Journal of Arid Environments 190 (2021) 104526

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Impacts of grazing by kangaroos and rabbits on vegetation and soils in a semi-arid conservation reserve

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ARTICLE INFO

Keywords:
Soil bulk density
Infiltration
Vegetation biomass
Introduced herbivores
Soil compaction
Calicivirus

ABSTRACT

Overgrazing by introduced herbivores is widely recognized as a threatening process in Australia's semi-arid rangelands. Comparatively, grazing by native herbivores is generally considered to have benign effects. Populations of introduced herbivores are controlled in conservation reserves, but populations of native kangaroos and wallabies are seldom subject to control. We investigated the impacts of rabbit and kangaroo grazing on vegetation and soils at Yathong Nature Reserve in semi-arid Australia during the dry conditions that prevailed in 2019. We conducted spotlight and dung surveys to measure the relative abundance of kangaroos and rabbits, and assessed understorey biomass, woody plant density, soil bulk density and water infiltration rates in selective herbivore exclosures that had been established in 1979, and nearby controls that all herbivores could access. Kangaroos were the dominant herbivores at the time of our study. Grazing by kangaroos decreased grass biomass, increased soil density and reduced the rate of water infiltration. Rabbits reduced woody plant density but had no detectable effect on understorey vegetation cover or soil attributes. Our findings question the existing paradigms about how grazing by kangaroos should be viewed and prompt the question: should kangaroo populations be managed within conservation reserves to reduce their impacts on ecosystems?

1. Introduction

Overgrazing is a threatening process in semi-arid and arid rangelands worldwide (Côté et al., 2004; Eldridge et al., 2016; Tiver and Andrew, 1997). Overgrazing occurs when the intensity and duration of total grazing pressure by herbivores is such that it causes a loss in productivity, including reduced vegetation cover, a shift in vegetation composition towards assemblages dominated by less palatable species, and changes to essential soil functions (Eldridge et al., 2016). Most literature on the impacts of grazing in arid lands focuses on livestock. However, any herbivore species, invasive or native, wild or domestic, has the potential to contribute to overgrazing (Côté et al., 2004; Short, 1985).

In Australia's semi-arid rangelands, conservation reserves have been established with the intention of enhancing biodiversity conservation by providing ecosystems with refuge from human activities associated with livestock grazing, including land clearing and hunting (Pressey, 1992). Grazing by rabbits (*Oryctolagus cuniculus)* is considered to be among the greatest threats to ecosystems in arid Australia (Mutze, 2017). Rabbit grazing removes palatable species, with particularly strong effects on woody shrubs (Auld, 1995; Forsyth et al., 2015; Mutze et al., 2016) and is linked to reduced vegetation biomass (Short, 1985). Typically, rabbit populations are controlled in conservation reserves in an effort to reduce their negative effects on ecosystems.

Kangaroo populations have irrupted across much of semi-arid Australia since European colonization of Australia. These irruptions are linked to the extirpation of their principal predator, the dingo, and the proliferation of artificial water points for livestock (Caughley et al., 1985; Fisher et al., 2021; Letnic and Crowther, 2013; Newsome, 1975). On commercially grazed properties kangaroos are often considered pests and their populations controlled because they compete with livestock for forage (McLeod and Hacker, 2020; Norbury and Norbury, 1992).

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https://doi.org/10.1016/j.jaridenv.2021.104526
Received 1 November 2020; Received in revised form 27 March 2021; Accepted 25 April 2021
Available online 4 May 2021
0140-1963/

Conversely, kangaroo populations are typically not controlled in conservation reserves because they are a native species. Consequently, kangaroos often exist at particularly high densities in conservation reserves in comparison to adjacent pastoral properties (Caughley et al., 1987).

