

RESEARCH ARTICLE

Geographic variation in mammal and reptile responses to fire and livestock grazing regimes

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Abstract

1. Changes in land use and fire regimes are a major threat to species and ecosystems worldwide. Species' responses to altered fire and livestock grazing likely vary depending on the local ecosystem and the attributes of the disturbance regimes.
2. We used single-species, single-season occupancy modelling to investigate the responses of 15 commonly occurring mammal and reptile species to fire and grazing regime attributes in an Australian subtropical woodland. Thirty-one hypotheses were formed based on species' responses to these regime attributes reported in other studies conducted in Australia. We expected that our hypotheses would be more likely to be supported when based on results from studies closer to our study area.
3. Of the 31 relationships we tested for, only six were consistent with the hypothesized responses for each species, and we were unable to discern any geographic patterns that made this consistency more likely. Seven mammal species' occupancy changed in response to a fire or grazing regime attribute. Four small mammals (eastern chestnut mouse *Pseudomys gracilicaudatus*, pale field rat *Rattus tunneyi*, delicate mouse *Pseudomys delicatulus*, central short-tailed mouse *Leggadina forresti*) and two large mammals (eastern grey kangaroo *Macropus giganteus*, red-necked wallaby *Macropus rufogriseus*) responded to different fire regime attributes. Pigs (*Sus scrofa*) had higher occupancy in more heavily grazed areas.
4. *Synthesis and applications.* Based on our findings, conservation land managers should be cautious in using species' responses to disturbance regimes from studies done in other bioregions to inform conservation practices in their local area. Factors that may have influenced the response of species to fire and livestock grazing in this region include the unique climate of the bioregion, prior land use history, previous large wildfires and recent above-average rainfall. Given the interspecies variability to fire regime attributes in this study area, we recommend maintaining variation in time since fire, time since late-dry-season

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fire and fire frequency in the landscape to accommodate the different fire history needs of individual species.

KEYWORDS

agriculture, burning, conservation, disturbance, ecology, management, occupancy

1 | INTRODUCTION

Fire and grazing disturbances are important ecological processes that shape fauna communities worldwide (White & Pickett, 1985). However, fire regimes have shifted dramatically in recent decades, particularly in tropical and subtropical woodlands and savannas (Russell-Smith et al., 2003). In addition, domestic livestock grazing now occurs across an estimated 25% of land globally, driving the degradation of many ecosystems (Asner et al., 2004). Both disturbances have been implicated in biodiversity declines and extinction of several vertebrate species (Kutt, Vanderduys, & O'Reagain, 2012; Santos, Hradsky, et al., 2022; Woinarski et al., 2015). Furthermore, fire and livestock grazing regimes vary regionally with climate and ecosystem, preventing generalisable conservation management. It is essential to understand how individual species respond to fire and grazing regimes in different ecosystems to manage land appropriately for conservation.

Ground-dwelling small mammals and reptiles are particularly vulnerable to fire and livestock grazing for several reasons. First, compared to larger species or those with the ability to fly, many small terrestrial mammals and reptiles often have a lower capacity to emigrate or move away from widespread disturbance (Hale et al., 2022). Second, fire and livestock grazing remove their food, shelter and nesting resources such as ground cover, shrubs and tree hollows (Kutt & Woinarski, 2007; Radford et al., 2015). Third, small mammals and reptiles become more vulnerable to predation by introduced mammals after the ground cover is removed by fire and grazing (McGregor et al., 2014).

Both short- and long-term impacts of fire and livestock grazing can shape ecosystems. Important fire regime attributes include time since the previous fire (Watson et al., 2012), severity (Lindenmayer et al., 2013), season, frequency and intensity (Gill, 1975). Grazing attributes include intensity, grazing treatment (e.g. constant, rotational and seasonal) or type of livestock (Neilly et al., 2018). The effect of these regime attributes on the ecosystem is highly dependent on environmental context such as rainfall and soil productivity (Yarnell et al., 2007). Approximately 43% of threatened Australian squamates and 88% of threatened Australian mammals are threatened by inappropriate fire regimes with high fire intensity and severity, high fire frequency and large fires correlated with the majority of population declines (Santos, Hradsky, et al., 2022; Santos, Sitters, et al., 2022). However, for several threatened mammals and reptiles, a lack of fire can also be problematic, primarily by reducing survival and breeding success (Santos, Hradsky, et al., 2022; Santos, Sitters, et al., 2022).

High-intensity grazing has typically caused declines in biodiversity of Australian fauna, but results have been more variable for low- and medium-level grazing (Neilly et al., 2018).

