Grazing by over-abundant native herbivores jeopardizes conservation goals in semi-arid reserves

Charlotte H. Millsa, Helen Waudbyb, c, Graeme Finlayson d, David Parkerb, Matthew Cameronb, Mike Letnic a, *

a School of BEES, UNSW, Sydney, NSW, 2052, Australia
b Biodiversity and Conservation, Environment, Energy and Science, NSW Department of Planning, Industry, and Environment, Albury, NSW, 2640, Australia
c Institute for Land, Water and Society, Charles Sturt University, Albury, NSW, 2640, Australia
d Bush Heritage Australia, PO Box 329 Flinders Lane, Melbourne, VIC, 8009, Australia

ABSTRACT

Relaxation of predation pressure following the removal of mammalian predators has led to the irruption of large herbivores and excessive levels of herbivory in many regions of the Earth. Conservation reserves in dryland regions aim to restore ecological processes and facilitate biodiversity conservation by functioning as refuges from grazing by livestock. However, grazing pressure in conservation reserves may be high and hamper conservation objectives because wild herbivore populations have irrupted in the surrounding landscape due to predator control as well as the absence of hunting and competition with livestock within reserves. Here, we assess the relative abundance of native herbivores (kangaroos) and introduced herbivores (rabbits) using driving transects and dung surveys, and use selective exclosures to assess wild herbivores’ impacts on vegetation and soils in four conservation reserves in semi-arid Australia. Kangaroos were the dominant herbivore in each reserve. Grazing by kangaroos and/or rabbits was linked to reduced complexity of understorey vegetation, grass cover, species richness of grasses, forbs and shrubs, the depletion of soil carbon and phosphorous, and increased soil bulk density. The marked impacts of grazing by wild herbivores, particularly kangaroos, on vegetation and soils that we report are symptomatic of overgrazing. Our study provides evidence that grazing by kangaroos may jeopardize conservation efforts across a large region of semi-arid Australia. We contend that managing the total grazing pressure exerted by wild herbivores is crucial to prevent overgrazing in dryland conservation reserves where herbivore populations are not regulated by predators.

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1. Introduction

Extermination of large mammalian predators and the ensuing relaxation of predation pressure has led to the irruption of large herbivores in many regions of the Earth (Gordon et al., 2004; Letnic and Ripple 2017; Oliva et al., 2019). In turn, excessive grazing and browsing by over-abundant wild herbivores in the absence of predators is a problem for conservation that has
hampered ecological restoration efforts in many places (Foster et al., 2014; Gordon et al., 2004; Mosley and Mundinger 2018). Readily apparent effects of overgrazing include shifts in the structure and composition of vegetation (Côté et al., 2004; Eldridge et al., 2018). Less noticeable are effects on the seed bank and ecosystem functions, including nutrient cycling, litter decomposition and the capacity of soils to absorb and retain moisture (Bressette et al., 2012; Eldridge et al., 2016). These latter effects can arise because removal of vegetation by herbivores and their trampling disrupt the supply of litter and nutrients to detritivores and the capacity of soils to absorb and retain moisture (Ludwig et al., 1996; Mahon and Crist 2019).

An objective of many dryland conservation reserves is to restore ecological processes and facilitate biodiversity conservation by functioning as a refuge from livestock grazing and other human activities such as hunting (Pressey 1992). However, dryland conservation reserves are often nested within a broader matrix of lands used for agricultural purposes, where predator populations have been suppressed and artificial water points provided to facilitate livestock production and wild-herbivore populations have subsequently irrupted (Lavery et al., 2018; Letnic et al., 2015). The widespread availability of water within the dryland conservation reserve–livestock grazing matrix opens all areas of a reserve to herbivores and other grazing-sensitive species experience very little relief from grazing pressures (Fensham and Fairfax 2008). Moreover, wild herbivore populations are often higher in conservation reserves than the surrounding landscape due to the absence of hunting and competition with livestock (Caughley et al., 1987; Chauhan and Sawarkar 1989; Gordon et al., 2004; Oliva et al., 2019). Consequently, there is great potential for excessive herbivory by wild herbivores to have adverse effects on the functioning of dryland conservation reserves that are counter to their biodiversity conservation objectives (Chauhan and Sawarkar 1989; Gordon et al., 2004; Morris and Letnic 2017; Oliva et al., 2019).

In Australia, the widespread extirpation of dingoes (Canis dingo) to facilitate sheep grazing has led to population irruptions of kangaroos (Osphranter spp.; Macropus spp.) and feral goats (Capra aegagrus hircus) across a large swathe of continent’s semi-arid lands (Caughley et al., 1987; Letnic and Ripple 2017; Letnic et al., 2012; Silcock et al., 2013). In addition, introduced rabbits (Oryctolagus cuniculus) are widespread and common herbivores throughout the region. Populations of rabbits and goats are usually controlled within conservation reserves. However, kangaroo populations are typically not controlled because they are native species and their grazing is deemed to be a natural process. Despite concern regarding the threat of over-grazing posed by over-abundant herbivores, little research is available on the effects of grazing by wild herbivores on conservation reserves in semi-arid Australia (Giljohann et al., 2017; Leigh et al., 1989; Prowse et al., 2019). In particular, the paucity of information on the impact of kangaroo irruptions on conservation reserves is alarming given the potential for impacts on the functioning of ecosystems and threatened species (Fensham et al., 2019; Hacker et al., 2020; Rees et al., 2017).

