded plots compared to control plots (control – exclude rabbit: CI = [-2.569, -0.250], P = 0.014) and the cover of alive and standing dead vegetation was higher inside

exclude all plots compared to openly grazed plots (control – exclude all: CI = [0.122, 0.594], P =0.008).

The densities of grass and Malvaceous species were higher compared to controls at all levels of kangaroo exclusion and was not affected by rabbit presence (Figure 4, Poaceae: control – exclude all, CI = [0.202, 1.705], P = 0.010; control – exclude kangaroo, CI = [0.273, 1.775], P = 0.006. Malvaceae: control – exclude all, CI = [0.310, 3.101], P = 0.020]; control – exclude kangaroo, CI = [0.0854, 3.069], P = 0.042). Forb species had a significantly lower density in rabbit only excluded plots compared to control plots (Forb species: control – exclude rabbit, CI = [-2.453, -0.228], P = 0.018). There was no difference in the density of native species among plots (P > 0.05). Species density response among plots for introduced species modelled poorly so we could not report a result. Plant species density grouped by annuals responded negatively under rabbit exclusion (Annual species: control – exclude all, CI = [-2.116, -0.249], P = 0.018; control – exclude kangaroo CI = [-0.996, -0.762], P = 0.788; control – exclude rabbit, CI = [-1.883, -0.078], P = 0.036) while perennial species responded positively when all herbivores were excluded compared to control plots (Perennial species: control – exclude all, CI = [0.868, 17.891], P = 0.032; control – exclude kangaroo CI = [-6.755, 9.149], P = 0.806; control – exclude rabbit, CI = [-7.542, 8.635], P = 0.876).

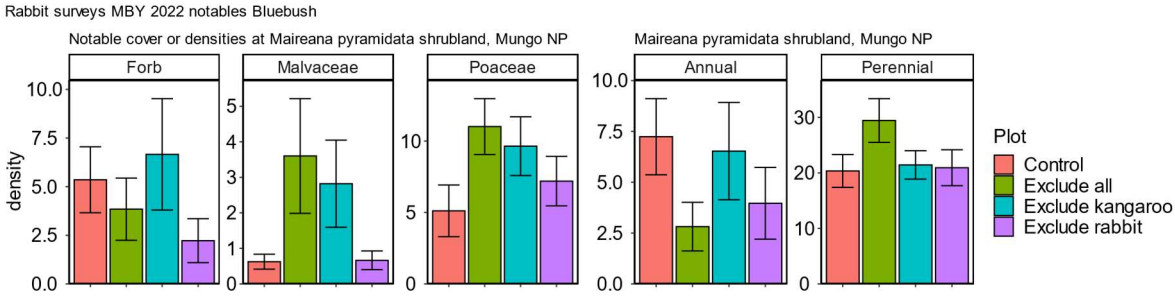


Figure 4: Densities of notable ground layer plant groups in the Mungo bluebush vegetation community.

Boolcoomatta chenopod shrubland

Plots at Boolcoomatta showed no significant differences in ground layer height (Figure 9, height: P > 0.05). Plots that excluded rabbits and not kangaroos had a lower species diversity compared to controls (control – exclude rabbit, CI = [-0.617, -0.0695], P = 0.016) and richness (control – exclude rabbit, CI = [-9.828, -1.796], P = 0.006). Plots that excluded rabbits produced significantly different community assemblages compared to those that permitted rabbits (Figure 10, manyany, control – exclude all, test statistic = 744.58, P = 0.006; control – exclude rabbit, test statistic = 721.96, P =

0.006; exclude kangaroo – exclude rabbit, test statistic = 548.69, P = 0.006). In addition, the two alternate rabbit excluded community assemblages differed among themselves conditioned on kangaroo presence (manyany, exclude all – exclude rabbit, test statistic = 569.39, P = 0.006). Removal of kangaroos with the permission of rabbits had no effect on the plant community assemblages compared to openly grazed plots (manyany, control – exclude kangaroo, test statistic = 976.00, P = 1.00) and removal of all herbivores compared to kangaroo only exclusion resulted in no significant differences in community assemblage (manyany, exclude all – exclude kangaroo, test statistic = 579.20, P = 1.00).