Correlative studies conducted on pastoral land suggest that kangaroo grazing has weaker effects on vegetation and soils than that of livestock and rabbits (Travers et al., 2018). However, where kangaroos occur at high densities their grazing can markedly reduce the standing biomass of grasses and the production of grass seed (Caughley et al., 1987; Mills et al., 2020; Norbury and Norbury, 1993; Rees et al., 2017). In addition, grazing by kangaroos has been linked to a reduction in the pools of soil carbon, nitrogen, and phosphorus (Morris and Letnic, 2017; Mills et al., 2020). Although both rabbits and kangaroos are widely perceived to be pests by pastoralists and rabbits are widely perceived as pests in conservation reserves, relatively few studies have compared their effects on vegetation and soils in conservation reserves (Prowse et al., 2019; Mills et al., 2020).

In 1979, researchers from Australia's Commonwealth Science and Industrial Research Organization (CSIRO) built selective exclosures Fig. 1 to investigate the effects of rabbits and kangaroos on vegetation in Yathong Nature Reserve in central New South Wales (Leigh et al., 1989). This research showed that rabbits had strong negative effects on the vegetation near their warrens and that kangaroos occurred at high densities and at times also had considerable effects on vegetation (Leigh et al., 1989). We revisited the exclosures built by Leigh et al. (1989) 40 years after their establishment to investigate the impacts of rabbits and kangaroos on vegetation and soil during a period of relatively dry conditions that prevailed in 2019. Rabbit populations have decreased since the study of (Leigh et al., 1989) because of the release of the calicivirus biological control agent (Sharp et al., 2001). Hence, it might be expected that rabbits' impacts may now be less than they were in the 1970s and 1980s. Our specific aims were to: 1) compare the relative abundances and activity of kangaroos and rabbits, and 2) compare the impacts that grazing by rabbits and kangaroos have on vegetation biomass, woody plants and soils under drought conditions.

2. Material and methods

2.1. Study site

Our study was conducted at Yathong Nature Reserve (32° 36′ S, 145° 30′ E) in semi-arid central New South Wales, Australia. The 1156 km^2 reserve was established as a conservation area and destocked in November 1971. The average maximum daytime temperature is 34.4 °C and the average minimum daytime temperature is 15.9 °C. Mean annual rainfall and the standard deviation of annual rainfall at the nearest weather station to Yathong are 369 mm and 147 mm, respectively ($n = 63$, Taringo Downs, 32° 24′ S, 145° 55′ E, Australian Bureau of Meteorology), although it varies greatly between years. In the calendar year preceding our study (2018) there was just 129 mm of rainfall at Yathong. Rainfall in the period January to July 2019 (239 mm) was close to average (226 mm) for the same time of year (Australian Bureau of Meteorology).

2.2. Grazing exclosures

To investigate the effects of rabbits and kangaroos on vegetation and soil we used selective grazing exclosures that were established in 1979 (Fig. 1, Leigh et al., 1989). The exclosures were located at two sites in areas situated on red-loam soils that had been cleared in the late 1800s. The dominant understorey species at the sites, included the grasses *Austrostipa scabra* and *Rytidosperma caespitosum*, and the forbs *Erodium crinum* and *Medicago lacinata*. Each site was characterized by sparsely scattered mature trees, including *Callitris glaucophylla*, *Casuarina cristata*, *Geijera parviflora* and *Alectryon oleifolius*. There were no woody shrubs in the exclosures at the time of their establishment (Leigh et al., 1989).

At one site there were 10 blocks of exclosures and at the other site there were 12 blocks of exclosures ($n = 22$). There were two treatments in each block, a 5 m × 5 m exclosure that excluded all herbivores, and a 5 m × 5 m exclosure that excluded kangaroos only. We used a 5 m × 5 m unfenced area directly to the north and matched to aspect and

Fig. 1. Exclosures and the surrounding landscape where control sites were situated at Yathong Nature Reserve in March 2019. Each exclosure consisted of a sub-exclosure that excluded kangaroos and a sub-exclosure that excluded all herbivores.

topography within 5 m of each exclosure block as a control site that all herbivores could access. Kangaroo exclosures were constructed of square-mesh ring-lock fence (10 cm × 10 cm mesh) and were approximately 70 cm high to exclude kangaroos, but allow access to rabbits (Leigh et al., 1989). The all herbivores excluded plots were constructed of fine wire netting (2.5 cm × 2.5 cm mesh) to exclude all herbivores, including rabbits, and were approximately 70 cm high (Leigh et al., 1989).