Here we investigate the effects of grazing by wild herbivores, including kangaroos and rabbits, on the structure, composition, and function of grassland ecosystems in four conservation reserves in semi-arid Australia. In each reserve we assessed the relative abundance of mammalian herbivores, and quantified vegetation structure, the composition of standing vegetation, and soil attributes. We expected that grazing by kangaroos and rabbits would reduce the cover and species richness of vegetation, compact the soil, and deplete soil nutrient pools (Eldridge et al., 2017; Leigh et al., 1989; Morris and Letnic 2017). For most variables, we expected that grazing by rabbits would have a greater negative impact than that of kangaroos. Kangaroos, as native herbivores, are widely considered to have relatively benign impacts because they have soft feet compared to hard-hooved ungulates, occur at lower densities than rabbits, and are highly mobile and can migrate before overgrazing occurs (Eldridge et al., 2017). Additionally, rabbits are thought to have a greater impact on soil nutrients and structure because burrowing and digging for habitat and food disrupts soil structure and promotes erosion (Eldridge et al., 2017).

2. Materials and methods

2.1. Study sites

The study was conducted in four conservation reserves in a region of semi-arid Australia (Fig. 1) where dingoes are rare due to intensive population control efforts and kangaroo populations have irrupted (Caughley et al., 1987; Letnic et al., 2012). Rabbits and feral goats are widespread throughout the region. The reserves, in order of increasing aridity, were Oolambeyan National Park (mean annual rainfall = 387 mm), Yathong Nature Reserve (mean annual rainfall = 369 mm), Mungo National Park (mean annual rainfall = 266 mm), and Boolcoomatta Station Reserve (mean annual rainfall = 199 mm). Oolambeyan, Yathong and Mungo are operated by a government conservation agency, the NSW National Parks and Wildlife Service. Boolcoomatta is operated by the non-government conservation organization, Bush Heritage Australia. All livestock was removed from the reserves when they were converted to conservation tenures, however the vegetation in some parts of Oolambeyan are managed for specific conservation objectives with targeted sheep grazing. At the time of the study in July to October 2018, drought conditions prevailed in south-eastern Australia and rainfall in the 12 months preceding our sampling at the nearest BOM weather station to the study areas (Bureau of Meteorology, 2018) was 256.4, 202.4, 169.7, 173.5 mm at Oolambeyan, Yathong, Mungo, and Boolcoomatta, respectively.

Feral goat populations at each of the reserves were subject to periodic control by mustering and/or shooting. Kangaroos are subject to lethal control at Boolcoomatta, but not at the other reserves. Rabbit populations had been controlled by destroying their warrens (ripping) at Boolcoomatta in 2012, and periodic ripping and poison baiting at Oolambeyan, Yathong and Mungo.
2.2. Herbivore abundances

To determine herbivore densities and relative abundance of kangaroo species, we counted mammals along belt transects by driving 15–20 km/h along single-lane unsealed roads with an observer standing on the back of a 4WD vehicle or observing from either side of the vehicle. During diurnal surveys the observer used binoculars to identify kangaroos to species level. During nocturnal surveys the observer used a 50 W spotlight to locate animals. However, because the light provided by the spotlight limited our visual acuity no attempt was made to classify kangaroos to species level and they were recorded simply as "kangaroo". When an animal was sighted, the perpendicular distance (m) from the road to the animal was estimated by the observer. We used a Bushnell Scout DX 1000 ARC rangefinder to calibrate our estimates of the perpendicular distance of each animal or group of animals from the road at first sighting. At each conservation reserve between July and October 2018 we conducted 1–2 nocturnal surveys of 25–40 km and 2–3 diurnal surveys of 30–54 km. If multiple surveys were conducted in a reserve, we completed them along different sections of road and pooled the survey results.

We used different indices for each survey type because the purpose of the surveys differed. Diurnal surveys aimed to determine the relative abundance of diurnally active herbivore species. Consequently, we indexed the abundances of the species sighted (Macropus giganteus, Osphranter rufus, Macropus fuliginosus) at each site as the number of individuals sighted per kilometre. Nocturnal surveys aimed to estimate the density of rabbits (Oryctolagus cuniculus) and kangaroos (Osphranter rufus and Macropus spp.) per km² using a belt width of 200 m either side of the vehicle. During nocturnal surveys, detectability of kangaroos was limited by the range of the spotlight beam to 100 m on either side of the vehicle. Rabbits were more difficult to detect than kangaroos because of their smaller body size. Overall, 95% of the rabbits we observed were within a 60 m belt on either side of the vehicle. Consequently, for rabbit density estimates we truncated the transect belt width to 60 m either side of the vehicle.