The covers of forbs, subshrubs, shrubs and the cover of the total of alive and standing dead vegetation were not different among herbivore exclusion plots (Figure 11, P > 0.05). Grass cover was significantly higher in plots that excluded all herbivores compared to control plots (grass: control – exclude all, [0.0633, 2.574], P = 0.044) while litter cover was lower in plots that excluded all herbivores compared to control plots (Litter: control – exclude all, CI = [-2.134, -0.208], P = 0.018).

In exclude all plots, the density of chenopod species was higher compared to controls (Figure 5, chenopod: control – exclude all, CI = [0.0180, 0.151], P = 0.012) while the density of woody species was lower (woody: control – exclude all, CI = [-1.302, -0.167], P = 0.012). Any herbivore exclusion significantly reduced the density of subshrubs with the largest absolute value effect coefficient associated with exclusion of both kangaroos and rabbits (subshrub: control – exclude all, CI = [-2.044, -0.369], P = 0.006; control – exclude kangaroo, CI = [-1.78, -0.140], P = 0.022; control – exclude rabbit, CI = [-1.673, -0.00445], P = 0.048). The exclusion of rabbits with permission of kangaroos resulted in a lower forb and *Euphorbia* forb species density compared to control plots (forbs: control – exclude rabbit, CI = [-2.479, -0.225], P = 0.022; *Euphorbia*: control – exclude rabbit, CI = [-76.710, -0.247], P = 0.034). There were no differences in the densities of native, introduced or annual species (P > 0.05) however perennial species density was significantly lower where kangaroos were excluded (Perennial, control – exclude all, CI =[-16.843, -3.182], P = 0.004; control – exclude kangaroo, CI = [-14.430, -0.585], P = 0.032); control – exclude rabbit, CI = [-12.837, 0.600], P = 0.088).

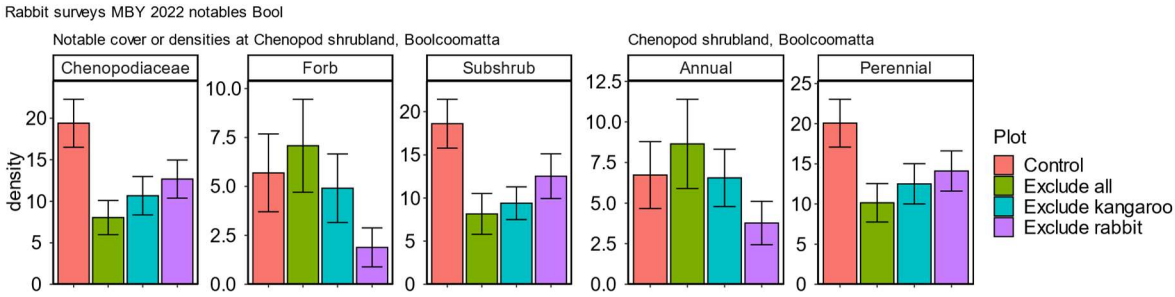


Figure 5: Densities of notable ground layer plant groups in the Boolcoomatta chenopod shrubland vegetation community.

Yathong grassy woodland

Plots at Yathong showed no significant difference in mean ground layer height among treatments (Figure 9, P > 0.05). Species diversity was lower in kangaroo only excluded plots compared to control plots (diversity, control – exclude kangaroo, CI = [-1.068, -0.242], P < 0.001) however species richness was not affected by herbivore exclusion (P > 0.05). The plant community assemblages among plots at Yathong were not significantly different (Figure 10, manyany, P > 0.05) however there were differences in the proportions of species groups.

Plots that excluded kangaroos had significantly more grass cover than those that permitted kangaroos (Figure 11, grass, control – exclude all, CI = [2.131, 38.449], P < 0.001; control – exclude kangaroo, CI = [2.231, 39.213], P = 0.022; control – exclude rabbit, CI = [-5.615, 30.201], P = 0.194). Plots that excluded only kangaroos also had significantly less cover of forbs, subshrubs, shrubs and chenopods (Figure 11, forb: control – exclude kangaroo, CI = [-4.740, -1.245], P = 0.002; subshrub: control – exclude kangaroo, CI = [-2.172, -0.0970], P = 0.036; shrub: control – exclude kangaroo, CI = [-5.293, -0.271], P = 0.028; chenopod: control – exclude kangaroo, CI = [-2.257, -0.367], P = 0.006). Overall, bare ground cover was significantly lower in exclude all plots compared to openly grazed control plots (bare: control – exclude all, CI = [-3.315, -0.284]; P = 0.024).

