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# Herbivores disrupt the flow of food resources to termites in dryland ecosystems

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## Abstract

Irruption of herbivore populations due to the extirpation of predators has led to dramatic changes in ecosystem functioning worldwide. Herbivores compete with other species for their primary source of nutrition, plant biomass. Such competition is typically considered to occur between species in closely related clades and functional groups but could also occur with detritivores that consume senescent plant biomass. In this study, we tested predictions that in ecosystems where herbivores are not regulated by predators, their indirect impacts on dead vegetation increase with primary productivity and extend to termites that feed on senescent vegetation. We compared dead vegetation cover and termite activity in herbivore exclosures and associated grazed plots at three locations situated along a rainfall gradient in arid Australia where kangaroo populations have irrupted. Dead vegetation cover and termite activity increased with rainfall in ungrazed plots but showed a negligible response to rainfall in grazed plots. Our results suggest that grazing can disrupt the flow of energy to detritivores and decouple the relationship between termite activity and primary productivity. Such disruption could have far-reaching impacts on arid ecosystems because many organisms sit within "brown food webs" that are sustained by energy derived from the decomposition of senescent plant tissues.

**KEYWORDS**
arid, brown food web, competition, detritivores, irruptive herbivores, rainfall gradient, termites

## INTRODUCTION

The populations of many of the Earth's large wild herbivores (body mass >10 kg) have undergone significant changes, with the populations and ranges of some species having declined and others having increased in abundance (Ripple et al., 2015). The removal of predators has been a key factor driving increased abundance of many herbivore species (Estes et al., 2011; Morris & Letnic, 2017). In some regions, deer, kangaroos, and camelids have increased to such an extent that they are considered overabundant (Apollonio et al., 2010; Côté et al., 2004; Letnic & Ripple, 2017; Oliva et al., 2019). Overabundant herbivores can have profound impacts on ecosystems (Forbes et al., 2019; Foster et al., 2014). Perhaps their most readily observed impact is the depletion of plant biomass due to their grazing and browsing (Côté et al., 2004; Fisher et al., 2021). However, herbivores'

impacts on ecosystems can extend to changes in nutrient cycling (Pineiro et al., 2010), soil processes (Mills et al., 2020), the productivity of ecosystems (Frank & McNaughton, 1993), fauna assemblages (Foster et al., 2014; Pringle et al., 2007), and the geomorphology of landscapes (Beschta & Ripple, 2012; Lyons et al., 2018).

Large herbivores compete with other species for their primary source of nutrition: plant biomass. Such interspecific competition is typically considered to occur between species within the same functional guild and between species in closely related clades, such as sympatric mammalian herbivores (Murray & Illius, 2000). However, this focus ignores many important interactions. For example, mammalian herbivores often compete for plant biomass with both arthropod herbivores and decomposer species that are typically considered to be in a different functional guild (Bardgett & Wardle, 2010). By consuming plant biomass, herbivores may suppress the abundance of detritivores by depriving them of carbon and other nutrients (Andriuzzi & Wall, 2017).

Detritivores facilitate the decomposition of plant material and transfer of nutrients through ecosystems (Yang & Gratton, 2014). Studies of herbivores' impacts on arthropod detritivores have primarily been conducted in productive ecosystems such as salt marshes, grasslands, and temperate woodlands and have obtained mixed results. Some studies show that herbivores can have deleterious effects on detritivore abundances due to a reduction in the availability of their food resource (Andresen et al., 1990; Barton et al., 2011; Bressette et al., 2012; Ford et al., 2013). However, other studies show that herbivores can also have positive effects on some decomposer species because their dung is a food resource for some species (Filazzola et al., 2020). Very few studies, to our knowledge, have investigated the link between vertebrate herbivores and invertebrate detritivores in less productive, arid ecosystems (Lagendijk et al., 2016) where plant biomass is sparse and there is considerable potential for detritivores to indirectly compete with herbivores for organic matter (Andriuzzi & Wall, 2017).

Many arid environments are characterized by a high temporal variability in rainfall, which dictates the main limiting factor for plant growth, the availability of moisture (Collins et al., 2014). In arid environments, irregular rainfall events trigger pulses of plant growth, which will henceforth be referred to as green pulses (Figure 1a) (Noy-Meir, 1973). Green pulses are often short-lived due to moisture limitations and the short lifespans of the ephemeral and annual plants that dominate arid plant assemblages (Schwinning & Sala, 2004). Pulses of vegetation growth typically trigger increases in populations of herbivores whose abundances are constrained by the availability of nutritious forage and track fluctuations in

forage availability with a lag time that is dependent on their life-history traits (Caughley et al., 1987; Fisher et al., 2021). Consequently, foraging by herbivores can have marked effects on green pulses when their populations are at the peak of their population cycles but only negligible effects at low points in their population cycles (Augustine & McNaughton, 2006; Choquenot & Forsyth, 2013; McCluney et al., 2012). The fraction of green pulses not consumed by herbivores eventually becomes senescent and creates a pulse of dead vegetation that we hereafter refer to as brown pulses (Figure 1a) (Cebrian, 1999). The brown fraction of the pulse is the biomass of senescent plant material available for consumption by detritivores (Chapin et al., 2002) that provides the energy for the "brown food web" involving detritivores and their predators (Moore et al., 2004).