We undertook dung surveys to provide an indication of herbivore activity in the vicinity of the exclosures in the months prior to our surveys. We counted groups of herbivore dung present on three 2 × 100 m belt transects. An index of grazing activity for each herbivore species (kangaroo; goat; rabbit) at each reserve was calculated as the total number of dung groups encountered per 1000 m² at each block, and then by calculating an average across all blocks at each conservation reserve.

2.3. Experimental approach herbivore exclosures

Within each reserve we surveyed the vegetation and soils across a network of selective herbivore exclosures between July and October 2018. The exclosures had been established for 8–18 years at the time of survey, and in each instance had been constructed after conservation reserves were established and livestock had been removed. All exclosures at Oolambayan were
in sections of the reserve that were not included in the sheep-grazing management regime. All enclosures were established after the release of the rabbit biological control agent calicivirus in 1995.

The age, size, and design of the herbivore enclosures differed between and within reserves (Table 1). At each reserve, enclosure plots were arranged in blocks that included 1–3 nearby (within <100 m) fenced enclosure plots and an unfenced open grazed plot situated on the same soil type. All blocks contained one open grazed plot (accessible by all herbivores) and other enclosure treatments that excluded all herbivores (excluded rabbits and large herbivores; accessible for small mammals and insects), excluded only large herbivores (kangaroos and goats), or excluded only rabbits. We surveyed 80 plots within 25 blocks across all reserves. The area surveyed within all plots was 25 × 25 m (625 m²), the size of the smallest enclosure plot.

While soil and vegetation types in plots differed among and within reserves, all plots within a block were situated on comparable soil and vegetation-types. Plots that excluded all herbivores, excluded kangaroos only, and excluded rabbits only were present at Boolcoomatta, Yathong and Mungo. At Oolambeyan, the only enclosures available were those that excluded all herbivores (n = 8) and those that excluded kangaroos, but not rabbits (n = 2) (Table 1). Where open grazed plots were not already demarcated within the block, we selected an area that matched the exclusion plots in topography, vegetation and soil type, within a 100 m radius of the enclosure plots (Table 1, Fig. 2).

2.4. Vegetation structure and composition

To examine differences in vegetation structure and composition between treatments we conducted vegetation complexity assessments, point-intercept ground cover assessments and counted species richness within the plot. We avoided areas directly under trees because of the potentially confounding effects of shading and litter fall.

Within each 25 m × 25 m plot we assessed the complexity of understory vegetation within four randomly located, non-overlapping, 5 × 5 m sub-plots. Vegetation complexity in each sub-plot was determined by recording the percentage of a 20 × 50 cm chequered board obscured by vegetation when observed from a distance of 5 m. The board is held perpendicular to the ground at four heights (0–20, 20–50, 50–100 and 100–150 cm) above ground level (Fox et al., 1996). We calculated vegetation complexity for the plot by taking an average percentage across all strata and all subplots. To examine differences in the ground cover of litter, grasses and forbs between treatments we used the point-intercept method in transects separated by 1 m that covered the entire 25 × 25 m plot. At each point, ground cover was classified as bare (including bare ground with cryptogam cover), litter, grass or forb and we calculated the percentage cover for each category. To estimate species richness in plots we conducted a systematic survey and recorded all species encountered, including dead plants that were rooted in the ground.

2.5. Soil function

To assess if the soil nutrient pool varied between treatments, we extracted 9 soil cores (10 × 10 cm in dimension) to a depth of 5 cm from random locations within each plot. We removed litter from the soil surface prior to sampling. Samples from each plot were bulked and composited before being stored in sealed bags.

For soil nutrient analysis, we took 200 g of soil from the composite sample, oven dried it at 40 °C and crushed it to <2 mm peds. We used Dumas high-temperature combustion, and a LECO CNS analyser to determine total carbon (%) and total nitrogen (%) concentrations. We extracted the above-ground portion of all vegetation within each plot with a 50 cm chequered board obscured by vegetation when observed from a distance of 5 m. The board is held perpendicular to the ground at four heights (0–20, 20–50, 50–100 and 100–150 cm) above ground level (Fox et al., 1996). We calculated vegetation complexity for the plot by taking an average percentage across all strata and all subplots.

