

Recent grazing reduces reptile richness but historic grazing filters reptiles based on their functional traits

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Abstract

1. Grazing by mammalian herbivores can alter vegetation structure and composition. It can therefore affect critical habitat features used by native wildlife for shelter, feeding, and breeding. This can have variable effects, which advantage or disadvantage particular species, depending on habitat requirements.
2. We tested the relative effects of recent and historic livestock grazing and recent rabbit and kangaroo grazing on all reptiles, and on specific groups of reptiles based on three functional traits: habitat preference (semi-arboreal, terrestrial, fossorial), activity pattern (diurnal, nocturnal), and primary foraging habitat (tree, litter, open).
3. We used structural equation modelling to assess the direct and indirect impacts of mammalian herbivores (livestock, and free-ranging kangaroos and rabbits) on reptile richness at 108 semi-arid woodland sites in eastern Australia. We used a trait-based approach to classify reptiles according to their: (a) habitat preference, (b) activity pattern, and (c) foraging preference.
4. We recorded 42 reptile species from 1,736 specimens caught over 13,824 trap nights. Sites grazed by rabbits were associated with greater richness of semi-arboreal species. Kangaroo grazing had virtually no effects on total richness or richness within trait groups. The effects of recent and historic livestock grazing differed among reptile trait groups. Increasing intensity of recent livestock grazing reduced the richness of most reptile groups directly, and indirectly suppressed the positive effect of native plant richness on reptile richness. The effects of historic livestock grazing, however, filtered reptiles based on their traits, reducing the richness of tree-shrub foraging reptiles only. Increasing woody cover had direct suppressive effects on all reptiles, but particularly open foragers and terrestrial species. Overall, the effects of recent livestock grazing were stronger than those of plant richness or woody cover.
5. *Synthesis and applications.* We demonstrate how grazing by all herbivores, both domestic and free-ranging, needs to be managed according to seasonal conditions in order to meet the conservation needs of semi-arid reptiles within landscapes dominated by livestock.

KEYWORDS

functional traits, grazing, herbivores, livestock, lizards, reptiles, skinks, species richness

1 | INTRODUCTION

The impacts of grazing on biodiversity are complex and typically span multiple spatial and temporal scales (Fischer, Lindenmayer, & Cowling, 2004; Olff & Ritchie, 1998). Grazing alters a number of fine-scale habitat features and food resources by increasing bare ground (Eldridge, Delgado-Baquerizo, Travers, Val, & Oliver, 2017), promoting woody plant cover and shifting vegetation composition and structure (Yates, Norton, & Hobbs, 2000). Grazing can also substantially reduce ecosystem resilience and can indirectly alter the response of wildlife to disturbances such as fire (Kutt & Woinarski, 2007) or drought (Howland, Stonjanovic, Gordon, Fletcher, & Lindenmayer, 2014). Several studies have highlighted the legacy effects of historic grazing on fauna, which can be vastly different to recent grazing effects (Kay et al., 2017).

The impact of grazing on faunal assemblages often depends on both the species and the configuration of land use across the landscape (Thompson, Nowakowski, Justin, & Donnelly, 2016). Grazing is generally known to benefit species that are adapted to open habitats and impact species that prefer denser vegetative cover (Schieltz & Rubenstein, 2016). Different species traits such as body size, diet preference, and activity patterns have been used to predict whether a given species or groups of species will perish or persist in a heavily grazed landscape. The complex interactions among grazing and faunal traits are poorly understood and occasionally the observed relationships and trends are somewhat unexpected. For example, grazing by domestic livestock has been shown to increase the abundance of nocturnal geckos (Donihue, Porensky, Fofopoulos, Rigionos, & Pringle, 2013) and spiders (Paschetta et al., 2013). These types of observations of species allow for simple connections to be made between common species traits and expected species responses in terms of their response to grazing. Despite clear links between grazing and some animal species, we lack a comprehensive understanding of the mechanisms by which grazing leads to changes in faunal diversity, particularly across large regional scales.

Australia's semi-arid regions support some of the richest assemblages of reptiles globally with high levels of endemism. These regions also have a relatively short (~230 years) history of grazing by domestic livestock. These make for an ideal system to explore the impacts of overgrazing on reptiles. Reptiles exhibit diverse responses to grazing-induced changes in ecosystems (Attum, Eason, Cobbs, & Baha El Din, 2006), and these are most pronounced in arid and semi-arid environments (Schieltz & Rubenstein, 2016). The broadscale distribution of reptiles in drylands is often strongly aligned with regional patterns in vegetation (Hughes, 2003). At the site or community level, however, reptile distribution is more strongly aligned with microhabitat features that are important for thermoregulation, foraging, nesting, and refuge (McElhinny, Gibbons, Brack, & Bauhus, 2006). These fine-scale habitat features are most often heavily affected by grazing, with recent grazing activity (i.e. over the past decade) often driving changes in vegetation community composition, and to a lesser extent, soil surface features such as the cover of litter or bare soil. Longer term historic grazing, however, is more likely to affect soil structure and nutrients

(Eldridge et al., 2017) and woody plant cover by removing germinants and therefore altering the rate of recruitment (Tiver & Andrew, 1997). Unlike the effects of recent grazing on plant community composition, the legacy effects of grazing are difficult to reverse. Understanding, therefore, the relative effects of current and historic grazing on reptiles is important if we are to predict outcomes for wildlife in response to different management actions.