Exclude only rabbit plots had significantly lower cover of *Marrubium vulgare* (Lamiaceae) compared to control plots (Figure 6, Lamiaceae, control – exclude rabbit, CI = [-98.908, -6.641], P = 0.006). There was no difference in the cover of native, introduced or perennial species among plots (P > 0.05) however, annual species cover was significantly lower in plots that only excluded kangaroos (Annual, control – exclude all, CI = [-6.991, 28.761], P = 0.226; control – exclude kangaroo, CI = [-100.483, -6.460], P < 0.001; control – exclude rabbit, CI = [-9.320, 27.242], P = 0.344). Although we didn't specifically quantify large shrub abundance, consistent with an effect measured previously at

Yathong (Braden *et al.* 2021), we observed the presence of juvenile and mature woody shrubs such as *Geijera parviflora* that were noticeably associated with exclosures that filtered out rabbits.

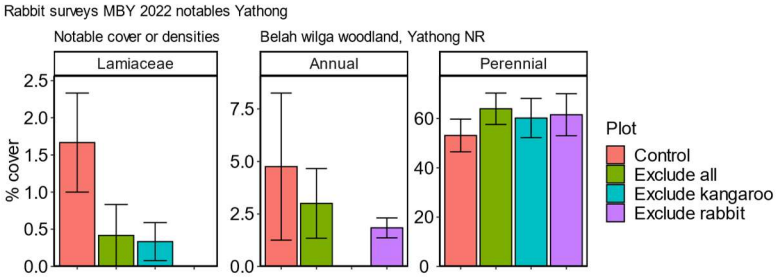


Figure 6: % Cover of notable ground layer plant groups in the Yathong woodland vegetation community.

Mungo Callitris woodland

Kangaroo exclusion resulted in significantly taller average plot height compared to controls in the *Callitris* woodland plots (Figure 9, control – exclude all, CI = [-1.627, -0.579], P < 0.001; control – exclude kangaroo, CI = [-1.284, -0.167], P = 0.018). Pairwise testing revealed exclude all plots heights were not significantly different from exclude kangaroo plots (exclude all – exclude kangaroo, CI = [-0.108, 0.800], pd = 0.936). Plots that permitted kangaroos had similar heights (control – exclude rabbit, CI = [-0.828, 0.401], P = 0.468 and were significantly lower than either kangaroo exclosure (exclude all – exclude rabbit, CI = [0.349, 1.399], pd > 0.999; exclude kangaroo – exclude rabbit, CI = [0.00472, 1.055], pd = 0.976).

There was no difference in species diversity among exclusion plots (Figure 9, P > 0.05) however, species richness was higher than controls in plots that only excluded rabbits and kangaroos (species richness: control – exclude all, CI = [0.739, 10.040], P = 0.026; control – exclude kangaroo, CI = [-6.395, 2.775], P = 0.402; control – exclude rabbit, CI = [-2.676, 6.701], P = 0.434). A combination of kangaroo permission and rabbit exclusion resulted in a significantly different plant community assemblage compared to control plots (Figure 10, manyany, control – exclude rabbit: test statistic = 650.91, P = 0.006) while there were no significant differences in assemblage among control – exclude all, control – exclude kangaroo or other plot pairs (manyany, P > 0.05).

All plots that excluded herbivores had lower bare ground cover (and higher alive and standing dead vegetation cover) than control plots (Figure 11, control – exclude all, CI = [-2.679, -1.146], P < 0.001; control – exclude kangaroo, CI = [-1.907, -0.689], P < 0.001; control – exclude rabbit, CI = [-1.357, -0.334], P = 0.006). Compared to control plots, litter cover was lower in exclude all plots (control –

exclude all, CI = [-15.142, -0.475], P = 0.040) and higher in exclude rabbit plots (control – exclude rabbit, CI = [2.571, 17.576], P = 0.006). Grass cover in all kangaroo exclusion plots was higher than in control plots (grass: control – exclude all, CI = [9.381, 35.627], P < 0.001; control – exclude kangaroo, CI = [3.171, 29.791], P = 0.018; exclude all - exclude kangaroo, CI = [-6.780, 18.118], pd = 0.786). Grass cover in rabbit excluded plots was not significantly higher than in control plots (control – exclude rabbit, CI = [-8.248, 20.153, P = 0.328), however there was an interaction were rabbit grazing in the absence of kangaroos resulted in grass cover that was not significantly different from plots grazed by kangaroos and not rabbits (exclude kangaroo – exclude rabbit, CI = [-2.441, 23.325], pd = 0.952). Forb, shrub and subshrub cover was unaffected by herbivore exclusion (P > 0.05).