<table>
<thead>
<tr>
<th>Conservation Reserve</th>
<th># Blocks</th>
<th>Treatments (80 plots total)</th>
<th>Survey Date</th>
<th>Established</th>
<th>Vegetation Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yathong</td>
<td>1</td>
<td>Open Grazed, Exclude Kangaroos/Rabbits/All (4)</td>
<td>July 2018</td>
<td>2003</td>
<td>Casuarina pauper woodland</td>
</tr>
<tr>
<td>Yathong</td>
<td>1</td>
<td>Open Grazed, Exclude Kangaroos/Rabbits/All (4)</td>
<td>July 2018</td>
<td>2003</td>
<td>Geijera parviflora woodland</td>
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<tr>
<td>Yathong</td>
<td>1</td>
<td>Open Grazed, Exclude Kangaroos/Rabbits/All (4)</td>
<td>July 2018</td>
<td>2005</td>
<td>Geijera parviflora woodland</td>
</tr>
<tr>
<td>Oolambeyan</td>
<td>2</td>
<td>Exclude All, Open Grazed (4)</td>
<td>August 2018</td>
<td>2003/2004</td>
<td>Acacia ovata woodland</td>
</tr>
<tr>
<td>Oolambeyan</td>
<td>1</td>
<td>Exclude All, Open Grazed (2)</td>
<td>August 2018</td>
<td>2003/2004</td>
<td>Casuarina pauper woodland</td>
</tr>
<tr>
<td>Oolambeyan</td>
<td>1</td>
<td>Exclude All, Open Grazed (2)</td>
<td>August 2018</td>
<td>2003/2004</td>
<td>Eucalyptus largiflora woodland</td>
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<tr>
<td>Oolambeyan</td>
<td>4</td>
<td>Exclude All, Open Grazed (8)</td>
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<td>2003/2004</td>
<td>Callitris glaucophyla woodland</td>
</tr>
<tr>
<td>Oolambeyan</td>
<td>1</td>
<td>Exclude Kangaroos, Open Grazed (2)</td>
<td>August 2018</td>
<td>2003/2004</td>
<td>Callitris glaucophyla woodland</td>
</tr>
<tr>
<td>Oolambeyan</td>
<td>1</td>
<td>Exclude Kangaroos, Open Grazed (2)</td>
<td>August 2018</td>
<td>2003/2004</td>
<td>Hakea leucopetra woodland</td>
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<tr>
<td>Mungo</td>
<td>2</td>
<td>Open Grazed, Exclude Kangaroos/Rabbits/All (8)</td>
<td>August 2018</td>
<td>2000</td>
<td>Callitris glaucophyla woodland</td>
</tr>
<tr>
<td>Mungo</td>
<td>2</td>
<td>Open Grazed, Exclude Kangaroos/Rabbits/All (8)</td>
<td>August 2018</td>
<td>2008</td>
<td>Maireana pyramidata shrubland</td>
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<tr>
<td>Mungo</td>
<td>2</td>
<td>Open Grazed, Exclude Kangaroos/Rabbits/All (8)</td>
<td>August 2018</td>
<td>2000</td>
<td>Maireana pyramidata shrubland</td>
</tr>
<tr>
<td>Boolcoomatta</td>
<td>2</td>
<td>Open Grazed, Exclude Kangaroos/Rabbits/All (8)</td>
<td>October 2018</td>
<td>2010</td>
<td>Acacia aneura woodland</td>
</tr>
<tr>
<td>Boolcoomatta</td>
<td>1</td>
<td>Open Grazed, Exclude Kangaroos/Rabbits/All (4)</td>
<td>October 2018</td>
<td>2010</td>
<td>Alectryon oleifolius, Maireana spp. Shrubland</td>
</tr>
<tr>
<td>Boolcoomatta</td>
<td>1</td>
<td>Open Grazed, Exclude Kangaroos/Rabbits/All (4)</td>
<td>October 2018</td>
<td>2010</td>
<td>Acacia spp., Maireana spp. Sandhill</td>
</tr>
</tbody>
</table>
nitrogen (%) content of soil, following methods 6B2b and 7A5 respectively from Rayment and Lyons (2011). Plant-available phosphorus (mg kg$^{-1}$) was analysed with the Bray I extraction method as per method 9E2 in Rayment and Lyons (2011).

To determine the effects of herbivore grazing on soil density we used a bulk density cylinder to collect samples. Five samples of an 86 cm$^3$ cylinder were extracted from each of the plots and composited. These samples were dried in the laboratory at 105 °C until a constant weight was reached ($\pm 1$ g) (McKenzie et al., 2002). Bulk density was calculated as the final mass divided by the volume of the samples. Particles $>2$ mm (e.g., stones) were removed using a sieve and their mass and volume subtracted to determine bulk density of particles $<2$ mm (McKenzie et al., 2002).

2.6. Statistical analyses

We used linear mixed effects models with grazing treatment, conservation reserve, and the interaction between grazing treatment and conservation reserve, as fixed factors. Although grazing treatment was the factor which we were primarily interested in understanding, we included the factor conservation reserve in our analyses to take into account variation between reserves due to variables such as rainfall, species pools and soil type. Exclosure block was specified as a random effect in analyses. All analyses were conducted using a Gaussian distribution. We used single degree of freedom contrasts to explore differences among treatment means when a significant ($P < 0.05$) main effect or interaction term was reported. We report significant contrasts only. All analyses were conducted using SPSS v24.90.