In this study, we examined the impacts of grazing by different herbivores on reptile richness in semi-arid woodland sites over 0.4 million km² of eastern Australia. Our objectives were to test the relative effects of recent and historic livestock grazing, and recent rabbit and kangaroo grazing on reptiles and on specific groups of reptiles based on three functional traits: (a) habitat preference (semi-arboreal, terrestrial, fossorial), (b) activity pattern (diurnal, nocturnal), and (c) primary foraging habitat (tree/shrub, litter, open). Trait based analyses allowed us to examine the relationships between grazing and different groups of reptiles based on their needs for particular substrates or habitat features for sheltering, foraging, and thermoregulation.

We had two hypotheses. First, we expected that any effects of grazing would differ among different types of herbivores (i.e. livestock vs rabbits vs kangaroos; recent vs historic livestock grazing) and the functional traits of reptiles linked to habitat preference, activity pattern, and foraging preference (Hypothesis 1). These responses are consistent with the known effects of grazing on habitat structure (Yates et al., 2000) and resulting effects on reptiles with different requirements for foraging or habitat, for example more litter (Brown, 2001) or bare soil, for example for thermoregulation (Frank, Dickman, Wardle, & Greenville, 2013). Second, we expected that the mechanisms underlying any herbivore effects on reptiles would be indirectly mediated by changes in environmental conditions, specifically litter, bare soil and woody plant cover, and native plant richness (Hypothesis 2). We explored these direct and indirect effects using structural equation modelling (SEM). Thus, livestock could physically alter reptile behaviour and therefore richness (Smith, Arnold, Sarre, Abensperg-Traun, & Steven, 1996) whereas the effects of smaller-bodied herbivores such as rabbits would likely be indirect via habitat alteration. Reptile assemblages might also be influenced by legacy effects of historic livestock grazing that alter woody plant cover (Tiver & Andrew, 1997). In contrast, we might expect recent livestock grazing effects would be related more to changes in plant composition (Travers, Eldridge, Dorrrough, Val, & Oliver, 2018) or native plant richness (Valentine, Roberts, & Schwarzkopf, 2007). Understanding how different herbivores, and recent and long-term livestock grazing can directly and indirectly affect reptile assemblages *via* their functional traits allows us to better understand how grazing drives changes in faunal diversity across spatial and temporal scales.

2 | MATERIALS AND METHODS

2.1 | The study area

The study area spanned 0.4 million km² of eastern Australia in central and western New South Wales. We surveyed 108 sites in total, which comprised 36 sites in each of three broad vegetation

communities dominated by either *Callitris glaucophylla* (Joy Thomps. and L. A. S. Johnson), *Eucalyptus largiflorens* (F. Muell), or *Eucalyptus camaldulensis* (Dehnh). Mean annual rainfall ranges from 385 to 460 mm, and average annual temperature is $\sim 18^{\circ}\text{C}$ and varied little across the study area. Soils are dominated by clay loams and loams. Sites were selected from a total pool of 451 where vegetation, soils, and grazing intensity data had previously been collected (Eldridge et al., 2017; Travers et al., 2018). Sites were selected to span the available range of grazing intensities (see below) and habitat conditions (i.e. groundstorey plant, woody plant, and litter cover; further details in Supporting Information Appendix S1).

2.2 | Assessment of habitat and grazing intensity data

At each site we positioned a 200 m long transect, which formed the central axis of the 2 ha survey plot (200 m \times 100 m). Along the transect we assessed the projected crown cover of trees (>4 m tall) and shrubs (>0.5 m) every 2 m. We placed five 25 m² (5 m \times 5 m) quadrats (hereafter “large quadrat”) every 50 m (i.e. 0, 50, 100, 150, and 200 m) along the transect. Within each large quadrat we centrally nested a smaller (0.5 m \times 0.5 m) quadrat (hereafter “small quadrat”). In each large quadrat we identified all plant species and assessed the cover of litter and bare soil. Site-level richness of native plants was calculated, and the cover of litter and bare soil averaged across the five large quadrats.