All herbivore exclusion increased the density of shrub species (shrub, control – exclude all, CI = [1.132, 4.379], P = 0.002; control – exclude kangaroo, CI = [1.999, 4.974], P < 0.001; control – exclude rabbit, CI = [1.439, 4.699], P < 0.001). Kangaroo exclusion reduced the density of forb species (forb, control – exclude all, CI = [-1.620, -0.0839], P = 0.03; control – exclude kangaroo, CI = [-1.532, -0.0581], P = 0.032). There was no difference in density of native species among plots (P > 0.05) however due to scarcity of introduced species, we could not model responses in their density. There were no significant differences in the densities of annual or perennial species among plots (P > 0.05). Exclusion of rabbits had a significant effect on the recruitment of *Callitris glaucophylla* where juveniles were only recorded as present inside exclude all and exclude rabbit fences (Figure 7 & 8). *Callitris glaucophylla* juveniles had a significantly higher density than control plots in the exclude only rabbit exclosures (control – exclude rabbit, CI = [0.641, 33.582], P = 0.036).

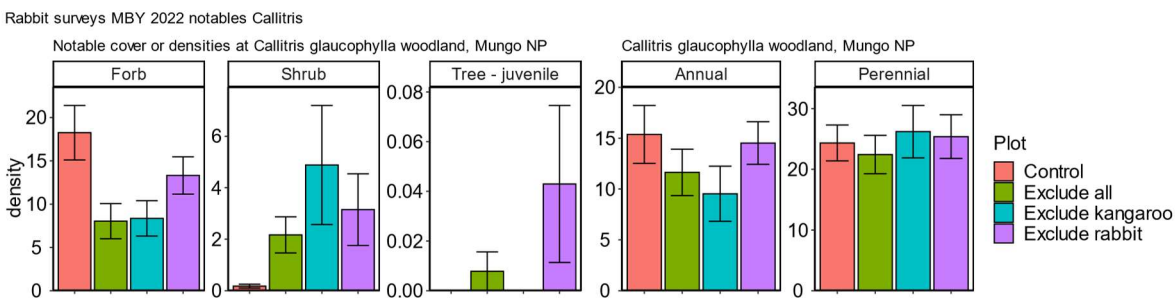


Figure 7: Densities of notable ground layer plant groups in the Mungo Callitris woodland vegetation community. Tree – juvenile refers to Callitris glaucophylla juveniles.

Figure 8: Callitris glaucophylla juveniles inside a combined kangaroo and rabbit exclosure in Mungo sand dune woodland. Mature individuals outside of fence in background. Exclosure built in 2000 by Soil Conservation Service, NSW.