3. Results

3.1. Herbivore abundances

Kangaroos were the most frequently observed herbivore during diurnal and nocturnal surveys at each reserve (Fig. 3). The relative abundance of kangaroo species varied among reserves. Red kangaroos ($O. rufus$) were recorded in all reserves and were the most abundant kangaroo species at Boolcoomatta, Oolambeyan and Mungo. Western grey kangaroos ($M. fuliginosis$) were recorded in all reserves and were the most abundant kangaroo species at Yathong. Eastern grey kangaroos ($M. giganteus$) were recorded during diurnal surveys at Oolambeyan and Yathong, but were not sighted at Mungo or Boolcoomatta (Fig. 3a). The density of all kangaroo species combined, estimated from nocturnal surveys, was 144.9 kangaroos per km$^2$ at Oolambeyan, 50 kangaroos per km$^2$ at Yathong, 17.29 kangaroos per km$^2$ at Mungo, and 7.3 kangaroos per km$^2$ at Boolcoomatta. No euros ($Osphranter robustus$) or feral goats ($Capra hircus$) were sighted during surveys.
Rabbits were recorded during nocturnal surveys at all reserves, but most frequently at Oolambeyan and least frequently at Boolcoomatta. Rabbit density was estimated to be 77.3 per km$^2$ at Oolambeyan, 37.4 per km$^2$ at Yathong, 21.6 per km$^2$ at Mungo and 1.0 per km$^2$ at Boolcoomatta.

Kangaroo dung was the most frequently encountered herbivore dung at each reserve (Fig. 3c). Rabbit dung was recorded at every reserve. Goat dung was encountered infrequently at Mungo and Boolcoomatta. No goat dung was encountered at Oolambeyan or Yathong.

3.2. Vegetation structure

We found a significant effect of treatment on vegetation complexity ($F_{3, 20.8} = 74.21, P < 0.001$), but no effect of reserve ($F_{3, 21.6} = 0.90, P < 0.46$) or interaction between treatment and reserve ($F_{8, 42.9} = 1.80, P < 0.10$; Fig. 4a). Vegetation complexity was greater in the all herbivores excluded plots (mean$\pm$1SE $0.82 \pm 0.12$) than in the open grazed plots ($P < 0.001$; mean$\pm$1SE $0.32 \pm 0.11$) and rabbit exclusion ($P < 0.001$; mean$\pm$1SE $0.48 \pm 0.17$) plots. Vegetation complexity was greater in the kangaroo exclusion plots (mean$\pm$1SE $0.64 \pm 0.13$) than it was in the open grazed ($P = 0.001$) and rabbit exclusion plots ($P = 0.02$).

We found no effect of treatment ($F_{3, 40.4} = 1.25, P = 0.3$) or interaction between treatment and reserve ($F_{8, 40.1} = 1.83, P = 0.1$) for litter cover, but there was an effect of reserve ($F_{1, 18.7} = 6.74, P = 0.003$). Litter cover was lower at Boolcoomatta (mean$\pm$1SE $12.7 \pm 0.72$) than at Mungo (mean$\pm$1SE $43.2 \pm 0.79$), Oolambeyan (mean$\pm$1SE $46.8 \pm 0.98$) and Yathong (mean$\pm$1SE $60.4 \pm 1.18$; Fig. 4d).

We found effects for treatment ($F_{3, 49} = 36.16, P = 0.001$), reserve ($F_{3, 21} = 5.43, P = 0.006$) and the interaction between treatment and reserve ($F_{8,49} = 4.87, P < 0.001$) for percentage grass cover (Fig. 4c). At Boolcoomatta, grass cover was greater in the all herbivores excluded and rabbit excluded plots ($P < 0.05$) than it was in the open grazed plots. At Mungo, grass cover was greater in the all herbivores excluded plots than it was in the open grazed plots ($P < 0.001$), rabbit excluded ($P < 0.001$) and kangaroos excluded plots ($P < 0.001$). At Oolambeyan, grass cover was greater in the all excluded than it was in the open grazed ($P < 0.001$) and kangaroo excluded plots ($P < 0.001$). At Yathong, grass cover was greater in the all herbivores excluded and rabbits excluded plots than it was in the open grazed plots (both $P < 0.001$). At Yathong, grass cover was also greater in the kangaroo excluded plots than it was in the open grazed and rabbits excluded plots (both $P < 0.001$).
We found an effect of reserve (F3,21 = 3.39, P = 0.02) but no effects for treatment (F3,46 = 1.85, P = 0.15) nor interaction between treatment and reserve (F3,46 = 0.34, P = 0.9) on the percentage cover of forbs (Fig. 4b). Forb cover was significantly greater at Oolambeyan (mean ± 1SE 20.4 ± 0.73) than it was at Boolcoomatta (P = 0.005; mean ± 1SE 4.7 ± 0.44) and Yathong (P = 0.024; mean ± 1SE 7.0 ± 0.57) while Mungo did not differ from other reserves (P > 0.05; mean ± 1SE 13.4 ± 0.67).