Despite research examining the effects of fire and grazing regimes on mammal and reptile populations across Australia (Santos, Hradsky, et al., 2022; Santos, Sitters, et al., 2022), there is still limited information on the effects of these regimes on biodiversity in many ecosystems. This issue arises because fire interval, climate, soil type, land use history and fauna and flora communities differ between ecosystems, leading to different intraspecific responses. Therefore, it is important to assess the consistency of species' responses to fire and grazing regimes across different bioregions to determine their applicability to inform land management in different areas.

We aimed to determine the responses of fauna to attributes of fire and livestock grazing regimes in an Australian subtropical woodland and compare these with responses of the same species in other systems across Australia. Based on published studies, we developed a suite of hypotheses about fauna species responses. We expected that the likelihood of a hypothesis being supported would be greater where it was drawn from studies in bioregions closer to our study region. The results of this study may be useful for developing strategies for the conservation of these species in subtropical woodlands where mammal and reptile responses to fire and grazing regimes are relatively understudied.

2 | MATERIALS AND METHODS

2.1 | Hypothesized responses to fire and livestock grazing regimes

We undertook a literature search to extract published information on how 15 mammal and reptile species found in our study area responded to fire and grazing regimes in different bioregions of Australia. We were interested in four fire variables: frequency, severity, seasonality and time since previous fire; and livestock grazing. We used Google Scholar and Web of Science with the following search queries: 'species scientific name' OR 'common name' AND 'fire' OR 'grazing' OR 'time since fire' OR 'late dry season fire'. We compiled peer-reviewed literature that used statistical tests between 1980 and 2022. From 2763 peer-reviewed articles we filtered the dataset and collated a total of 71 individual responses of species to fire and livestock grazing regime attributes from 47 separate papers (see Data sources section). We recorded the influence

of fire and livestock grazing variables on a species as positive, negative or non-significant and the study's bioregion. This information was used to hypothesise whether each species would have a positive, negative or non-significant response to fire and grazing regime attributes in subtropical woodlands (S1). Where studies had conflicting responses, we chose the majority response, or if there was no majority, the response that occurred in the closest geographic location to our study. Three species had no literature on their response to fire and livestock grazing variables: the central short-tailed mouse (*Leggadina forresti*), eastern pebble-mound mouse (*Pseudomys patrius*) and pig (*Sus scrofa*).

2.2 | Study area

Our study was conducted on Carnarvon Station Reserve (−24.85196, 147.63398) and neighbouring farmland in central Queensland, Australia. The 59,000-ha reserve is adjacent to Carnarvon National Park and together forms the largest remaining area of woodland in the Brigalow Belt bioregion (Figure 1). Average temperature ranges from 3.1°C to 22.2°C during winter and 18°C to 34°C during summer, with average annual rainfall of 682.5 mm (Bureau of Meteorology, 2022). Carnarvon Station Reserve was used for livestock grazing until 2001 when it was purchased by Bush Heritage Australia. Management of the reserve aims to maintain or increase biodiversity, while neighbouring properties are managed for cattle grazing. Sites were spread evenly across two main vegetation communities: basalt soil with *Eucalyptus* woodland and sandstone-derived soil with *Callitris*/*Angophora* woodland.

2.3 | Fauna surveys

We used white-flash Reconyx Hyperfire HC550 and W2 cameras to detect species across 48 sites, spaced a minimum of 1.7 km apart. Cameras were deployed for 6 weeks at each site during two seasons: spring to summer (August 2020 to January 2021) and summer to autumn (January 2021 to June 2021). We chose to use a 6-week sampling duration per season to align better with the assumption of closed populations, and we set site as a random effect in occupancy models to address the repeated measure (two seasons per site for a total of 96 samples). At each 100 m × 20 m site, three cameras (one HC550 and two W2) were deployed and set 50 m apart in a straight line. Due to the limited number of cameras, we rotated them between sites. Reconyx Hyperfire W2 models were set to the same ISO (800) and shutter speed (1/120th) as the Reconyx Hyperfire HC550 models to reduce variability between camera trap models. All cameras were set to operate 24 h a day and take three photos per trigger with no delay between photos or triggers and high sensitivity. We considered 1 h between consecutive photos an independent detection event. Cameras were secured to a metal bracket in a vertical position 1 m above the