When the exclosures were initially established they were placed at varying distances from rabbit warrens so that researchers could examine the grazing impacts of rabbits and kangaroos at different proximities to rabbit warrens (Leigh et al., 1989). In the intervening period extensive rabbit control has been undertaken in the reserve, so the original rabbit warrens were not always present and new warrens may have formed. Consequently, we restricted our analyses to comparisons between the three exclosure treatments. If response variables differed between the kangaroos excluded plots and control we interpreted the difference to be related to kangaroo grazing. If response variables differed between the Exclude all plots and Exclude kangaroo plots then we interpreted the difference to be related to rabbit grazing. If the response variables differed only between the Exclude all plots and control plots we interpreted the effect to be related to rabbit grazing.

2.3. Herbivore assemblages

We conducted nocturnal distance sampling surveys to determine the relative densities of kangaroos and rabbits near the grazing exclosures, in March and July 2019. We drove at 15 km/h along single lane unsealed roads at night while an observer used a 50 W spotlight to locate animals. When animals were sighted, the number of kangaroos and rabbits seen and their estimated perpendicular distance from the track were recorded. 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". Previous research in the area indicates that red kangaroos (*Osphranter rufus*), eastern grey kangaroos (*Macropus giganteus*) and western grey kangaroos (*Macropus fuliginosus*) are present in the area with red kangaroos being the most abundant species (Mills et al., 2020). 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. We surveyed 35 km in March 2019 and 38 km in July 2019.

At the time the study was undertaken, feral goats were present in the reserve, but subject to intensive population-control activities. To index feral goat densities, we conducted diurnal driving surveys by driving 15–20 km/h along the same roads used for nocturnal surveys with observers seated inside the vehicle scanning for goats on either side of the vehicle. We conducted a total of 30 km of daytime surveys in both March 2019 and July 2019.

In March 2019 and July 2019 we counted dung near the two exclosure sites to obtain an indication of herbivore activity in the months prior to our surveys. We counted the total number of groups of herbivore dung present on three 2 × 100 m belt transects. An index of grazing activity for each herbivore species (kangaroo; goat; rabbit) was calculated as the total number of dung groups encountered per 1000 m^2.

2.4. Vegetation and soil function

Within each exclosure and control plot we measured vegetation biomass, the number of woody plants present, soil bulk density, and the water infiltration rate. We conducted two survey trips, one in March 2019 and another in July 2019. Vegetation biomass was measured on both sampling occasions, while the number of woody plants present, soil bulk density, and the rate of water infiltration were measured during or from samples collected during the July 2019 sampling period.

We measured vegetation biomass using the same methods as Leigh et al. (1989). On each sampling occasion we randomly placed one 0.5 m^2 quadrat in each exclosure. We clipped all vegetation from within each quadrat and oven-dried the samples at 60 °C until a constant mass was reached (around 24 h). Biomass samples were identified to species and the biomass of each species weighed. We calculated biomass per m^2 of grasses and forbs, and total plant biomass. During the July sampling period we ensured that the quadrat did not overlap with the area that was clipped in the March sampling period. To determine the impacts of different herbivore species on woody vegetation, we recorded the number of woody plants present in plots. All woody plants we encountered were assumed to have sprouted since the establishment of the exclosures because the species lists published in Leigh et al. (1989) did not include any woody plants.

We used a bulk density cylinder (86 cm^3 volume) to collect samples to assess soil bulk density. Three samples were extracted from each plot and composited. Samples were dried in the laboratory at 105 °C until a constant mass was reached (±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 2 mm sieve, and their mass and volume subtracted to determine bulk density of particles < 2 mm (McKenzie et al., 2002). To measure water infiltration rate, we poured 35 mL of water into a 4 cm diameter cylinder fixed to the ground and recorded the number of seconds it took until the water was absorbed by the soil. We measured infiltration once in each plot.