### 3.3. Vegetation composition

We found effects of treatment (F3,58 = 23.54, P = 0.001) and reserve on grass species richness (F3,58 = 6.64, P = 0.001), but no interaction between treatment and reserve (F3,58 = 1.84, P = 0.087; Fig. 5a). Grass species richness was greater in the all herbivores excluded plots (mean ± 1SE 2.86 ± 0.25) than it was in the open grazed (P < 0.001; mean ± 1SE 0.64 ± 0.18), rabbit exclusion (P < 0.001; mean ± 1SE 0.67 ± 0.18), and kangaroo exclusion plots (P = 0.03; mean ± 1SE 2 ± 0.26). Grass species richness was greater in the kangaroo exclusion than in the open grazed plots (P < 0.001). Grass species richness was greater at Boolcoomatta (P = 0.042; mean ± 1SE 1.9 ± 0.33) and Oolambeyan (P = 0.005; mean ± 1SE 2.1 ± 0.29) than it was in Yathong (mean ± 1SE 1.0 ± 0.25). Grass species richness was greater in Oolambeyan (P = 0.003; mean ± 1SE 2.1 ± 0.29) than it was in Mungo (mean ± 1SE 1.2 ± 0.18).

We found an effect of treatment (F3,38,4 = 16.56, P < 0.001) on forb species richness but no effect of reserve (F1,18,2 = 0.58, P = 0.64) nor interaction between treatment and reserve (F1,38,1 = 1.49, P = 0.194; Fig. 5b). Forb species richness was greater in the all herbivores excluded treatment (mean ± 1SE 9.1 ± 0.40) than it was in the rabbit exclusion (mean ± 1SE 4.9 ± 0.44), kangaroo exclusion (mean ± 1SE 5.6 ± 0.40) and open grazed (mean ± 1SE 4.8 ± 0.34) treatments (all P < 0.001).

We found significant effects of treatment (F3,45,4 = 7.876, P < 0.001) and reserve (F3,20,8 = 6.677, P = 0.03) on shrub species richness, but no interaction between treatment and reserve (F3,40,3 = 1.133, P = 0.36; Fig. 5c). Shrub species richness was greater in the all herbivores excluded (mean ± 1SE 3.0 ± 0.28) and rabbit exclusion plots (mean ± 1SE 3.2 ± 0.36) than it was in the open grazed plots (mean ± 1SE 1.7 ± 0.24) (both P < 0.001). Shrub species richness was also greater in the all herbivores excluded plots than in the kangaroo excluded plots (P = 0.04; mean ± 1SE 2.5 ± 0.34). Shrub species richness was greater at Boolcoomatta (mean ± 1SE 4.5 ± 0.32) than at Oolambeyan (<0.001; mean ± 1SE 1.3 ± 0.27), Yathong (P = 0.014; mean ± 1SE 2.1 ± 0.32) and Mungo (P = 0.01; mean ± 1SE 2.4 ± 0.22).

### 3.4. Soil function

We observed a significant effect of treatment (F3,37,5 = 3.38, P = 0.03), but no effect of reserve (F3,18,6 = 1.61, P = 0.22) nor interaction between treatment and reserve (F3,37,3 = 1.02, P = 0.43) on Bray 1 phosphorus (Fig. 6a). On average, Bray 1 phosphorus was greater in the kangaroo exclusion (mean ± 1SE 25.7 ± 0.1) than in the open grazed (P = 0.003; mean ± 1SE 19.4 ± 0.07) or rabbit exclusion plots (P = 0.004; mean ± 1SE 15.7 ± 0.11) and there was no difference between the all herbivores excluded plot (mean ± 1SE 19.9 ± 0.09) and the other treatments (P > 0.05).
Fig. 5. Mean total species richness in each treatment at each conservation reserve for a) grasses, b) forbs and c) shrubs. Reserves are presented in order of increasing aridity from left to right. Error bars are ±1 SEM.

Fig. 6. Mean values for soil results a) phosphorous, b) carbon, c) nitrogen and d) bulk density for each combination of treatment and conservation reserve. Reserves are presented in order of increasing aridity from left to right. Error bars are ±1 SEM.
We found effects of treatment \((F_{3,44} = 4.15, P = 0.01)\), reserve \((F_{3,20} = 20.09, P < 0.001)\) and an interaction between treatment and reserve \((F_{8,44} = 2.71, P = 0.016)\) for soil percentage carbon (Fig. 6b). At Mungo, soil percentage carbon was greater in the all exclusion \((P < 0.001)\), rabbit exclusion \((P = 0.017)\) and kangaroo exclusion \((P < 0.001)\) plots than it was in the open grazed plots. At Oolambeyan, soil percentage carbon was greater in the all herbivore exclusion \((P < 0.001)\) and kangaroo exclusion \((P = 0.004)\) plots than it was in the open grazed plots. Soil percentage carbon did not differ between treatments at Yathong or Boolcoomatta.