Over time, as green pulses come and go, senescing vegetation will accumulate, although the biomass available to detritivores might be reduced in situations where herbivores occur at high population densities. We predicted that herbivores would indirectly influence brown pulses and detritivore biomass by reducing the biomass of green pulses (Figure 1a). Following theoretical modeling describing the relationship between herbivore and plant abundances across a productivity gradient in ecosystems with unpredictable rainfall (Choquenot & Forsyth, 2013; Oksanen et al., 1981), we also predicted that with increases in rainfall, greater primary productivity would facilitate higher densities of herbivores whose grazing would increasingly deplete plant biomass along that gradient. By consuming and, in the process, killing plants at the juvenile stage, this grazing decouples the relationship between rainfall and green pulses (Figure 1b) (Choquenot & Forsyth, 2013; Letnic & Ripple, 2017). Given the link between green and brown pulses, a decoupling of the relationship between rainfall and vegetation growth is also expected to decouple the relationships between rainfall and brown pulses and between brown pulses and detritivore activity.

In arid ecosystems, termites are one of the principal arthropod detritivores (Whitford, 2000) and feed on a variety of resources including senescent grasses forbs and coarse woody debris (Donovan et al., 2001). Termites consume the brown fraction of growth pulses. Thus, it is conceivable that they indirectly compete with mammalian herbivores that consume the green fraction of growth pulses. Support of this idea comes from studies of the impacts of large herbivores on termites in the savanna ecosystems of Africa that found that large herbivores can have a negative effect on termite consumption of litter (Buitenwerf et al., 2011; Gosling et al., 2016). However, relatively little is known about the impacts that herbivores have on termites in arid ecosystems (Abensperg-Traun, 1992; Braithwaite et al., 1988; Holt et al., 1996). A study
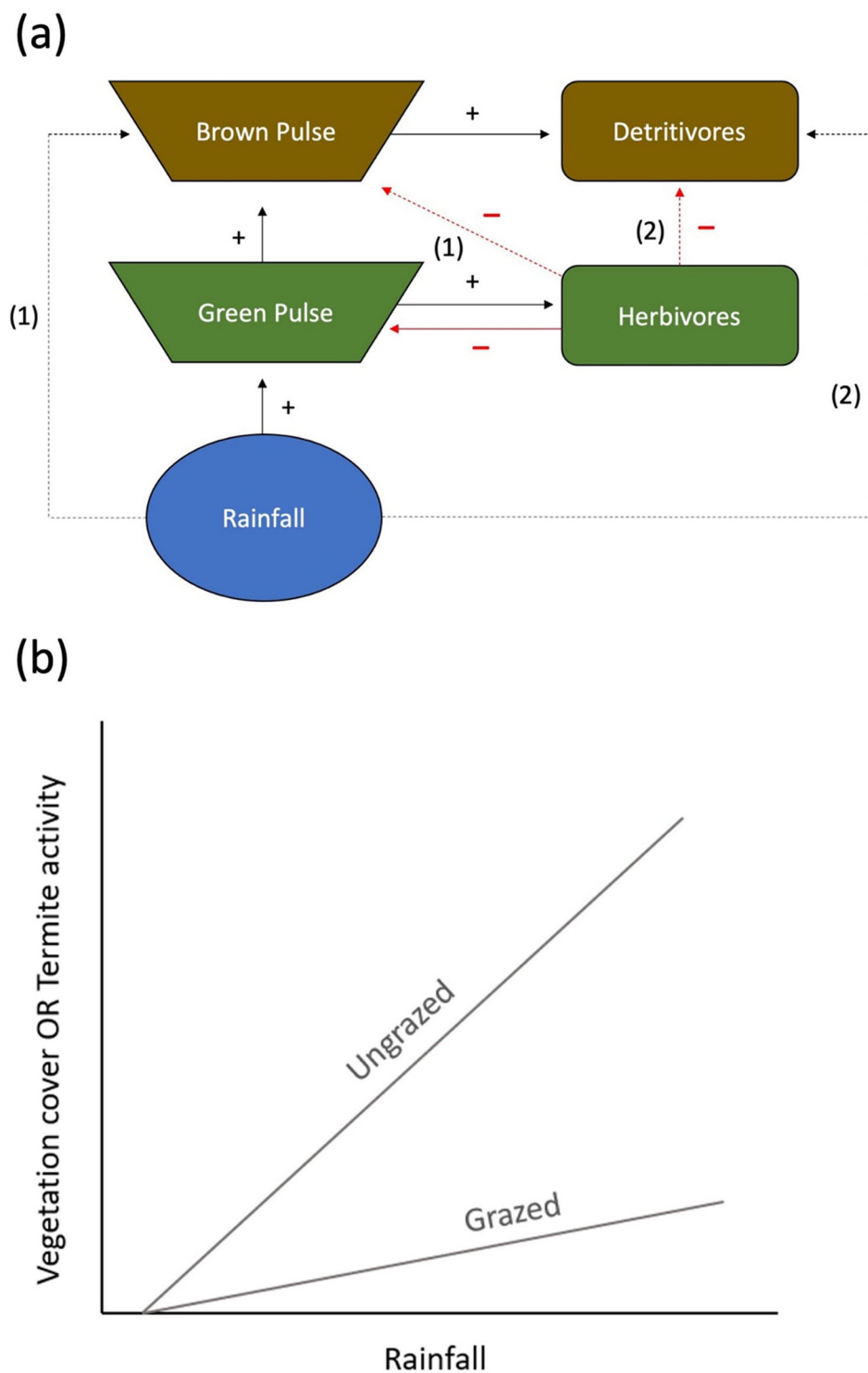
**FIGURE 1** (a) Model of direct (solid lines) and indirect (dashed lines) interactions that determine the size of the green pulse, brown pulse, and detritivore biomass in relation to rainfall and herbivory. The black lines represent positive interactions, while the red lines represent negative interactions. The numbers refer to the hypotheses that we tested. (b) The predicted relationship between vegetation cover or termite activity versus rainfall in ungrazed plots where herbivores are absent and in grazed plots.

from semiarid Australia found that grazing by livestock had little effect on termite abundance and community composition (Abensperg-Traun, 1992), although studies from Australia's tropical savannas have found grazing to have adverse effects on termite abundance and species richness (Braithwaite et al., 1988; Holt et al., 1996).