Grazing was assessed using measures of recent and historic grazing pressure. To assess historic grazing, we measured the width and depth of all livestock tracks crossing the 200 m transect to calculate the total cross-sectional area (cm²/200 m). To assess recent grazing, we counted dung pellets of different herbivores in both the small and large quadrats, separately, for each type of herbivore. Dung and pellet counts have been used widely to estimate the abundance of large herbivores including Eastern Grey Kangaroos (*Macropus fuliginosus*; Johnson & Jarman, 1987) and the accumulation of dung by sheep has been shown to be a highly reliable method of assessing paddock stocking differences (Lange & Willcocks, 1978). Kangaroo (*Macropus* spp.), “rabbit” (i.e. rabbits and hares; *Oryctolagus cuniculus* L. and *Lepus europaeus* Pallas), and “sheep” (which included sheep *Ovis aries* L., and goats *Capra hircus* L.) dung pellets were counted in the small quadrats, and cattle dung (*Bos taurus* L.), sheep, rabbit, and kangaroo dung pellets were counted in the large quadrats. Dung samples from each site were collected, oven dried at 60°C, and weighed to estimate the mass of individual pellets, or in the case of cattle, dung events. The average mass of dung was then used to calculate the total mass of each type of dung per hectare for each herbivore (see Eldridge et al., 2017). For this study we combined dung data from cattle and sheep into a single category (“livestock”). Dung mass was highly variable among communities (CV%: M: 136.4; range: 38.7–300 (Supporting Information Table S1)).

2.3 | Reptile surveys

Each site was surveyed over four consecutive days and nights over the 2014–2015 Austral summer during periods when reptiles were most active. Three survey methods (pitfall trapping, funnel trapping, and timed diurnal active searches) were used at each site to assess the reptile assemblage, and multiple sites sampled during the same period. Active searching (two periods of 30 min) of leaf litter, logs, rocks, bark, and other ground debris was undertaken in mid-morning or early afternoon, avoiding the hottest periods when reptile activity is often suppressed. Two types of pitfall traps were used, 20 L buckets (400 mm \times 290 mm) and PVC pipes (150 mm \times 600 mm) to maximise captures since the trapability of some families of reptiles differs between buckets and pipes (Thompson, Thompson, & Withers, 2005). Sixteen pitfall traps were arranged in four arrays at each site, each array 50 m apart, positioned near the 50, 100, 150, and 200 m locations on the 200 m transect. Each trap array consisted of four pitfall traps positioned 5 m apart, with an alternating bucket and pipe arrangement. A fibreglass flywire drift fence (30 cm \times 25 m) was erected at each array to direct animals towards the pit traps.

2.4 | Statistical analyses

Reptile data were combined over all sampling methods, dates, and sites ($n = 108$) to provide a measure of total richness and richness within nine functional groups (Table 1). This resulted in four analyses, one for each of the following datasets: (a) all reptiles combined, (b) habitat preference (semi-arboreal, terrestrial, fossorial), (c) activity pattern (nocturnal, diurnal), and (d) foraging preference (tree, litter, open).

Structural equation modelling (Grace, 2006) was used to obtain a systems level understanding of the effects of grazing and four environmental variables on the richness of reptiles within the three trait groups (Figure 1). Unlike ANOVA, SEM takes into account the effects of all other variables (such as the cover of bare soil cover, litter and woody plants, and native plant richness) when considering the direct relationship between grazing and reptile richness. The number of sites in this study ($n = 108$) meant that we had to be prudent in our selection of grazing and habitat predictors to include within the SEM. First, we combined cattle and sheep dung into one attribute (livestock) as these herbivores are “managed” and their effects on plants and soils are relatively similar, unlike residual, free-ranging herbivores (kangaroos and rabbits), which vary markedly in their ecosystem effects (Eldridge et al., 2017; Travers et al., 2018). Second, we restricted the number of habitat predictors in our models to four measures. We selected (a) tree and shrub cover (henceforth “woody cover”) as this could be influenced by long-term historic grazing effects and would be an important habitat structure for semi-arboreal and tree foraging reptiles; (b) native plant richness, as this is strongly influenced by both recent and historic grazing (Travers et al., 2018) and could affect a number of reptile species based on their foraging and sheltering needs; (c) litter cover, as there is evidence that recent grazing has an impact on litter and reptiles (Yates et al., 2000) and it is critical habitat for litter foraging reptile species

TABLE 1 The richness of reptiles recorded during the study according to their functional traits based on their habitat preference (semi-arboreal, terrestrial, fossorial), time of peak activity (diurnal, nocturnal), and primary foraging site (tree, litter, open). Note due to limited data, we pooled data for arboreal and semi-arboreal species (hereafter “semi-arboreal”); for fossorial, semi-fossorial, and cryptozoic species (hereafter “fossorial”); and for tree and shrub foragers (hereafter “tree forager”)

Activity	Foraging	Terrestrial	Semi-Arboreal	Fossorial
Diurnal	Open	13	3	0
	Litter	4	0	2
	Tree	0	3	0
Nocturnal	Open	8	1	1
	Litter	1	0	3
	Tree	0	2	0

(Lindenmayer et al., 2008); and (d) the cover of bare soil, because bare soil has been identified in many studies as being highly correlated with reptile richness, particularly agamids (Read, 2002) and those that forage in open bare ground (Michael, Wood, Crane, Montague-Drake, & Lindenmayer, 2014). Bare soil is also often associated with heavy livestock or rabbit grazing (Eldridge & Simpson, 2001; Eldridge, Val, & James, 2011, Table 2).