We found an effect of reserve \((F_{3,14,3} = 22.51, P < 0.001)\), but no effect of treatment \((F_{3,36,2} = 0.40, P = 0.2)\) nor interaction between treatment and reserve \((F_{3,35,9} = 1.28, P = 0.29)\) for soil percentage nitrogen (Fig. 6c). On average, soil percentage nitrogen was greater at Oolambeyan \((\text{mean}\pm\text{1SE} 0.14\pm 0.05)\) than the other reserves \((P < 0.01)\) and was greater at Yathong \((\text{mean}\pm\text{1SE} 0.09\pm 0.04)\) than at Boolcoomatta \((P = 0.01; \text{mean}\pm\text{1SE} 0.05\pm 0.05)\). Soil percentage nitrogen did not differ between Mungo \((\text{mean}\pm\text{1SE} 0.6\pm 0.20)\) and the other reserves \((P > 0.05)\).

We found effects for treatment \((F_{3,47,0} = 3.25, P = 0.031)\), reserve \((F_{1,217} = 10.26, P < 0.001)\), but no interaction between treatment and reserve for soil bulk density \((F_{8,46,8} = 1.82, P = 0.097)\). On average, soil bulk density was lower in the kangaroo exclosures \((\text{mean}\pm\text{1SE} 1.4\pm 0.10)\) than open grazed plots (Fig. 6d; \(P = 0.008; \text{mean}\pm\text{1SE} 1.5\pm 0.07)\) and did not differ between other treatments \((\text{mean}\pm\text{1SE} 1.09)\) all herbivores excluded \(1.4\pm 0.09\); rabbit exclusion \(1.4\pm 0.10)\). Soil bulk density was greater at Boolcoomatta \((\text{mean}\pm\text{1SE} 1.6\pm 0.10)\) than it was at Mungo \((P < 0.001; \text{mean}\pm\text{1SE} 1.4\pm 0.07)\), Oolambeyan \((P < 0.001; \text{mean}\pm\text{1SE} 1.3\pm 0.08)\) and Yathong \((P = 0.004; \text{mean}\pm\text{1SE} 1.4\pm 0.08)\). Additionally, soil bulk density was greater at Mungo than it was at Oolambeyan \((P = 0.048)\).

4. Discussion

Grazing by wild herbivores had effects on the vegetation and soils of four widely separated semi-arid conservation reserves that were symptomatic of overgrazing. Kangaroos were the most abundant herbivore at all the conservation reserves. Grazing by both kangaroos and rabbits was linked to a reduction in the complexity of understorey vegetation, the cover of grasses, species richness of forbs and the depletion of soil carbon. Grazing by rabbits was linked to a reduction in shrub species richness. Grazing by kangaroos was linked to reduced species richness of grasses, depletion of the soil phosphorus pool, and increased soil bulk density. Our findings show that grazing by kangaroos contributes to degradation of vegetation and soils in conservation reserves which historically has largely been attributed to the grazing impacts of introduced species (Leigh et al., 1989; Russell et al., 2011). More generally, our results illustrate how disruptive wild-herbivore populations can have impacts that are counter to the objectives of conservation reserves in regions where apex predators have been extirpated.

Our diurnal and nocturnal surveys revealed that kangaroo and rabbit abundances decreased with aridity and that kangaroos were the most abundant herbivores in each conservation reserve at the time of sampling. At the time of sampling, feral goats occurred at much lower densities than kangaroos or rabbits. We did not observe goats during driving surveys and goat dung was recorded infrequently during dung surveys. Thus, we are confident that the impacts on the structure, composition and function of ecosystems that we report were linked primarily to kangaroo and rabbit grazing.

Kangaroo assemblages varied among reserves, with red kangaroos being the dominant species at Oolambeyan, Boolcoomatta and Mungo and western grey kangaroos the dominant species at Yathong. While each kangaroo species varies in its dietary preferences (Caughley et al., 1987; Dawson 2012), the effects of kangaroo grazing on vegetation structure and composition, and soil function were generally consistent between reserves indicating that the effects of the different kangaroo species on vegetation and soils were similar.

Consistent with the findings of previous studies, grazing by rabbits suppressed the species richness of woody shrubs and forbs, and grass cover (Denham and Auld 2004; Foran 1986; Leigh et al., 1989; Travers et al., 2018). Additionally, rabbit grazing was linked to decreased soil carbon levels at Mungo. Most studies of rabbits’ impacts on soils have investigated effects mediated by their warrens, diggings, and dung heaps (Eldridge et al., 2006; Eldridge and Simpson 2002), but not on soils in the surrounding landscape. Our results demonstrate that rabbits’ impacts on soils are evident in the broader landscape irrespective of focal points for their activity. Furthermore, rabbit populations in all the reserves were subject to lethal control methods, although not necessarily consistently or similarly across reserves. It is widely appreciated that maintaining appropriate durations and intensities of rabbit control activities is critical to management of total grazing pressure (Mutze et al., 2016). Nevertheless, our results show that rabbits can have measurable impacts on vegetation and soils even when their populations are subject to control measures, and in the likely presence of the biological control agents myxomatosis and rabbit calicivirus.