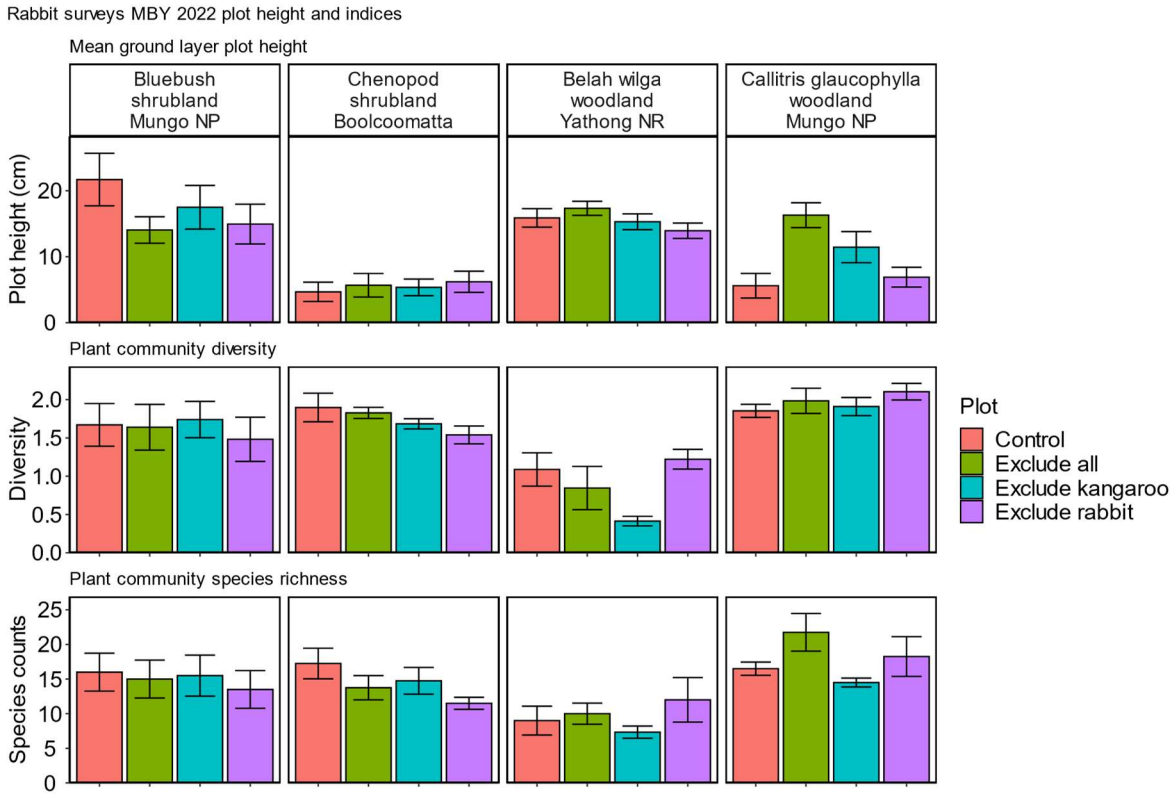


Figure 9: Mean plot height, species diversity and species richness among herbivore exclusion treatments at Boolcoomatta, Mungo and Yathong reserves.