Prior to analyses, we subtracted each community effect for a given attribute (the difference between the community mean [μ_c] and the grand mean [μ]), resulting in a “centred” dataset with a more appropriate regression line (Supporting Information Figure S1). Any natural variation among samples remains inherent in the data after this “centring” process but it effectively removed differences among communities, allowing us to undertake one analysis using all data rather than separate, community-specific analyses. All subsequent analyses were performed using centred variables. All exogenous variables (woody cover, litter cover, bare soil cover, native plant richness; Supporting Information Table S2), and the five grazing variables (cattle, sheep/goats, rabbits, kangaroos, historic grazing) were also standardised (z-transformed).

We undertook four analyses examining the effects on all reptiles combined, and our three trait groups of habitat preference, peak activity period, and foraging habitat. As all the relationships were linear, there was no need to model quadratic relationships. Our *a priori* model (Figure 1) was compared with the variance-covariance matrix to assess the overall goodness-of-fit, using the χ^2 statistic. The goodness-of-fit test estimates how well our data are reflected

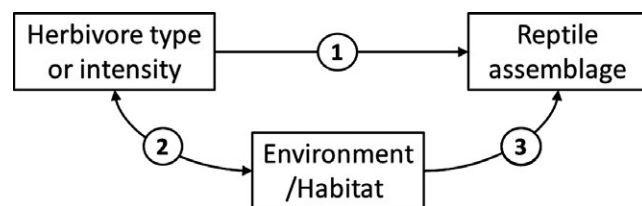


FIGURE 1 *A priori* model showing the predicted effects of herbivores on the reptile assemblage. Effects can be indirect (Pathway 3 via 2) when herbivores alter their environment and therefore habitat for reptiles, or direct (Pathway 1), such as when herbivores affect the behaviour of reptiles by their physical presence

by the *a priori* structure. Thus, high probability values indicate that these models are highly plausible causal structures underlying the observed correlations. Analyses were performed using the AMOS 22 (IBM, Chicago, IL, USA) software. The model with the strongest measures of fit (e.g. low χ^2 , high Goodness of Fit Index and high Normal Fit Index, or low root mean square error of approximation) were interpreted as showing the best fit to our data. The strength and sign of relationships among the variables is represented by path

TABLE 2 Hypothesised mechanisms underlying the grazing-habitat-reptile *a priori* model in Figure 1. + positive effect, – negative effect

Path	Hypothesised mechanism(s)
1	(–) Livestock can directly interfere with the behaviour and activity of wildlife (Schielz & Rubenstein, 2016) affecting breeding activity and success (Popotnik & Giuliano, 2000) and livestock trampling cause losses and ultimately affect the persistence of some species (Smith et al., 1996)
2	(–) Grazing by livestock and rabbits reduces tree and shrub regeneration (Tiver & Andrew, 1997), increases bare soil (Eldridge et al., 2017), may modify the litter layer (Bromham, Cardillo, Bennett, & Elgar, 1999), and have mixed effects on native plant richness (Eldridge et al., 2017; Travers et al., 2018). These in turn could represent shifts in prey items as changing habitat with (–) intensive livestock grazing reduces the density of ant mounds (Beever & Herrick, 2006), spider holes (Read, 2002), and Orthoptera abundance (Wasiolka, Blaum, Jeltsch, & Henschel, 2009)
3	(+) Trees provide critical habitat for arboreal and semi-arboreal reptiles (Brown, Dorrough, & Ramsey, 2011) by providing shade and litter (Brown, 2001), which are important for thermoregulation and shelter (Webb et al., 2005). (+) Litter provides critical foraging and sheltering habitat for litter foragers and other terrestrial species (Smith et al., 1996; Webb et al., 2005). (+/–) Bare soil provides basking sites for thermoregulation by Agamids and larger diurnal reptiles (Frank et al., 2013). Bare soil favours “sit and wait” foraging strategies, such as fossorial or nocturnal species (Pianka, 1967; Read, 2002). (+) Native plant richness is correlated with reptile abundance (Brown et al., 2011) and composition (Jellinek, Driscoll, & Kirkpatrick, 2004); reptile richness declines with increasing exotic plants (Jellinek et al., 2004)

coefficients, which are analogous to partial correlation coefficients (Grace, 2006). Our *a priori* model attained a good fit by all criteria, and thus no *post hoc* alterations were made. With a good model fit, we were free to interpret the path coefficients of the model and their associated *p* values.

3 | RESULTS

3.1 | Reptile sampling

We recorded 1,736 reptiles, from 42 species, over a total of 13,824 trap nights and 108 hr of habitat searches (Supporting Information Table S3). The overall trapping rate was 8.1 individuals per 100 trap nights and 5.5 individuals per hour of diurnal searching. Thirty-four species (eight families) were recorded from pitfall trapping, 29 species (six families) from funnel traps, and 16 species (five families) from diurnal searches. The richness and abundance of reptiles recorded per site ranged from 1 to 10 species and 1 to 42 individuals. The skink *Morethia boulengeri* was the most widespread and frequently recorded, present at 90% of sites and accounting for 44% of all reptile records. Other frequently recorded species were *Cryptoblepharus pannosus* (60% of sites; 17% of records) and *Menetia greyii* (40% of sites; 7% of records). Nine species were recorded at less than 10% of sites.