Here, we assess the impact of herbivory on vegetation cover and termite activity using large herbivore exclusion

plots across three conservation reserves situated along a rainfall gradient in arid Australia. Kangaroo populations have long been considered overabundant following wet periods across much of arid Australia, including in our study region, due to the extirpation of their primary predator, the dingo (*Canis dingo*), as well as the introduction of artificial water points (Caughley et al., 1987; Letnic & Ripple, 2017). In this region, grazing by kangaroos can have marked effects on vegetation, particularly the grasses and forbs on which they primarily feed (Mills et al., 2020; Prowse et al., 2019). Thus, we hypothesized that grazing by kangaroos would dampen or decouple the relationship between rainfall-driven vegetation growth pulses of grasses and forbs that are the main components of their diets (Bailey et al., 1971; Dawson & Ellis, 1994; Griffiths & Barker, 1966) and the activity of detritivorous termites that feed on senescent grasses and forbs and their litter (Wijas, Lim, & Cornwell, 2022). Specifically, we predicted that (1) cover of dead vegetation would increase with rainfall and decline with grazing by kangaroos, (2) termite activity would similarly increase with rainfall and decline with grazing by kangaroos, and (3) kangaroos would dampen the response of vegetation cover and termite activity to rainfall (Figure 1b). Finally, we predicted that termite species composition would differ across herbivore treatments, with grass and litter feeding termites such as *Drepanotermes* spp. being more prevalent inside herbivore exclosures. We focused our measurements of vegetation cover on dead vegetation for two reasons. First, because the green pulse in arid ecosystems is ephemeral and our sampling involved periodic snapshots of vegetation, we considered the response of dead cover to be a better indicator of herbivores' cumulative impacts on vegetation. Second, we focused on dead vegetation cover because this is the primary food resource for termites.

## METHODS

### Study area

The study was carried out at three conservation reserves situated along a semiarid to arid rainfall gradient in southeastern Australia. Because rainfall is linked to primary productivity and plant cover in arid environments, other factors such as soil carbon and soil nitrogen also increase with rainfall, whereas soil phosphorus tends to decrease (Delgado-Baquerizo et al., 2013; Ding et al., 2021; Mills et al., 2020). Temperature is relatively similar across the reserves, with Yathong and Mungo having an average daily temperature of 17°C and Boolcoomatta having an average temperature of 18°C. The sites in order of increasing mean annual rainfall (MAR) were Boolcoomatta Reserve (220 mm MAR), Mungo National Park (280 mm MAR), and Yathong Nature Reserve (360 mm MAR) (Figure 2).

Drought conditions prevailed throughout southeastern Australia during the years preceding our study (Appendix S1: Figure S1). This was evidenced by well below average rainfall at all sites ranging from 101 mm at Boolcoomatta and 128 mm at Mungo to 295 mm at Yathong in the 12 months preceding our study. Yathong and Mungo are managed by a government agency, the NSW National Parks and Wildlife Service, while Boolcoomatta is managed by the non-governmental organization Bush Heritage Australia. No livestock were present on any of the reserves; however, small numbers of feral goats occur on each of the reserves. Soil types varied across the reserves, although exclosures were positioned on similar loamy soils within each reserve.

### Herbivore exclusion experiment

To undertake our experiment at a large spatial scale and obtain relevant ecological information, we had to undertake our experiment across herbivore exclosures that were not originally constructed for this experiment and therefore were built during different years with different dimensions (Appendix S1: Table S1). The herbivore exclosures were constructed with "marsupial mesh" (50 × 50 mm) designed to exclude large herbivores and built at least 10 years ago. The fences of the exclosures were at least 1.6 m in height and thus were tall enough to prevent kangaroos and feral goats from accessing them (Appendix S1: Figure S2). Each herbivore exclosure had an associated control demarcated by four posts within 100 m of it, and both together will be referred to as a block. There were four blocks in Boolcoomatta, eight in Mungo, and three in Yathong. Although vegetation type varied across blocks, it was kept constant within each block. The herbivore exclosures effectively excluded large herbivores such as kangaroos and goats, though at the time of the study goats were rare on each reserve. Rabbits and predators of termites such as echidnas or lizards were able to access the exclosures because the mesh was coarse enough not to impede their movements. Hence, any effect of the exclosures on vegetation or termites was due to the grazing impacts of large herbivores but not those of rabbits or termite predators.