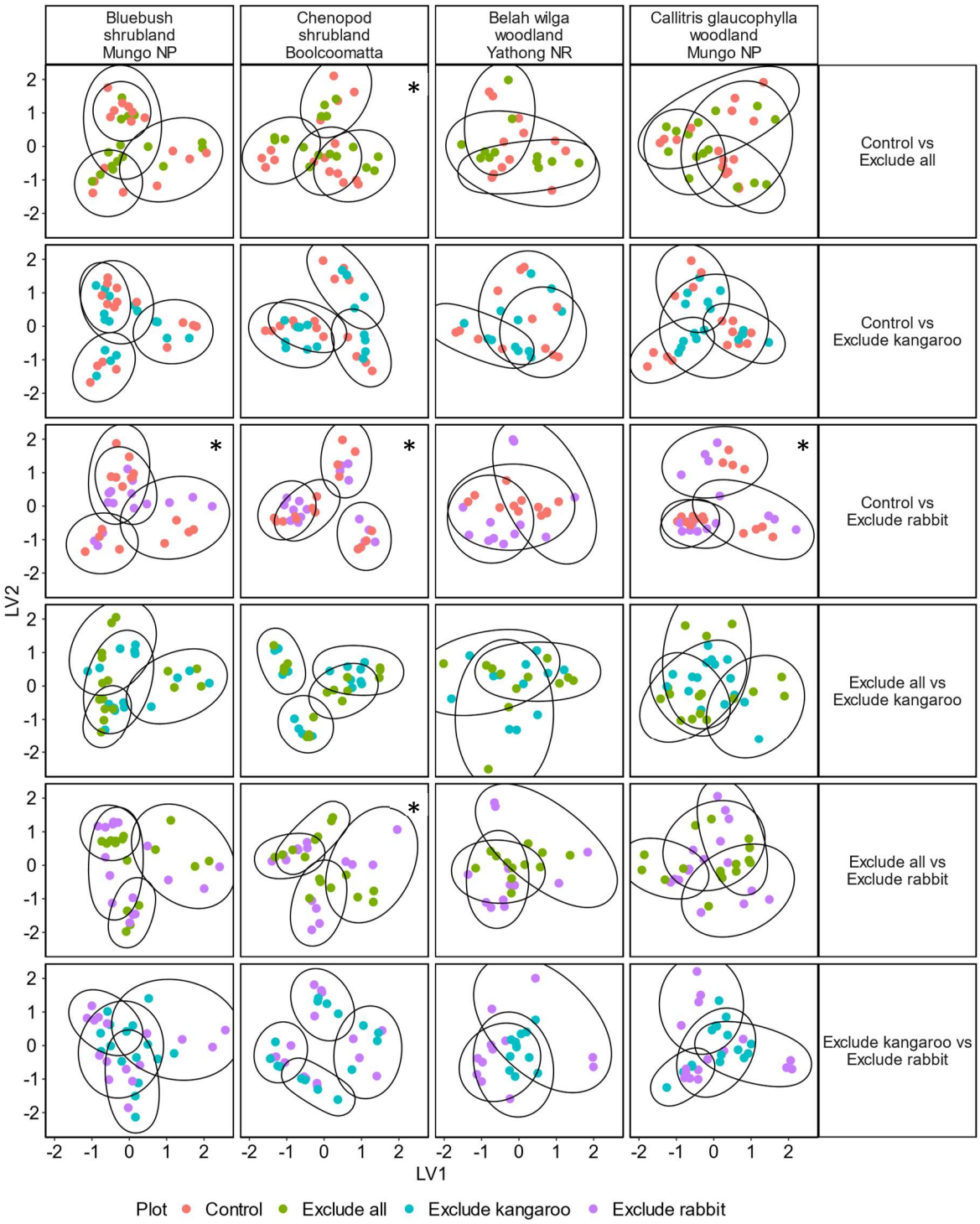


Figure 10: Ordination showing plant species assemblage relationships among plot samples by treatment pair at each vegetation community. Point coordinates are positioned by latent variables derived from the multivariate generalised linear mixed models used in analyses. Ellipses enclose sample points associated with each fence block. Samples or blocks close to each other have more similar plant species assemblages compared to those that are distant. The multivariate mixed effect modelling takes into account the 'block' random effects present. For example, at Boolcoomatta, four blocks in three different vegetation communities were sampled and at other locations there was natural variation among blocks within communities sampled. Treatment pair effects at each community are calculated from the aggregate of treatment pair effects estimated at each block (ellipse). Statistically significant treatment pair effects are marked (*).