3.2 | Effects of grazing and environmental variables on reptiles

Our structural equation models indicated that the effects of livestock grazing on reptiles differed markedly between recent (LIV) and historic (TRK) livestock grazing (Figure 2a). Increases in recent livestock grazing reduced reptile richness overall, and reduced all groups of reptiles except semi-arboreal (ARB) species (Figure 2). Our models suggest that recent grazing acts by suppressing the positive effect of native plant richness on reptile richness (Figure 2a). Increases in historic livestock grazing had fewer effects on different reptile groups and a much lower overall negative effect on reptile richness (Figure 2a–d). Increasing intensity of historic grazing was also associated with a direct negative effect on tree foraging species richness (TRE; Figure 2d). Our models also showed that increases in native plant richness were generally strongly positive, particularly for diurnal, fossorial, semi-arboreal, and tree foraging species (Figure 2a–d). They also show that woody cover regulated the grazing effect, with higher levels of woody cover reducing the negative effects of grazing. Greater woody cover also reduced reptile richness overall, and most strongly for terrestrial (TER) species and open (OPN) foragers. Increasing litter cover was also associated with increases in semi-arboreal and tree foraging species (Figure 2c,d).

Kangaroo grazing had a direct negative effect on the richness of nocturnal reptiles but no effects on other groups (Figure 2b) or on any environmental measures (Figure 2a–d). Similar to the livestock effect, rabbits reduced reptile richness by suppressing the positive effect of native plant richness (Figure 2a). Rabbit grazing was also associated with a direct positive effect on the richness of semi-arboreal species.

The standardised total effects (sum of direct plus indirect effects) from our models showed that recent livestock grazing had the strongest effects on reptile assemblage, followed by woody cover and native plant richness (Table 3). They also highlight the contrasting overall effects of historic livestock grazing on reptiles, with few effects on reptiles overall (STE = 0.04) and increases in reptiles based on their habitat and foraging preferences with increasing richness of terrestrial (STE = 0.15) and open foragers (STE = 0.12), but reductions in the richness of semi-arboreal (STE = -0.17) and other tree foragers (STE = -0.20). Similarly rabbit grazing increased the richness of semi-arboreal species (STE = 0.19), but reduced in terrestrial (STE = -0.16) and to a lesser extent nocturnal (STE = -0.11) species richness. Litter cover also had a strong negative overall effect on fossorial richness (STE = -0.16) but an equally strong positive effect on the richness of semi-arboreal (STE = 0.17) reptiles (Table 3).

4 | DISCUSSION

Recent livestock grazing had a detrimental impact on reptiles, reducing community richness of all species, irrespective of their habitat, foraging preferences or activity patterns. A long history of livestock grazing was also associated with reductions in richness of reptiles with a semi-arboreal habit and those that foraged in trees. Of our free-ranging herbivores, increased rabbit grazing only increased semi-arboreal reptiles, while kangaroo grazing had few overall effects. Our results therefore provide mixed support for our hypothesis of a trait-specific effect of grazing on reptile richness. However, our results do indicate that grazing indirectly filters species by suppressing the positive effects of native plant richness, which in turn reduces the richness of several types of reptiles (fossorial, semi-arboreal, diurnal, and tree foraging species).

The loss of reptile richness was a pervasive impact associated with recent livestock grazing and was inconsistent with our first hypothesis. Recent livestock grazing effects were generally strong and consistently negative, with the standardised total effects, the sum of all direct and indirect effects, ranging from -0.18 to -0.40 (Table 3). Overall, the effects of livestock grazing on the reptile community were stronger than the effects of woody cover or native plant richness. The direct, and therefore unexplained, effects of recent livestock grazing are likely due to trampling or behavioural responses of reptiles to the presence of livestock, which could alter the manner in which different species are able to avoid large animals (Schieltz & Rubenstein, 2016). Increasing levels of recent livestock grazing could simplify reptile communities by disturbing the surface layers, thereby influencing temperature fluctuations and the thermal qualities of surface soils (Theisinger & Ratianarivo, 2015) and potentially favour species that prefer patchy or shallow litter layers over those that prefer to move through deep litter such as *Lerista* spp. Based on the effects of kangaroo grazing, there was also little support for our first hypothesis, with our only real effect being a negative relationship with nocturnal species, which we find hard to explain. These results reinforce previous research results