### Vegetation cover

To assess the impact of large herbivore grazing on vegetation cover, we measured ground cover and vegetation cover in each exclosure block in November 2019 and on
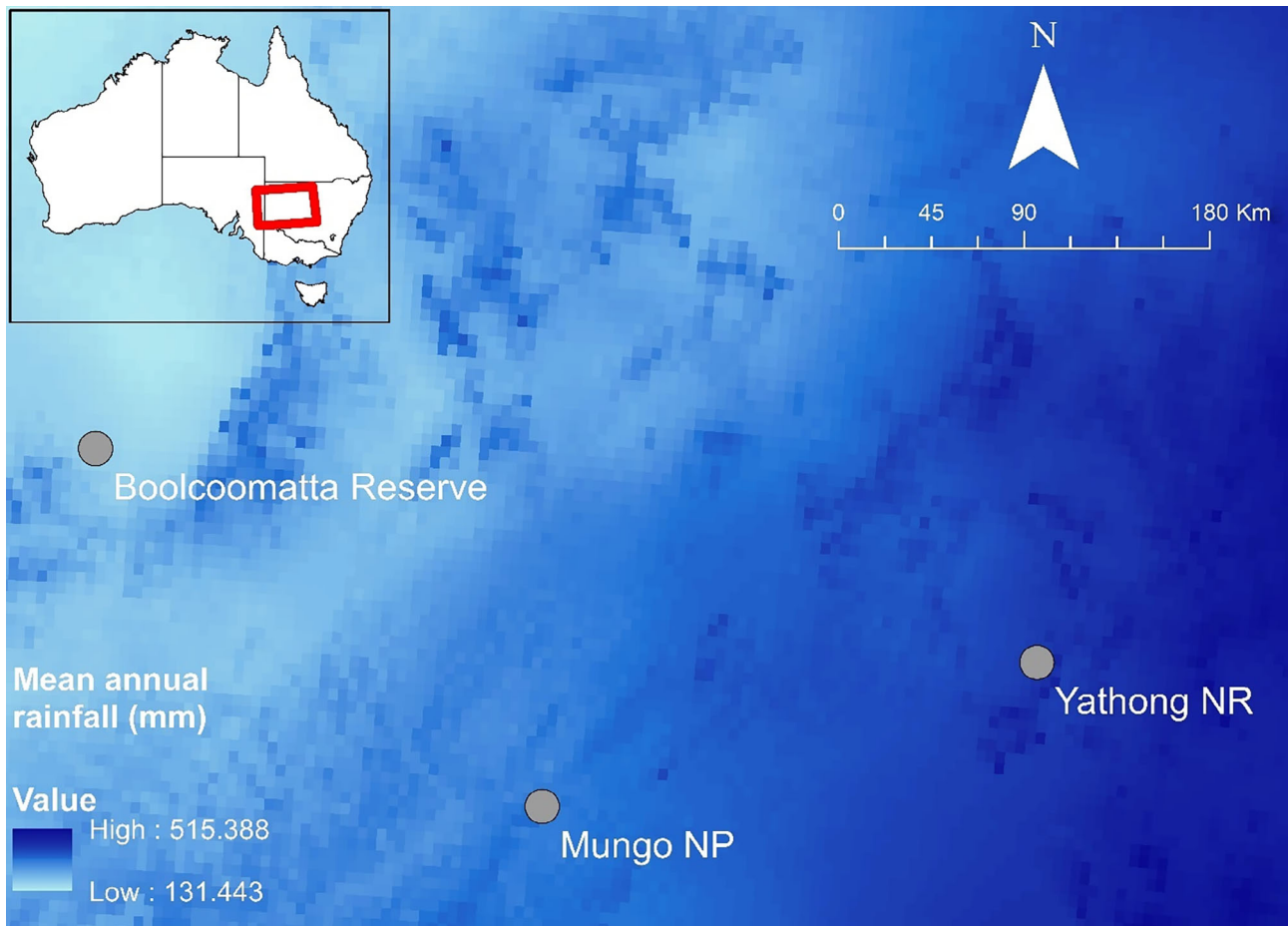
**FIGURE 2**   Map of study sites (gray circles) showing location of Yathong Nature Reserve, Mungo National Park, and Boolcoomatta Reserve and mean annual rainfall. Inset shows location of study region within Australia.

another sampling occasion conducted between March and July 2020 (Appendix S1: Table S1). Vegetation cover was measured using point intercept surveys over a 25 × 25-m area where the type of vegetation was assessed every meter along 25 parallel transects spaced 1 m apart. For the exclosures in Mungo and Boolcoomatta, a random 25 × 25-m area was chosen while for Yathong we sampled the whole 25 × 25-m area. The categories of ground cover and vegetation scored were bare ground, litter, dead forb, and dead grass. For further analysis, we calculated dead vegetation cover as the sum of dead forbs and grasses in addition to litter in each exclosure and its associated control.

## Termite community and activity

Because termites in arid Australia form nests that are typically underground and are thus difficult to locate (Wijas, Lim, & Cornwell, 2022), we used toilet paper rolls as cellulose baits to index termite activity on each plot (Davies et al., 2021). In November 2019, we deployed

12 toilet paper rolls (400 sheet rolls, unscented and unbleached) to index termite activity in each plot. The rolls were set out in three rows spaced 10 m apart, with four rolls spaced 5 m apart in each row. Due to COVID-19-related restrictions on our movements, the toilet paper rolls were collected at different times within each reserve as specified in Appendix S1: Table S1 within a maximum deployment period of 7 months. On collection, we visually estimated the percentage of toilet paper consumed from each roll and calculated the average for each plot to quantify the activity of termites (Coggan et al., 2016).

In addition to measuring the activity of termites, we assessed the termite species composition of each exclosure and control by extracting soldier specimens from the toilet paper rolls when these were collected and by actively searching for termites through the digging of trenches in November 2019. We set out two crossing diagonal 30-m transects in each exclosure and dug out 10 × 10 × 10-cm pits every 2 m along each transect and searched for live termites for 1 person min at each pit. If live termites were found, we collected a specimen from the soldier caste to identify the termite species.

We identified the termite specimens collected to species level using species identification keys and taxonomic description papers (Gay, 1968; Hill, 1942; Watson & Perry, 1981) and by comparing our specimens to referenced specimens in the Australian National Insect Collection. We recorded the number of times each species was found in a pit or on toilet paper bait and used the relative abundance of each species within each plot for further analysis.