2.5. Statistical analyses

We used the '*Distance*' package version 0.9.8 (Miller et al., 2019) in R version 3.6.1 (R Core Team, 2019) to estimate large herbivore density from nocturnal surveys. Based on detection curves, we used an effective strip width (distance from the vehicle) of 100 m for kangaroos and 75 m for rabbits. We used Kolmogorov-Smirnov and Cramer-von Mises tests in the '*Distance*' package to check goodness of fit ($P > 0.05$) and determine a set of plausible models for our data. We used model selection using AIC and selected the half-normal key function with cosine adjustment term for our data (Miller et al., 2019).

Linear mixed effects models were run with SPSS 24.0. Treatment, date and the interaction between treatment and date were independent fixed factors in linear mixed effects models for total biomass, grass biomass and forb biomass. To correct skewed distributions, total biomass, grass biomass, forb biomass and water infiltration rate were log transformed. For variables that were only measured on one sampling occasion (number of woody plants, bulk density, rate of water infiltration), treatment was specified as a fixed factor. Models for all variables used a Gaussian distribution. Plot nested within location was a random factor. In instances when main effects were significant ($P < 0.05$) post-hoc tests were performed using Fishers Least Significant Difference (LSD) test.

3. Results

3.1. Herbivore abundance

Our nocturnal distance sampling estimated rabbit density to be 1.4 ± 0.6 individuals/km^2 in March and 1.6 ± 0.8 individuals/km^2 in July. Our nocturnal distance sampling estimated kangaroo density to be 49.9 ± 24.2 individuals/km^2 in March and 39.9 ± 6.3 individuals/km^2 in July. No feral goats were seen during the diurnal surveys. Kangaroo dung was the most frequently encountered dung at both sites (Fig. 2). Rabbit dung was recorded at both sites (Fig. 2). Dung from other herbivore species was not encountered at either site.

3.2. Vegetation

The number of woody stems in plots was significantly affected by treatment (Fig. 3a; $F_{2,42} = 5.47$, $P < 0.08$). More woody plants were present in the Exclude all plots than in the Control plots ($P = 0.002$), but

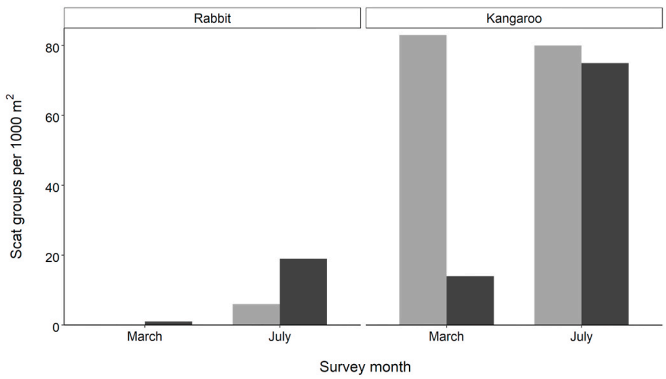

Fig. 2. Number of scat groups per 1000 m^2 found on transects at each site on each sampling occasion (March 2019 and July 2019). Bar shading indicates site (n = 2).

the number of woody stems did not differ between the Kangaroos excluded and Control plots ($P = 0.1$) or between the Kangaroos excluded and Exclude all plots ($P > 0.1$).

Neither treatment ($F_{2,105} = 2.95$, $P = 0.057$) or time of sampling ($F_{1,105} = 1.51$, $P > 0.05$) affected total biomass. However, a significant interaction term ($F_{2,105} = 6.66$, $P = 0.002$) indicated that total biomass responded differently between treatments between sampling periods (Fig. 3a). Total biomass increased between sampling trips in the Control plots, but not in the Exclude kangaroos or Exclude all plots ($P < 0.001$). During the March sampling trip, total biomass was greater in the Exclude all plots ($P < 0.001$) and Exclude kangaroos plots ($P < 0.001$) than in the Control plots, but there were no differences in total biomass among treatments during July.