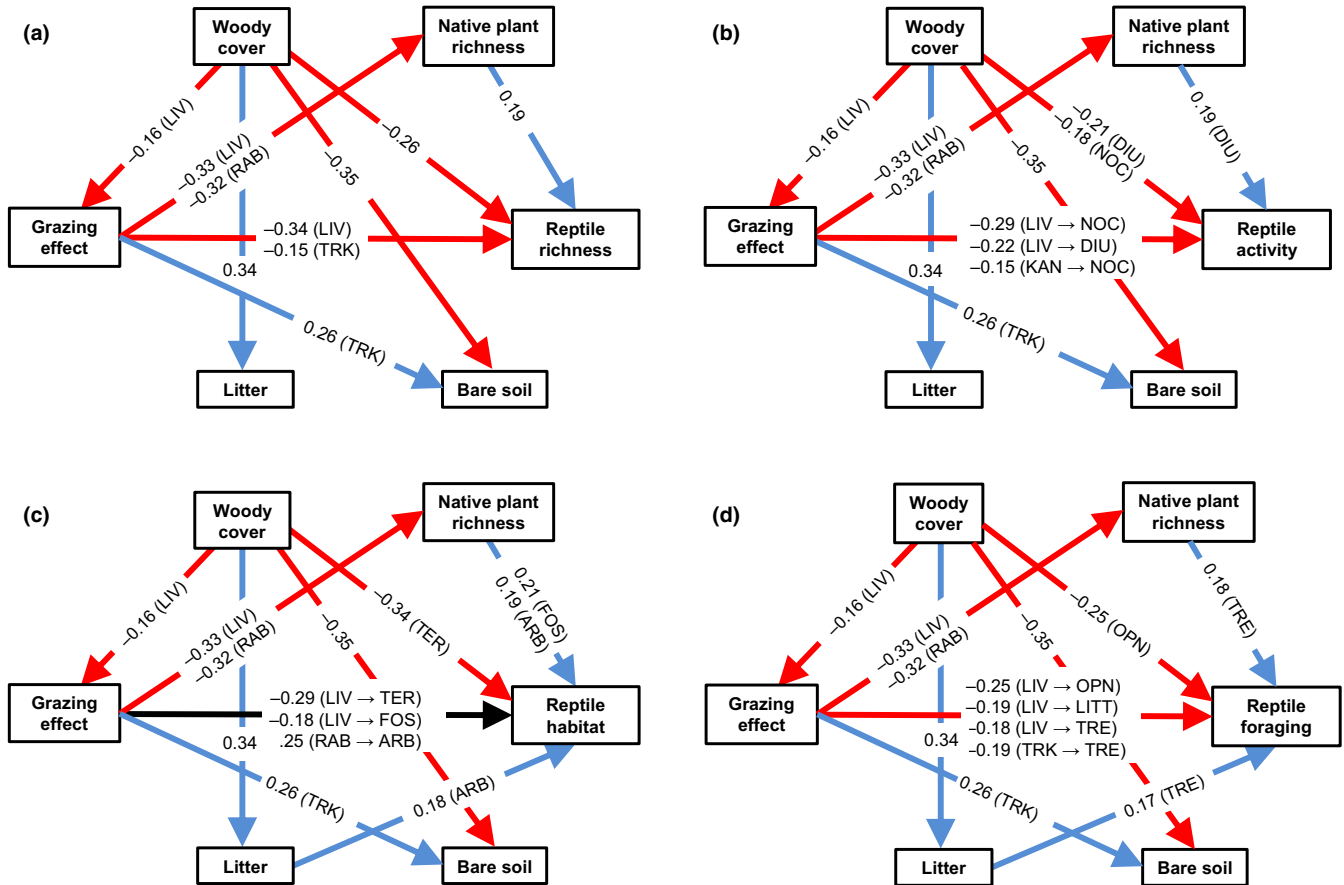


FIGURE 2 Structural equation model of the significant ($p < 0.05$) direct and indirect effects of grazing (recent grazing by cattle/sheep/goats, rabbits, and kangaroos; historic grazing by cattle/sheep/goats), tree cover, litter cover, bare soil, and native plant richness on the richness of (a) all reptiles, (b) reptiles by activity (diurnal, nocturnal), and (c) reptiles by habitat type (semi-arboreal, terrestrial, fossorial), (d) reptiles by foraging preference (tree, open, litter). The arrows (standardised path coefficients) indicate the direction and magnitude of the effect of one variable upon another. For example, for reptile activity (b), grazing by livestock is associated with reduced richness, but rabbit grazing is associated with greater richness, of diurnal reptiles. Similarly, increased historic grazing (tracks) and reduced kangaroo grazing are associated with more bare soil. All models, increasing levels of historic grazing are associated with reduced soil carbon (-0.28 LIV \rightarrow DIU, 0.17 RAB \rightarrow DIU). Grazing codes: LIV = livestock (cattle, sheep/goats), RAB = rabbits, KAN = kangaroo, TRK = tracks (historic grazing). Habitat codes: ARB = semi-arboreal (including arboreal), TER = terrestrial, FOS = fossorial (including cryptozoic). Activity codes: DIU = diurnal, NOC = nocturnal. Foraging codes: TRE = tree or shrub, LIT = litter, OPN = open. Model statistics: Total reptile richness: $\chi^2 = 3.04$, $df = 6$, $p = 0.80$, $R^2 = 0.42$. Habitat model: $\chi^2 = 4.17$, $df = 7$, $p = 0.76$, $R^2 = 0.18, 0.38, 0.24$ for semi-arboreal, terrestrial, and fossorial, respectively. Activity model: $\chi^2 = 3.04$, $df = 7$, $p = 0.88$, $R^2 = 0.25, 0.32$ for diurnal and nocturnal, respectively. Foraging model: $\chi^2 = 3.48$, $df = 7$, $p = 0.84$, $R^2 = 0.19, 0.24, 0.35$ for tree, litter, and open, respectively