## Herbivore abundances and grazing pressure

To index herbivore densities in the vicinity of the exclosures in each reserve, we carried out diurnal surveys on each sampling occasion. The diurnal surveys were carried out in the late afternoon, which is when the excluded herbivores, kangaroos and goats, could be readily observed. The surveys were carried out from a vehicle moving at 15 km/h, and fauna within 100 m of the road were recorded. During each sampling period at each site, we undertook one to four surveys from 4.5 to 32 km, amounting to a total of 23.8 to 45.9 km of diurnal surveys depending on the sampling period and site. To compare abundances across reserves, we averaged the total abundance of animals sighted per kilometer across the two sampled periods.

To measure the relative grazing pressure of different herbivore species, we walked along three 100-m transects around each block and recorded the presence or absence of dung every meter to species or genus for kangaroos. For this study, the different kangaroo species were grouped into one category as we wanted to assess the overall impact of kangaroo herbivory on the ecosystem. As the dung counts were carried out over 100-m transects, we converted these to percentages. For further analysis, we calculated the percentage of dung encountered across the three 100-m transects around each block on each sampling occasion.

## Analysis

To account for grazing pressure and vegetation change over the period during which the termite baits were in the ground, we averaged rainfall in the past 12 months, percentage dung cover, herbivore density counts, and dead vegetation cover over the two sampling periods.

To assess grazing pressure, we ran generalized linear mixed-effects models using the lme4 package in R (Pinheiro et al., 2017), with average percentage dung encountered as a response variable against the fixed factors site and species. Given the nature of the count data

for the dung surveys, we rounded the percentage values to the closest integer and applied a Poisson distribution to our model. Block was specified as a random factor to account for the difference in vegetation types across the rainfall gradient.

To assess the impact of large herbivore grazing on available resources for termites and termite activity, we ran linear mixed-effects models for dead vegetation cover and for monthly toilet paper consumed as response variables. The fixed predictor variables were average rainfall in the past 12 months, herbivore exclusion (ungrazed/grazed), and their interaction. Block was specified as a random factor to account for the variance in vegetation cover and termite activity across different plots. To investigate the relationship between resource availability and termite activity, we ran a linear mixed model with bait consumption as a response variable and dead vegetation cover as an explanatory variable. Site was included as a random factor.

To assess the difference in termite species composition across the different herbivore treatments, we used a multivariate generalized linear model fitting a Poisson distribution. We used the model-based approach from the mvabund package in R (Wang et al., 2012), with average rainfall in the past 12 months, herbivore exclusion, and their interaction as explanatory variables. The relative abundance of each termite species was used as a response variable. We only included species that were observed at more than one site to increase model accuracy. We tested for significance with a threshold alpha $= 0.05$ through an ANOVA with likelihood ratio tests and Monte Carlo resampling with 999 samples.

## RESULTS

Kangaroos were the most abundant herbivore at each reserve (Figure 3a). Goats were observed at Mungo and Boolcoomatta, but their abundance was less than 10% of that of kangaroos at these sites (Figure 3a). Kangaroo dung was the dung type most frequently encountered in dung surveys at all sites (Appendix S1: Table S2, Figure 3b).

The cover of dead vegetation increased with mean annual rainfall on both grazed and ungrazed plots (Table 1). However, the response exhibited by dead vegetation cover to rainfall was muted on grazed plots (Table 1, Figure 4).

Bait consumption in ungrazed plots increased with rainfall but showed a negligible response to rainfall in grazed plots (Table 2, Figure 5). Bait consumption increased with dead vegetation cover (Appendix S1: Figure S3, Table S3). We found termites from five genera that feed on a variety of substrates, including grass, dung, wood, and litter (Appendix S1: Table S4). The species of termites we most
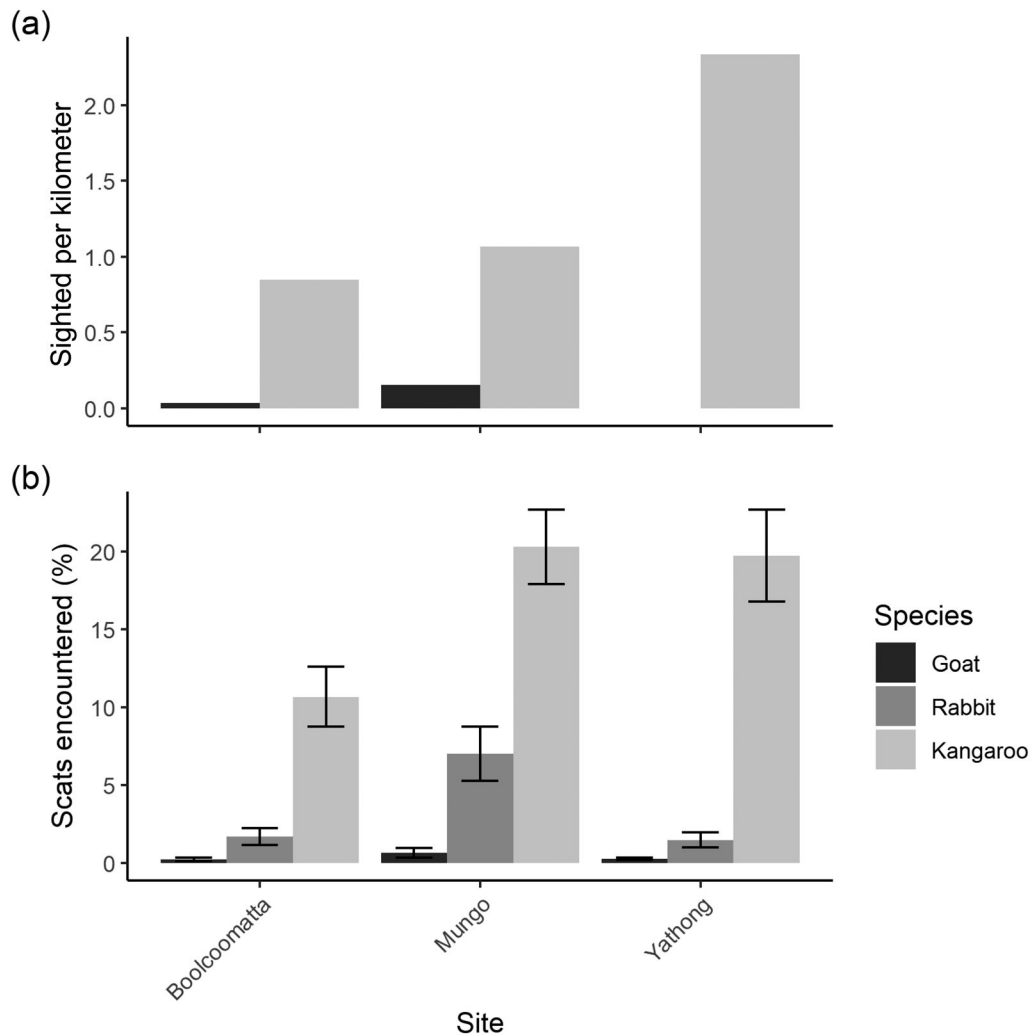
**FIGURE 3** (a) Average number of herbivores sighted per kilometer between the two sampling periods across the three study sites during diurnal surveys and (b) average percentage dung encountered ($\pm 1$ SE) along dung surveys across the three study sites. The sites are arranged in order of increasing mean annual precipitation.