Treatment ($F_{2,105} = 11.38$, $P < 0.001$), sampling period ($F_{1,105} = 8.74$, $P < 0.01$) and an interaction between treatment and sampling period ($F_{2,105} = 3.41$, $P < 0.05$) affected grass biomass. Grass biomass responded differently between treatments over time and increased between March and July in the kangaroo exclusion plots, but not in the other treatments (Fig. 3c). During the March sampling trip, grass biomass was greater in the Exclude all plots ($P < 0.001$) and Kangaroos excluded treatments ($P < 0.001$) than in the Control plots. Grass biomass did not differ between the Exclude all plots and Kangaroos excluded plots ($P > 0.9$). Treatments did not affect grass biomass during the July sampling trip.

There was an effect of sampling period ($F_{1,105} = 16.67$, $P < 0.001$), but no effect of treatment ($F_{2,105} = 0.15$, $P = 0.55$) or the interaction between treatment and sampling period on forb biomass ($F_{1,105} = 1.95$, $P > 0.1$). Forb biomass increased on all plots between the March and July sampling periods ($P < 0.001$).

3.3. Soil function

Soil bulk density sieved to less than 2 mm differed between treatments ($F_{2,63} = 31.02$, $P < 0.001$) and was lower in the Exclude (all vs. control $P < 0.001$) and Kangaroos excluded (kangaroo vs. control, $P < 0.001$) than in the Control plots where all herbivores had access (Fig. 4a). Soil bulk density did not differ between the Exclude all plots and the Kangaroos excluded plots ($P > 0.5$) (see Fig. 4a).

Water infiltration rate differed between treatments (Fig. 4b; $F_{2,63} = 7.34$, $P < 0.001$). Infiltration rate was greater in the Exclude kangaroo plots than in the Exclude all plots ($P = 0.001$) and Control plots ($P = 0.002$). Water infiltration rates did not differ between Exclude all plots and Exclude kangaroos plots ($P > 0.89$).

4. Discussion

Dung counts and spotlight surveys showed that kangaroos were the

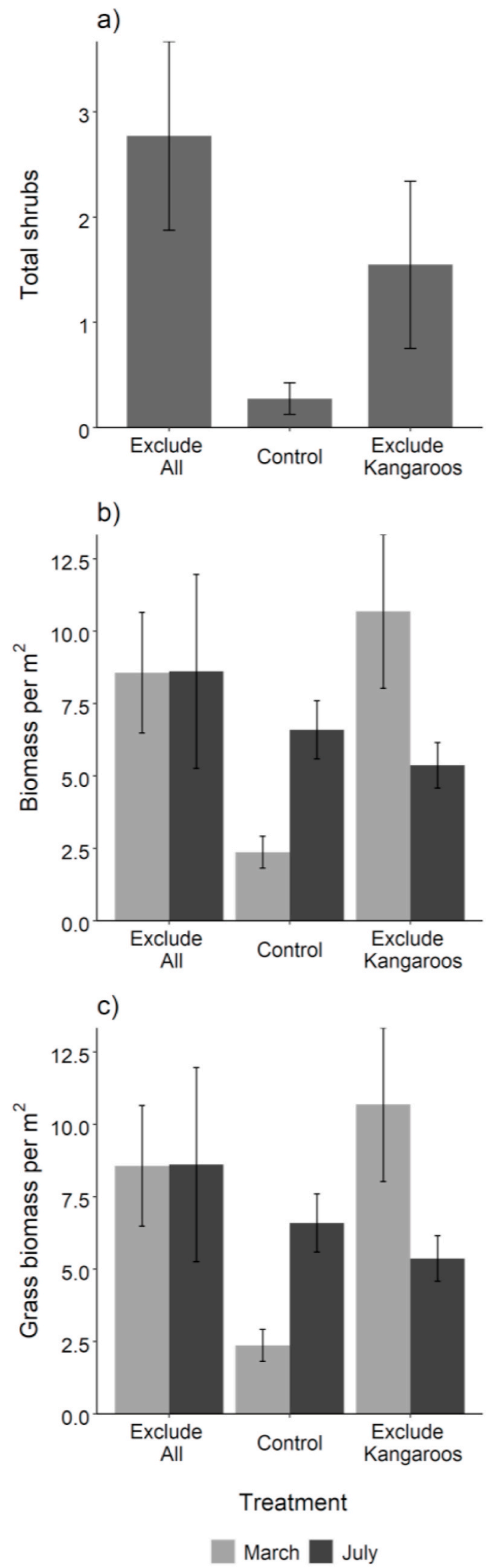

Fig. 3. Mean a) density of woody plants (Total shrubs), b) Total biomass and c) Grass biomass in the exclude all herbivores, exclude kangaroos exclosures and the control plots on each sampling occasion. Density of woody plants (Total shrubs) was assessed in March 2019. Total biomass and grass biomass were assessed in March 2019 and July 2019. Error bars represent ±1 standard error.