Importantly, our results show that grazing by kangaroos had marked effects on vegetation and soils that were symptomatic of overgrazing. Kangaroo grazing was linked to reduced understorey vegetation complexity, grass cover, and grass and forb species richness, depletion of the soil carbon and phosphorous pools, and increased soil bulk density. These findings are consistent with previous studies which have investigated kangaroos’ impacts on vegetation and soils in the absence of livestock (Caughley et al., 1987; Morris and Letnic 2017; Norbury et al., 1993; Short 1985) but contrast with research showing that grazing by macropods at unknown densities maximised species richness in times of high rainfall (Fensham et al., 2011). Our results highlight that grazing by high density kangaroo populations can have severe effects on ecosystems during drought.
The effects of intensive grazing by wild herbivores that we report have broad repercussions for ecosystem assembly and function. For example, reduced plant cover affects animals that rely on grasses or forbs for shelter and food (Barton et al., 2011; Howland et al., 2016; Rees et al., 2017), and soil compaction may diminish water infiltration (Val et al., 2019). Two of the conservation reserves included in our study, Oolambeyan and Boolcoomatta are important refuges for a Critically Endangered ground-nesting bird, the plains-wanderer (Pedionomus torquatus). Optimally managing grazing pressure is crucial for plains-wanderers because they have specific habitat requirements and abandon grasslands that are too dense or become too sparse through overgrazing (Baker-Gabb et al., 1990). Consequently, denudation of vegetation by livestock and rabbits is considered to be threat to plains-wanderers (Baker-Gabb et al., 1990). However, our results show that grazing by kangaroos can affect vegetation and soils in similar ways to grazing by livestock and rabbits.

Irruptions of mammalian herbivores where mammalian predators have been extirpated is a global phenomenon that often poses intractable problems for biodiversity conservation and ecological restoration because of social issues that need to be taken into consideration when managing their populations (Nilsen et al., 2007; Thondhlana et al., 2020). In North America, cervid populations have irrupted following the extirpation of wolves and the increased grazing pressure has negatively affected over 100 plant species (Côté et al., 2004; Crête et al., 2001). To address the grazing impacts of deer, Cuyahoga Valley National Park has culled deer populations (Dougherty et al., 2003) and wolves were reintroduced to Yellowstone National Park (Smith et al., 2003). However, in many regions where native herbivore populations have irrupted community opposition has hindered the re-establishment of predators or culling to levels optimal for biodiversity conservation (Austin et al., 2013; Martin et al., 2020). In the case of kangaroos in Australia, on pastoral lands they are often culled to reduce their impacts on pastures or harvested with the dual aim of reducing their impacts on pastures and supporting a meat-harvest industry (McLeod and Hacker 2020). In this context conservation reserves are widely considered to be refuges where kangaroos can live unharmed because they are a native species and their grazing is often deemed to be a benign natural process (Cooney et al., 2012; Wilson and Edwards 2019).

However, the marked impacts of grazing by wild herbivores which we report could be regarded as detrimental for biodiversity conservation and counter to the aims of conservation reserves (Prowse et al., 2019). Indeed, our findings raise questions about native herbivore management on conservation reserves, including: what density of kangaroos is acceptable from a biodiversity and threatened species conservation perspective, and, should kangaroo populations be managed in conservation reserves to reduce their grazing impacts? These questions are inextricably linked to the broader problem of shifting baselines and in particular uncertainty about what abundances of herbivores should be considered "natural" or desirable in landscapes where there are competing land-uses and there is little understanding of the densities at which herbivores existed prior to modern times (Caughley et al., 1987; Gordon et al., 2004). However, we argue that population management of wild herbivores, irrespective of whether they are native or introduced, is critical to ensure that overgrazing does not occur in conservation reserves and contend that it may now be time to consider management measures for kangaroo populations in Australia’s conservation reserves to prevent overgrazing and the degradation of biodiversity.

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Data availability

Data are available from Figshare Digital Repository: https://doi.org/10.6084/m9.figshare.13323248.v124JaMUXRoohttps://datadryad.org/stash/share/ZTQque0On0V5i8DFP8d4-VG7CCVknxg1w24JaMUXRoo.

Authors' contributions

ML, HW and MC conceived the project; ML, HW and CM designed methodology; CM, HW, DP, GF and ML collected the data; ML led data analysis with assistance from CM; ML and CM led the writing of the manuscript with critical input from all authors. All authors gave final approval for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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