**TABLE 1** Model output of linear mixed-effects models for total vegetation cover, live vegetation cover, and dead vegetation cover against rainfall, herbivore treatment (grazed/ungrazed), and their interaction.

| Predictor | Estimate | CI | $p$ |
|---|---|---|---|
| Intercept | 6.58 | −8.54 to 21.70 | 0.367 |
| Rainfall | 0.10 | 0.02 to 0.18 | **0.021** |
| Treatment (ungrazed) | −4.55 | −13.92 to 4.82 | 0.325 |
| Rainfall:treatment (ungrazed) | 0.06 | 0.00 to 0.11 | **0.036** |

*Note*: *p*-values in bold are significant. The insignificance of the intercept values indicates that the fitted lines for grazed plots may intersect with 0. Random effects: $\sigma^2 = 16.17$, $\tau_{00\ \text{set}} = 67.95$, ICC = 0.81, $N_{\text{set}} = 14$. Observations = 28; conditional $R^2 = 0.897$.

encountered included *Heterotermes ferox* ($n = 55$), *Amitermes germanus* ($n = 22$), *Amitermes colonus* ($n = 13$), and *Drepanotermes perniger* ($n = 10$). There was no difference in termite community composition across the rainfall gradient ($\text{LRT}_{1,26} = 22.46$, $p = 0.087$) and across herbivore exclusion treatments ($\text{LRT}_{1,26} = 11.54$, $p = 0.37$), and there was no interaction between rainfall and herbivore treatment ($\text{LRT}_{1,26} = 7.05$, $p = 0.43$).

## DISCUSSION

Our results provide evidence that in areas where large herbivores are very abundant in more productive drylands, they can disrupt the flow of food resources to detritivores by limiting the accumulation of senescent plant material. In accordance with Hypothesis 1, the cover of dead vegetation cover increased with rainfall, but the response was lower on grazed than ungrazed plots. In accordance with Hypothesis 2, termite activity
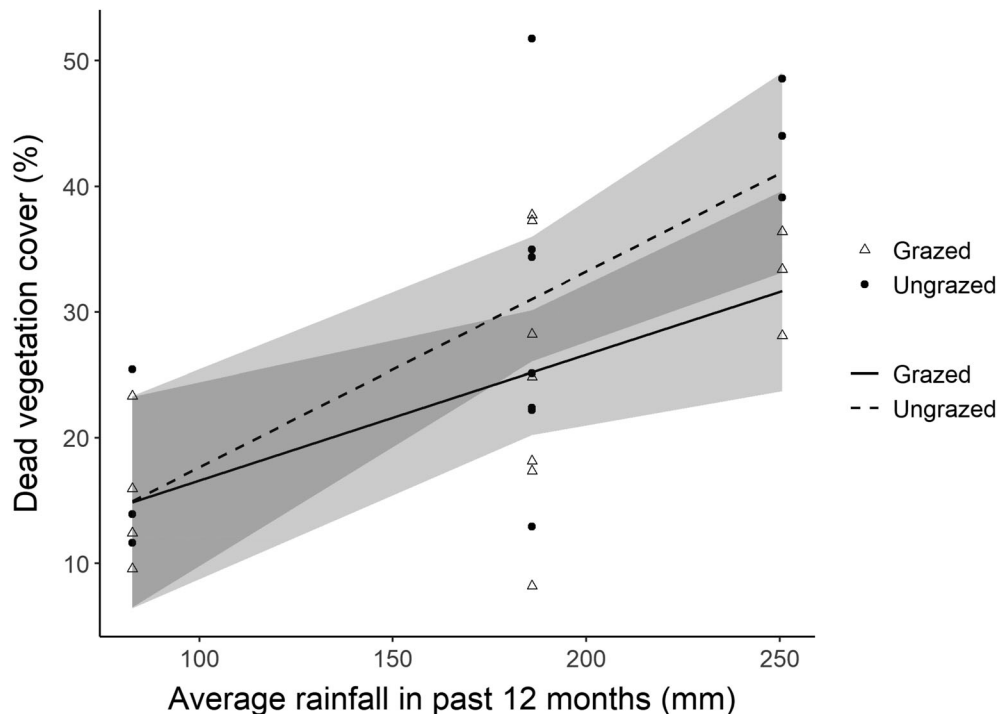
**FIGURE 4** Percentage cover of dead vegetation within grazed (open symbols) and ungrazed plots (solid symbols) plotted against average rainfall in the past 12 months. The solid and dashed lines (±95% CI) represent fitted values from the linear mixed effects models for percentage cover in grazed and ungrazed plots, respectively.