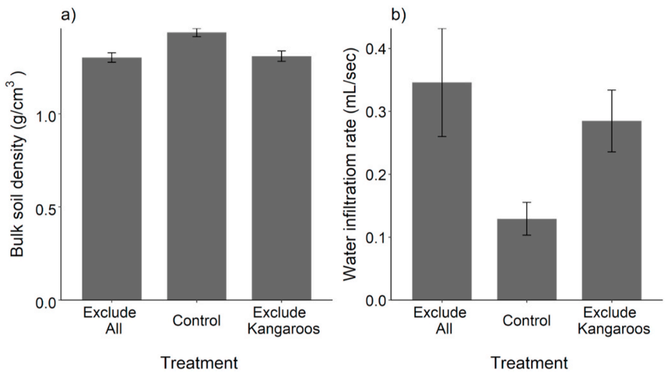

Fig. 4. Mean a) Bulk density (soil < 2 mm) and b) water infiltration rate in plots where all herbivores were excluded, plots where kangaroos only were excluded and grazed control plots where all herbivores had access. Error bars represent ±1 standard error.

most abundant herbivore at Yathong when our study was conducted during a period of average rainfall and just after a period of prolonged drought. Similarly, Leigh et al. (1989) found that rabbits were the most abundant herbivores in the reserve during periods of wet conditions between 1979 and 1984, but kangaroos were the most numerous herbivore during the 1981–1982 drought. Rabbit grazing was linked to a reduced number of woody plant stems while kangaroo grazing was linked to reduced total understorey biomass, grass biomass, soil bulk density and water infiltration rate. Our results provide evidence that grazing by both rabbits and kangaroos adversely affects vegetation and soils in semi-arid ecosystems, but in notably different ways.

The grazing treatment had no effect on forb biomass, however, total biomass and grass biomass responded to the grazing treatment. Both Total biomass (the sum of grass and forb biomass) and grass biomass were greater in the Exclude all and Exclude kangaroos plots in the March sampling trip when conditions were quite dry but did not differ between treatments during the wetter conditions that prevailed during the July sampling trip. The strong suppressive effect of kangaroo grazing on total biomass and grass biomass demonstrated in our study during a period of relatively dry conditions accords with the findings of other studies from arid Australia which have investigated the grazing impacts of kangaroos (Morris and Letnic, 2017; Mills et al., 2020; Norbury and Norbury, 1993; Rees et al., 2017).

Interestingly, Leigh et al. (1989) found that grazing by both rabbits and kangaroos influenced grass biomass, while our results show that only grazing by kangaroos affected grass biomass. The limited effect of rabbits on grass biomass during our study, even though grass is their preferred forage (Leigh et al., 1989) could be due to their low abundance during the dry conditions which prevailed when our study was conducted in combination with a general reduction in rabbit numbers since the introduction of calicivirus in 1996 (Sharp et al., 2001). Our finding that the density of woody plants was greatest in plots from which rabbits were excluded (Exclude all) suggests that grazing by rabbits has limited the recruitment of woody plants in the landscape surrounding the exclosures. This finding is consistent with previous studies showing that rabbits readily consume shrub seedlings, limiting the recruitment of woody plants (Auld, 1995; Cooke, 2012; Lange and Graham, 1983).

Soil bulk density was lower and the rate of water infiltration was greater in the Exclude all herbivores and Kangaroos excluded treatments than in the Controls. This finding suggests that trampling by kangaroos causes soil compaction and diminishes the capacity of soils to absorb water. Taken together with previous studies showing that kangaroo grazing can compact the soil and deplete the soil nutrient pool (Morris and Letnic, 2017; Mills et al., 2020) our study provides evidence that grazing by relatively high-density kangaroo populations can have detrimental effects on soil functions.