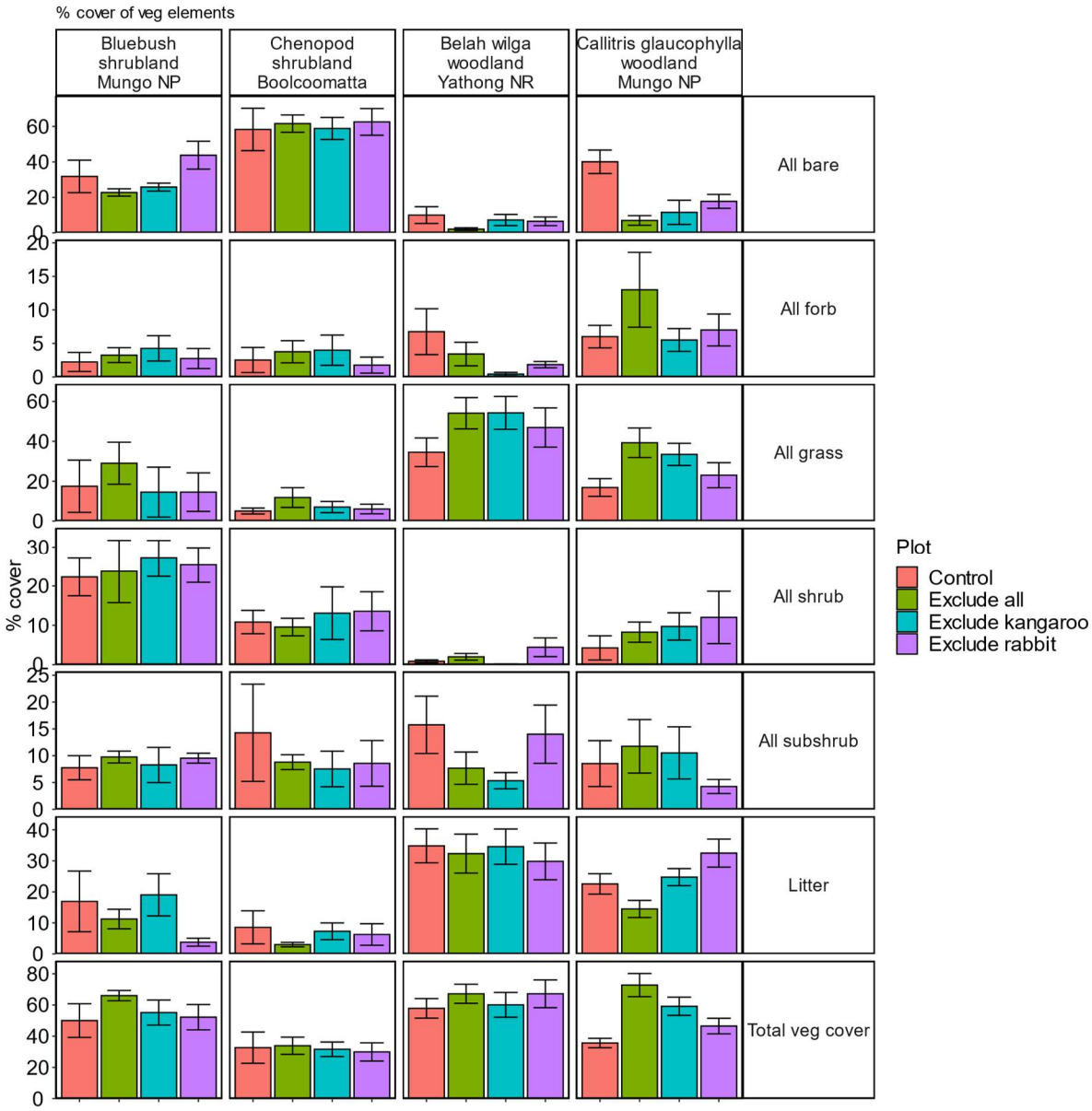


Figure 11 :Percent cover of growth forms, bare ground and total alive and standing dead vegetation.

Discussion

We found ground layer plant community and structure effects were often associated with plots that excluded rabbits and not kangaroos when compared to plots that allowed grazing by both herbivores. For example, when rabbits were excluded and kangaroos permitted, the Mungo bluebush community and Mungo *Callitris* communities was significantly altered compared with other combinations of herbivore exclusion. Boolcoomatta demonstrated a higher sensitivity to the Mungo and Yathong sites revealing an alternate community in the absence of rabbits regardless of kangaroo presence. As kangaroo only exclusion had little effect on plant communities compared to the openly grazed communities this indicates that kangaroo grazing is benign to the ground layer flora in the absence of rabbits while rabbit grazing is having an opposite effect, a conclusion also reached by Mutze *et al.* (2016a) and Travers *et al.* (2018).

Our results suggest potential mechanisms linking ground layer flora assemblage to herbivore taxa. In the Mungo *Callitris* woodland, kangaroo exclusion resulted in a taller ground layer and higher grass cover than in openly grazed plots however this did not affect the cover of other forbs, shrubs or subshrubs. Interaction with rabbit herbivory shaped the recruitment of *Callitris glaucophylla*. Under any rabbit exclusion, *C. glaucophylla* juveniles were present, consistent with (Leigh *et al.* 1989; Travers *et al.* 2019; Zimmer *et al.* 2017) however there was a significantly higher density of juveniles when kangaroos were allowed to graze. This indicates that kangaroo grazing has little effect on *Callitris* while rabbit grazing is inhibiting recruitment. In the absence of rabbits, *Callitris* recruitment may be enhanced where grass dominance is reduced by kangaroo grazing. This is similar to observations in an Australian temperate grassy woodland where forb cover and species richness benefit when dominant grasses are suppressed by grazing (Tremont 1994; Tremont and Mcintyre 1994).

At the Yathong woodland, removal of kangaroos resulted in higher grass cover than kangaroo grazed plots. As at the Mungo *Callitris* woodland, complete herbivore exclusion did not affect the cover of forbs, shrubs or subshrubs however an interaction with rabbit grazing strongly affected the cover of the introduced species *Marrubium vulgare* (Lamiaceae). *Marrubium* was present in plots with rabbits and plots that excluded all herbivores however was absent in where kangaroos grazed and not rabbits. At Yathong, *Marrubium* abundance is associated with rabbit activity (Cooke 2012), and our result supports hypothesis (2) and observations by Travers *et al.* (2018) and Mutze *et al.* (2016a) that introduced plant abundance is supported by rabbit activity. Our result, however, suggests that

Marrubium may be removed, over time, by kangaroo grazing, similar to observations in Mutze *et al.* (2016a).