demonstrating few if any effects of kangaroo grazing on plants and soils in these semi-arid woodlands (Eldridge et al., 2017; Travers et al., 2018), though higher kangaroo densities can affect reptiles (Howland et al., 2014).

Trait-specific effects of grazing on reptile communities are consistent with the large body of research on ground-foraging species from arid and semi-arid environments (Neilly, O'Reagain, Vanderwal, & Schwarzkopf, 2018; Rotem et al., 2015). A growing body of literature suggests that grazing favours species that prefer open habitats (Schielitz & Rubenstein, 2016). Although we did not detect any significant effects of bare soil on reptile richness, we did find a greater area of bare soil at sites with a stronger history of livestock grazing. It is also possible that the reptile abundance, rather than richness, changes in response to changes in bare soil. Increases in

both historic livestock grazing and recent rabbit grazing were associated with a greater richness of some reptile groups depending on their habitat and foraging preferences, and activity patterns, providing some support for the first hypothesis. Strong legacy effects of livestock grazing directly reduced the richness of tree foraging reptiles, and standardised total effects showed strong reduction in both semi-arboreal species and tree foraging species, which have a 56% overlap of species. Similarly, our standardised total effects show that increased rabbit grazing was associated with greater richness of semi-arboreal species, but reduced terrestrial and nocturnal species richness. This might at first seem difficult to reconcile, but semi-arboreal reptiles such as the bearded dragon (*Pogona vitticeps*) also spend considerable time on the ground, so are likely affected by changes in ground cover. Prolonged livestock grazing and rabbit

TABLE 3 Standardised total effects (STE: sum of direct plus indirect effects) derived from the structural equation modelling of recent livestock grazing, historic livestock grazing, native plant richness, tree cover, litter cover, and bare soil cover on different reptile richness. Semi-arboreal includes arboreal and semi-arboreal species. Fossorial includes fossorial and cryptozoic species

Reptile richness	Recent livestock grazing	Historic livestock grazing	Recent rabbit grazing	Recent kangaroo grazing	Native plant richness	Woody cover	Litter cover	Bare soil
All reptiles	-0.40	0.04	-0.02	-0.12	0.19	-0.23	0.05	0.08
Diurnal	-0.28	-0.01	0.06	-0.04	0.19	-0.16	0.04	-0.03
Nocturnal	-0.32	0.06	-0.11	-0.16	0.08	-0.18	0.02	0.17
Semi-arboreal	-0.18	-0.17	0.19	-0.11	0.20	0.02	0.17	0.09
Terrestrial	-0.31	0.15	-0.16	-0.05	0.05	-0.30	0.03	0.05
Fossorial	-0.27	-0.01	-0.06	-0.12	0.19	-0.03	-0.16	0.01
Tree foragers	-0.22	-0.20	-0.02	-0.12	0.19	-0.09	0.17	0.03
Litter foragers	-0.27	0.06	-0.06	0.04	0.03	-0.02	-0.02	-0.09
Open foragers	-0.25	0.12	0.03	0.04	0.03	-0.28	-0.01	0.17

grazing are also known to drive substantial changes in plant composition by enhancing exotic plant species at the expense of native plants (Travers et al., 2018) and are also associated with greater cover of bare ground (Tiver & Andrew, 1997). Thus, increased rabbit grazing and sites with a strong history of livestock grazing would likely have stronger effects on species that are sensitive to changes in both ground and plant cover, that is, the semi-arboreal taxa.