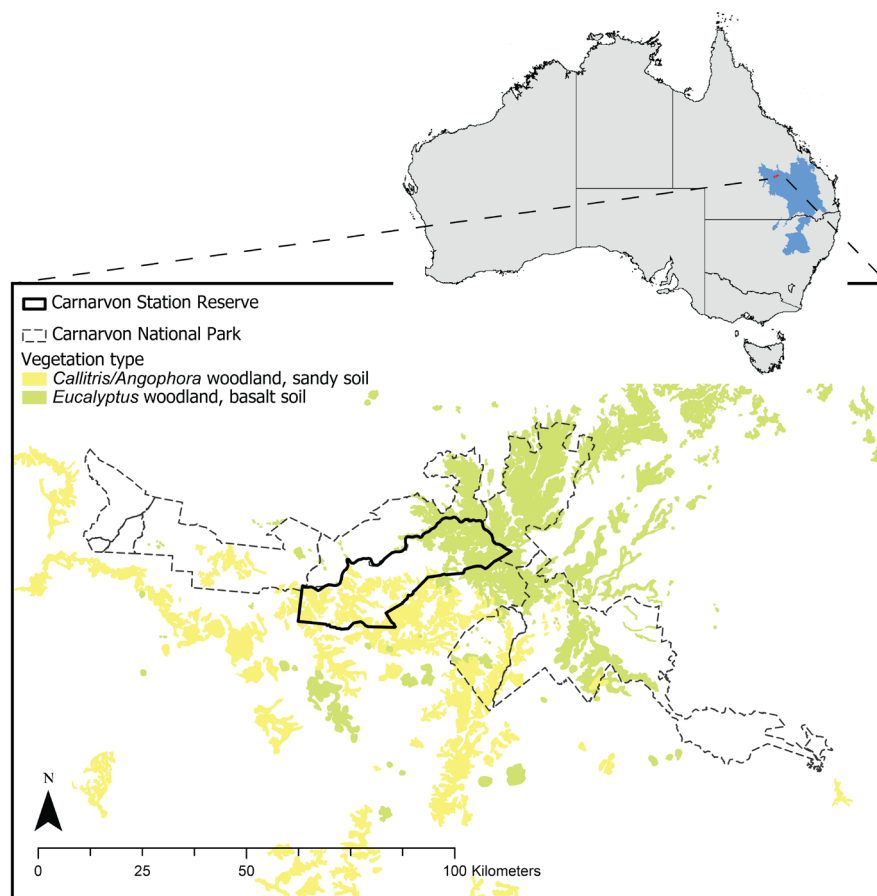
ground facing downwards. A peanut butter, honey and oat bait ball was placed inside a mesh tea strainer and attached to the centre of a 30 cm × 30 cm cork board which was secured to the ground directly underneath the camera (Dixon et al., 2018). This non-traditional camera trap deployment facilitated accurate identifications of small vertebrates by (1) reducing the amount of vegetation present in the field of view, (2) ensuring a consistent distance of animals to the camera lens thereby allowing size comparisons between species and the cork board and (3) allowing for consistent views of the head and body length in proportion to tail length – an important diagnostic feature of many rodent species. The cork board also created a temperature differential to ensure cameras were reliably triggered by reptiles (Welbourne et al., 2017). Baiting camera traps may mask some of the effects of disturbance by attracting animals from non-disturbed areas, making occupancy appear higher than in reality. However, this is a common method used for camera trapping (Stirnemann et al., 2015) and was deemed necessary given the relatively low density of fauna species in our study area. After 6 weeks, the cameras were retrieved, and all photos were downloaded and processed in Colorado Parks and Wildlife Warehouse V 4.0. Mammals and reptiles captured on camera were identified to species level except for *Planigale maculata* and *Planigale tenuirostris*, which were grouped as *Planigale* species because they could not be reliably distinguished from camera trap photos using this setup. All research methodologies were approved by the University of Queensland's Animal Ethics Committee (permit number SAFS/273/19/BUSH HERITAGE AUSTRALIA) and Queensland Department of Environment and Science (permit numbers WA0018208 and WA0019067).

2.4 | Fire and grazing covariates

We assessed grazing pressure in two ways: first, by counting the number of cow pats within four 20 m × 20 m plots at each site ($n = 96$) (James, 2003); and second, by using a 0–3 scale for grazing intensity. Zero (ungrazed by livestock) indicated no signs of livestock presence, one (lightly grazed) indicated signs of cropped grass clumps and the presence of a few livestock scats or tracks, two (moderately grazed) indicated signs of cropped grass clumps, numerous livestock scats, some trampling and/or bare soil and three (heavily grazed) indicated that grass was extensively and heavily cropped, with low grass cover, bare soil, erosion and a high number of livestock scats (Ludwig et al., 2000). These standard methods to assess grazing intensity have been used reliably in semi-arid woodlands in Queensland (James, 2003; Ludwig et al., 2000).