Kangaroo grazing in the absence of rabbits did not result in an alternate ground layer plant community at Yathong and this result is consistent with observation by Leigh *et al.* (1989) who suggests that the pasture at Yathong may be in a new stable state as a result of past overgrazing by rabbits, kangaroos and livestock. Consistent with Leigh *et al.* (1989), we found species richness was unaffected by herbivore exclusion, however, plots that excluded kangaroos and not rabbits were less diverse with a higher cover of grass and lower cover of forbs, shrubs and subshrubs compared to openly grazed plots. This may be because under a higher cover of grass, forbs, shrubs and subshrubs are persisting in the absence of grazing, however, rabbit grazing may be reducing the abundance of these growth forms which may be weakened under competitive stress from the dominant grasses (Noy-Meir *et al.* 1989).

The lower productivity shrubland communities showed sensitivity to both kangaroo and rabbit herbivory, which is consistent with hypothesis (3) that lower productivity sites are more sensitive to grazing effects. Grass cover was higher in plots that only excluded all herbivores at Boolcoomatta and removal of either herbivore reduced the density of subshrub species (predominantly *Sclecolaena* spp.) which is evidence of grazing induced *Sclerolaena* increase (Andrew and Lange 1986; Landsberg *et al.* 1997). A lower density of perennial species was associated kangaroo exclusion while forb density was lower where rabbits were excluded and not kangaroos. These interactive effects of herbivores have resulted in two different alternate plant communities relative to control plots where complete herbivore removal is associated with higher grass cover, and less subshrubs than controls. Removal of rabbits only resulted in lower forb densities compared to controls, less grass cover compared to complete exclusion, less subshrub density compared to combined grazing and a lower species richness and diversity compared to controls.

As for Boolcoomatta, forb density in the Mungo bluebush was lower in plots that excluded rabbits only and this was associated with an alternative plant community. Annual species density was lower in plots that excluded rabbits, which supports hypothesis (2) that annual abundance is associated with rabbit grazing.

Across the four vegetation communities, we found that kangaroo grazing is having neutral to beneficial effects on the ground layer flora assemblage, facilitating *Callitris* recruitment, removing the pasture weed *Marrubium vulgare*, reducing the dominance of competitive grasses and shifting plant

communities in the absence of rabbit grazing. This result is intuitive given that kangaroos and Australian rangeland flora have had a long evolutionary history (Travers *et al.* 2018).

In the absence of change to ground layer plant community composition in the presence of rabbits and even with kangaroo exclusion, Australian rangelands are likely being suspended in a degraded state with increased weeds, inhibited woody species recruitment and *Sclerolaena* increase. This is despite the residual rabbit densities compared those of pre-1950s biological control. There was insufficient evidence to support hypothesis (1) where rabbit exclusion, compared to grazing, did not increase species richness across the four vegetation communities. This may be because the vegetation in its present state has already been shaped by a history of rabbit grazing and species that could potentially be gained in rabbit exclosures have been lost from the seed bank by historic grazing (Leigh *et al.* 1989; Travers *et al.* 2018).

While our study assessed the effects of rabbit and kangaroo herbivory inside conservation reserves free from livestock, in the broader context of Australian rangelands, removal of rabbits may be helpful for rangeland conservation, however, livestock and goat grazing will continue to present similar challenges that work against rangeland conservation goals (Travers *et al.* 2018). In the context of de-stocked reserves, our study provides evidence that despite Australian rangelands having endured decades of uncontrolled rabbit destruction, continued rabbit control and elimination may facilitate rangeland recovery in semi-arid and arid regions, a conclusion similar to (Mutze *et al.* 2016a). In addition, recovery may be enhanced by continued grazing by kangaroos which reduce competition by grasses and can remove introduced pasture species. Although grazing can induce an increase in *Sclerolaena* spp. in arid sites, we found that this effect was lessened by the removal of rabbits or kangaroos. While kangaroos may be helpful in rangeland restoration we caution against allowing kangaroo overpopulation which may lead to overgrazing and associated soil degradation during dry periods (Mills *et al.* 2020).

Expenditure

Funding for this project was provided by Foundation for Rabbit-Free Australia Inc. under grant SA2021-01.

Table 4: Summary of plant survey expenses

Survey	Item	Cost ($)
Mungo 2022	Vehicle use	1 955
	Food, volunteer travel and misc supplies	656
Boolcoomatta – Yathong 2022	Vehicle use	2 300
	Food and misc supplies	245
	Total	5 156

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