Our models also provide some insights into possible underlying mechanisms, or indirect effects of grazing on reptile richness, via changes to habitat features, consistent with our second hypothesis. Recent grazing by livestock and rabbits reduced the richness of reptiles overall by suppressing the positive effect of native plant richness on reptiles, but also filtered species via this mechanism with the strongest negative effects on tree foraging, fossorial, semi-arboreal, and diurnal species. Our fossorial species were dominated by nocturnal (NOC, 67%) species such as small skinks (*Lerista* spp.) and blind snakes (*Ramphotyphlops* spp.) that forage for termites, ant eggs, and ant pupae, in litter and soil (Abensperg-Traun & Steven, 1997), and *Brachyurophis*, a snake that feeds primarily on fossorial skinks (How & Shine, 1999). It is possible that changes in native plants alter food sources for these species, but the ecology of fossorial reptiles is generally poorly understood (How & Shine, 1999). For diurnal, semi-arboreal and other tree foraging species, native plant richness is likely a proxy for other key microhabitat features that reptiles rely upon, such as habitat structure and complexity (Garden, McAlpine, Possingham, & Jones, 2007), which decline with livestock grazing (Val, Eldridge, Travers, & Oliver, 2018) but were not included in our models. Native plants may also provide a greater range of resources for reptiles, reduce climatic fluctuations (Herrera & Dudley, 2003), or provide better quality refugia from predators (Valentine et al., 2007). Thus there are many ways whereby native plant richness might affect critical reptile habitat such as habitat composition, thermoregulation and foraging substrates, food availability, and the provision of refuge sites, for different reptiles (Martin & Murray, 2011).

Increases in woody cover were associated with greater litter cover. Increasing litter was directly associated with greater richness

of semi-arboreal and woody plant foraging species (i.e. tree and shrub foraging species) and had a strong negative standardised total effect on fossorial species. Greater litter cover may not necessarily reflect better quality reptile habitat or a better substrate for foraging, because litter varies greatly in depth, quality, and substrate composition, which may explain why litter cover did not alter litter-foraging species richness. The positive effects of litter on semi-arboreal and woody plant foraging species is perhaps associated with the fact that large trees produce large quantities of litter and also provide extensive habitat or foraging structures for these types of reptiles. Although greater woody cover may increase the abundance of tree foraging, and arboreal and semi-arboreal species, not all trees provide suitable habitat. Thus a site with a few large habitat trees but lower overall woody cover may be more important for promoting species richness than a high density of small trees (MacNally, Cunningham, Barker, Horner, & Thomson, 2011; Tews et al., 2004). Moreover, increases in woody cover directly affected both nocturnal and diurnal species, and specifically, terrestrial and open foragers. Increasing woody cover can reduce spatial and temporal variation in surface temperature for heliotherms and thigmotherms (Martin & Murray, 2011; Melville & Schulte, 2001; Webb, Shine, & Pringle, 2005) and likely effects reptiles by altering surface layer complexity, interspecific competition, and predation rates (Toft, 1985).

Active thinning of tree and shrub regrowth are increasingly being used under the assumption that thinning will have positive biodiversity benefits. Our results show, however, that woody cover has a significant effect on reptile assemblages by suppressing terrestrial open foraging reptile group. In our study, the terrestrial open group was also the more common generalist species that also benefited from the effects of increasing grazing pressure. As demonstrated elsewhere, thinning to reduce woody plant density would likely benefit terrestrial open foraging generalists, possibly at the expense of other groups with more specialised habitat requirements (Attum et al., 2006; Jones, 1981). Furthermore, our study shows that woody cover regulates the negative effects of livestock grazing on reptiles. Therefore, promoting management actions to reduce woody cover will likely exacerbate the

negative effects of livestock grazing on those groups sensitive to a loss of structure and benefit more common generalist species.

Our study highlights the need to adopt sustainable grazing practices to prevent the loss of reptiles. Land managers need to consider the total grazing pressure, that is the combined effects of free-ranging herbivores as well as livestock. Furthermore, greater effort needs to be made to improve grazing management during droughts. Fauna are likely to be most susceptible in drought when resources are depleted and competition for scarce food items is intense. Implementing sustainable grazing practices under these conditions is therefore imperative for the survival of fauna, including that of reptiles.

5 | CONCLUSIONS

We found that the rabbit grazing and the legacy effects of livestock grazing, filtered reptile assemblages based on traits related to habitat and foraging needs, while recent livestock grazing activity reduced the richness of all reptiles, irrespective of their traits. Unlike the effects of recent grazing, longer term legacy effects of grazing are more difficult to reverse. Over longer time periods, therefore, grazing is likely to produce some reptiles that are “winners” and others that are “losers”. Ultimately, the effect of increased grazing may be to shift the structure of the reptile assemblage towards one dominated by a few widespread generalists at the expense of specialists, as has been shown globally (Martin & Murray, 2011). Over decadal time periods, however, any legacy effects of continual declines in plant species richness induced by grazing will likely manifest itself as more bare soil and fewer native plants. These changes will likely be exacerbated by reduced rainfall and increased temperatures associated with global changes in climate. A greater ability to manage all herbivores is critical if we are to balance the effects of livestock grazing to meet the needs of an increasing global population with the need to sustain habitat for reptile and other organisms.

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AUTHORS' CONTRIBUTIONS

J.V., D.J.E., I.O., and S.K.T. conceived and designed the study; J.V., S.K.T., D.J.E., and contractors collected the data; D.J.E., J.V., T.B.K., and S.K.T. analysed the data; J.V. led the writing of the manuscript,

and all authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data on grazing and reptile richness are deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.nh773s0> (Val, Travers, Oliver, Koen, & Eldridge, 2018).

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SUPPORTING INFORMATION

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

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