**TABLE 2** Model output of linear mixed-effects models for termite bait consumption against rainfall, herbivore treatment (grazed/ungrazed), and their interaction.

| Predictor | Estimate | CI | p |
|---|---|---|---|
| Intercept | 1.24 | −1.17 to 3.65 | 0.297 |
| Rainfall | 0.00 | −0.01 to 0.02 | 0.642 |
| Treatment (ungrazed) | −2.44 | −5.13 to 0.24 | 0.073 |
| Rainfall:treatment (ungrazed) | 0.02 | 0.00 to 0.03 | **0.014** |

Note: p-values in bold are significant. The insignificance of the intercept values indicates that the fitted lines for grazed plots may intersect with 0. Random effects: $\sigma^2 = 1.33$, $\tau_{00\ set} = 0.81$, ICC = 0.38, $N_{set} = 14$. Observations = 28; conditional $R^2 = 0.592$.

was greater as rainfall increased, but their activity was reduced in plots where herbivores were present. In accordance with Hypothesis 3, we found that the response of dead vegetation cover and termite activity to rainfall was dampened by kangaroo grazing. In what follows, we discuss our results in the context of previous studies on herbivores' impacts on ecosystems and our rainfall-vegetation pulse model (Figure 1a).

The arid landscapes of southeastern Australia are used predominantly for livestock grazing, except for a few protected areas managed by state governments and non-government organizations (Bryan et al., 2016). These

protected areas function as refuges from livestock grazing, but the threat of overgrazing may persist if there are high densities of wild herbivores (Mills et al., 2020; Prowse et al., 2019). The wild herbivores in our study region were kangaroos (*Osphranter rufus*, *Osphranter robustus*, *Macropus giganteus*, *Macropus fuliginosus*), rabbits, and feral goats. Diurnal surveys and dung count data indicate that the grazing effects we report were due predominantly to kangaroos, as goats were in lower numbers than kangaroos in each of the reserves at the time of the study.

Consistent with previous studies from arid Australia where kangaroo populations have irrupted, our results show that grazing by kangaroos suppressed vegetation cover (Mills et al., 2020; Rees et al., 2017). However, because kangaroos prefer to feed on living vegetation (Dawson, 2012), our interpretation of the finding that kangaroos suppressed dead vegetation cover is that grazing by kangaroos limited the accumulation of senescent plant biomass. This could have occurred because living plants inside of the exclosures were less likely to have been grazed upon by kangaroos and these plants were subsequently able to senesce (Jaman et al., 2022). We contend that the grazing impact of kangaroos increased along the rainfall gradient because the potential for vegetation growth increased with moisture availability, and this higher productivity allowed the landscape to support a higher density of kangaroos (Cairns & Grigg, 1993;
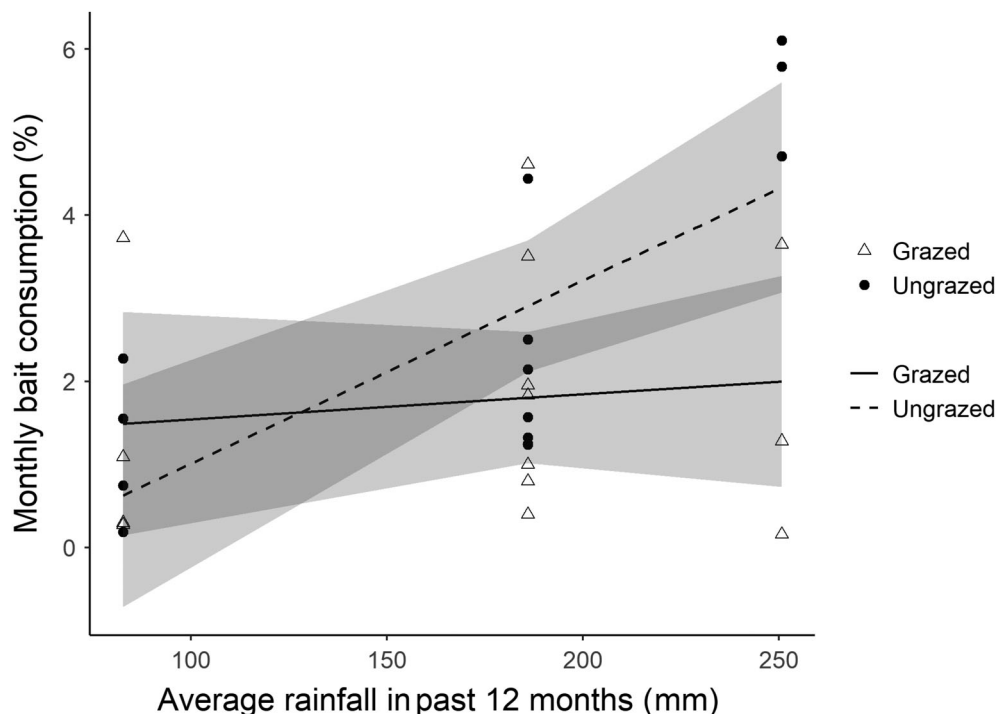
**F I G U R E 5**  Bait consumption by termites in grazed (solid symbols) and ungrazed plots (open symbols) plotted against average rainfall in the past 12 months. The solid line and dashed lines (±95% CI) represent fitted values from the linear mixed-effects models for percentage of bait consumed by termites in grazed and ungrazed plots, respectively.