Rabbits had little effect on soils and neither water infiltration rate or bulk density differed between the all herbivores excluded treatment and the kangaroo excluded treatment. In contrast, other studies have demonstrated that rabbit grazing is associated with depleted soil nutrients (Eldridge and Koen, 2008) and that water infiltration rates are lower (Eldridge et al., 2017) near rabbit warrens. The absence of a rabbit effect on soils may be related to the low abundances of rabbits and the absence of rabbit warrens near the exclosures at the time of our study.

A potential shortcoming of our study was the design of the exclosure plots. One border of the Exclude all plots and Exclude kangaroo plots was shared and at just 5 m × 5 m they were small in comparison to herbivore exclusion plots used in some other studies (Mills et al., 2020; Morris and Letnic, 2017; Zimmer et al., 2017). Consequently, the exclosure plots we used were very susceptible to edge effects. Nonetheless, the results demonstrated distinct differences in the vegetation and soils of the different treatments consistent with those observed in previous studies investigating the impacts of kangaroo and rabbit grazing in semi-arid and arid regions of Australia (Mills et al., 2020; Morris and Letnic, 2017; Mutze, 2017).

A key finding of our study is that kangaroos and not rabbits were the dominant grazers at Yathong Nature Reserve during the drought conditions which prevailed when the study was undertaken. Indeed, the effects of kangaroos on grass biomass and soil compaction in our study were symptomatic of overgrazing (Allan and Neil, 1991; Eldridge et al., 2016). While it is widely appreciated that kangaroo populations have irrupted across much of semi-arid Australia (Letnic and Ripple, 2017; Newsome, 1975; Pople et al., 2000), their populations are not usually managed in conservation reserves despite the fact that they can have detrimental effects on vegetation and soils (Fisher et al., 2021; Morris and Letnic, 2017; Prowse et al., 2019). However, it is important to consider that our observations were conducted over a brief time-frame during a period of drought while the exclosures had actually been in place for 40 years. Thus, it likely that some of the effects that we report such as those on woody plant density and soil compaction were legacies of the long-term exclosure of herbivores rather than herbivores' effects at the time of the study. Furthermore, it is important to note also, that the effects we report may also be legacies of periods when herbivore densities, particularly rabbit densities, were higher than at the period in time when we conducted our study.

Viewed more broadly, the situation with kangaroo overabundance in semi-arid Australia is paralleled by irruptions of ungulates in other parts of the world. In North America cervid populations have irrupted following the extirpation of wolves (Crête et al., 2001) and the increased grazing pressure has negatively affected over 100 plant species (Côté et al., 2004; Crête et al., 2001). Consequently, measures have been enacted in some conservation reserves to reduce deer population densities and their impacts, including the reintroduction of wolves in Yellowstone National Park (Smith et al., 2003) and culling of deer in Cuyahoga Valley National Park (Dougherty et al., 2003). We contend that as kangaroo effects on vegetation and soils are indicative of overgrazing, it may now be time to consider similar management measures for kangaroo populations in Australia's conservation reserves to mitigate their impacts on ecosystems (Barton et al., 2011; Prowse et al., 2019).

Funding

This research was supported by an Australian Research Council grant to ML and WC (DP180101477).

Data availability statement

Data will be made available through the Dryad Digital Data Repository or through a GitHub repository depending on journal preference.

Author contribution.

J. Braden, C. Mills, H. Waudby, W. Cornwell and M. Letnic conceptualized and designed the study. J. Braden and C. Mills conducted the fieldwork. J. Braden, C. Mills, W. Cornwell and M. Letnic conducted the analyses. J. Braden and C. Mills conducted the data collection and formal analysis. All author contributed to the writing.

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.

Acknowledgements

We would like to thank Alice Si and Laura Lopresti for assistance with fieldwork and staff at NSW National Parks and Wildlife Service for help coordinating field trips.

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