Caughley et al., 1984; Letnic & Crowther, 2013). As kangaroo abundance increased, we speculate that their impact on dead vegetation cover increased due to higher grazing pressure on green plant tissues (Choquenot & Forsyth, 2013; Oksanen et al., 1981), which in turn hindered the senescence of plant material. The drought conditions during our study may have emphasized the influence of herbivores on vegetation compared with wetter periods, but it is important to note that prolonged periods of dry conditions and associated periods of intensive grazing by herbivores are not unusual in arid Australia (McCluney et al., 2012; Morton et al., 2011).

Similar to their impacts on dead vegetation cover, kangaroos had an increasingly strong influence on termite activity along the rainfall gradient. This was evidenced by the fact that the site with the highest rainfall had the greatest difference in bait consumption between grazed and ungrazed plots. This trend in termite activity in relation to rainfall mirrored the effect that grazing by kangaroos had on dead vegetation cover and is consistent with studies showing that termite activity increases along with soil moisture (Abensperg-Traun, 1991; Mackay et al., 1986). We contend that as mean annual rainfall increased, kangaroos consumed an increasingly larger proportion of the green growth pulse before it had the opportunity to senesce and, therefore, become available as a food resource for termites. This decoupling of the termite

response to rainfall when kangaroos were present suggests that the availability of senescent plant material is a limiting factor for termites in arid environments. In addition, the similarity in termite species composition across treatments suggests that the lower termite activity in grazed sites was due to lower termite biomass rather than a shift in the composition of termite assemblages. While most termite species in our study area also feed on dung (Wijas, Lim, & Cornwell, 2022), our results suggest that as rainfall increases, the addition of excreta from herbivores is not enough to compensate for the reduction in senescing vegetation biomass due to grazing pressure.

Our results contrast with results from cold unproductive ecosystems where herbivores have been found to increase detritivore abundances (Tuomi et al., 2019). In unproductive cold ecosystems, it has been found that high herbivory pressure occurring outside the growing season leads to a reduction in perennial vegetation cover, favoring palatable vegetation growth during the growing season, which enhances detritivore activity. In addition, it has been found that dung and urine from herbivores enhance the growth of palatable plants, which also indirectly favors detritivores (Olofsson, Strak, & Oksanen, 2004; Olofsson et al., 2014). In contrast to cold unproductive ecosystems, we contend that in our study region, detritivore abundance is suppressed by grazing because primary productivity is so low, particularly

during dry periods, that there is little opportunity for senescent plant biomass to accumulate. This is because most of the photosynthetically active vegetation is consumed by herbivores before it can senesce.

A potential shortcoming of our study was that we made use of long-standing herbivore exclosures that were built at different times and that were not specifically designed for our experiment. Thus, a potential confounding factor affecting our experimental design was that the exclosures at the most arid site were also the most recently built. However, we think it is unlikely that the patterns in vegetation cover and termite activity that we attribute to a gradient in rainfall and primary productivity were due to exclosure age. Our reasoning for this is that rainfall-driven boom/bust dynamics are the principal driver of the dynamics of the annual grasses and forbs that kangaroos primarily eat in our study region (Noy-Meir, 1973; Reynolds et al., 2004). Across the region, rainfalls trigger the growth of grasses and forbs that, if not eaten by herbivores, gradually decay due to consumption by termites and breakdown by other factors such as physical breakdown by wind, photodegradation, and fungi (Okin, 2010). Therefore, we would expect that any effects of kangaroos on vegetation would be observed rapidly after the construction of the exclosures, and, given that the youngest exclosures were built over 10 years ago, there would have been ample time for several boom and bust cycles of vegetation growth to occur.

To conclude, our results provide evidence that mammalian herbivores may indirectly compete with and suppress the activity of detritivores in arid environments by limiting the accumulation of senescent plant biomass and in so doing disrupt the development of brown pulses. We hypothesize that consumption of plant biomass before it has the opportunity to senesce by overabundant herbivores may disrupt the functioning of brown food webs that involve decomposers and their predators (Moore et al., 2004; Wijas, Finlayson, & Letnic, 2022). Such disruption in brown food webs could have far-reaching impacts on arid ecosystems, especially during drought periods, because many organisms either directly or indirectly rely on the energy and nutrients provided by the decomposition of senescent plant biomass. For example, in arid ecosystems termites are important prey for many vertebrates (Abensperg-Traun, 1994; Pianka, 1986). We recommend that further studies be undertaken to understand the indirect effects that the disruption of brown food webs by overabundant herbivores has on the functioning of arid ecosystems.

## AUTHOR CONTRIBUTIONS

Baptiste J. Wijas and Mike Letnic conceived the ideas and designed methodology. Baptiste J. Wijas collected the data, analyzed the data, and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Wijas, 2023a) are available in Dryad at https://doi.org/10.5061/dryad.cz8w9gj5f. R script (Wijas, 2023b) is available in Zenodo at https://doi.org/10.5281/zenodo.7353143.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.