We assigned one measurement of fire severity to each 100 m × 20 m site based on a scale of 0–3 adapted from Lindenmayer et al. (2008) where 0 indicated no sign of fire, 1 indicated the understory had been burnt, 2 indicated the midstory was burnt and 3 indicated the overstory had been burnt. Spatial fire history (from 2009 to 2021) was mapped in ArcGIS software using data from Landsat

FIGURE 1 A map of Carnarvon Station Reserve in the context of Australia and the Brigalow Belt bioregion (blue). Yellow shows *Callitris/Angophora* woodland on sandy soil, green shows *Eucalyptus* woodland on basalt soil.



Fire Scars Queensland Series, Sentinel-2 Fire Scars Queensland Series and North Australia Fire Information and assigned one value for each sample. We used the previous 12 years of fire history because this data was mapped to a finer and more accurate spatial scale in and around the reserve compared to older fire history data. A 12-year time frame allowed us to avoid wrongly categorizing fire history for samples while still giving good variation in fire frequency across samples and encompassing the fire return intervals for these woodland ecosystems (range 3–10 years). Vegetation in our study region is driest in the late-dry season (July to December); therefore, fires in this period are predominantly hotter and more widespread than fires occurring from January to June. Other studies have found late-dry-season fires have a significant effect on small mammal and reptile species across a variety of ecosystems; therefore, we included it as a fire regime attribute (Santos, Hradsky, et al., 2022; Santos, Sitters, et al., 2022). From these data, we obtained the following covariates for analysis: vegetation type, grazing intensity, fire severity (0–3), fire frequency (fires per 12 years), time since last fire (0–12 years), frequency of late-dry-season fires (fires per 12 years) and time since last late-dry-season fire (0–12 years) (S2).

2.5 | Occupancy modelling

We used occupancy modelling to examine changes in the occupancy of our study species due to environmental covariates (e.g. burning

and grazing) while accounting for imperfect detection of species (MacKenzie et al., 2002). In line with model assumptions, we assumed species occupancy for a sample remained constant for the duration of each season (6 weeks), species were not falsely identified, and that seasons and sites were independent (MacKenzie et al., 2002). Detection histories containing presence/absence data (0 = species not detected; 1 = species detected) were generated for each species. We collapsed detection histories into 7-day sampling occasions to reduce the frequency of zeros and increase species detection probabilities, so each sample contained a total of six sampling occasions per 6-week season. Only full 1-week periods were retained, so if a camera malfunctioned, the corresponding week was omitted from detection and occupancy analysis.

We assessed naïve occupancy for each species by summing the total number of samples with at least one detection and dividing by the total number of samples ($n=96$). We ran models with occupancy and detection held constant to assess the detection probability of species across all samples. Species that were present in fewer than eight samples or that had a detection probability <0.15 were excluded as they did not have enough information regarding presence/absence to reliably determine their response to fire and grazing covariates (Guillera-Aroita et al., 2010). For these species, occupancy models either did not converge or produced large estimates and standard errors. We also excluded cattle and horses as we were interested in the effects of these animals via grazing, not their responses to site characteristics.

Before undertaking modelling, we used Spearman's product moment correlations to determine whether numeric detection or occupancy covariates were strongly correlated (>0.6) and, if so, only one of the pair was retained. Time since late-dry-season fire was retained over frequency of late-dry-season fire ($R = -0.7$) and number of cow pats was retained over grazing intensity score ($R = 0.89$) as our measure of livestock grazing intensity. A chi-square test found that vegetation type and fire severity were highly correlated ($\chi^2 = 18.8$, $p < 0.01$). Vegetation type was also found to be highly correlated with grazing intensity ($\chi^2 = 12.96$, $p < 0.01$) and time since late-dry-season fire ($\chi^2 = 19.5$, $p < 0.01$) using a Kruskal-Wallis test. Given our primary aim was to assess the effects of fire and grazing regime attributes on species, we removed vegetation type from further analyses. All covariates were centred and standardized to z-scores before model fitting.

2.6 | Power analysis

We ran a simulation-based power analysis using the *powerAnalysis()* function in the *unmarked* package (Fiske & Chandler, 2011) to better understand when our ability to detect an effect was likely to exceed the generally acceptable power threshold of 0.8 (Guillera-Arroita & Lahoz-Monfort, 2012). We estimated the power of our study design using four effect sizes (0.2, 0.4, 0.6 and 0.8) for both occupancy and detection covariates, keeping alpha (type 1 error rate) at 0.05, the number of samples at 96 and using 1000 simulations. Statistical effects of fire or grazing were only likely to be detected if there was a 1.99 times higher or lower likelihood of detection (effect size >0.38) or a 3.56 times higher or lower likelihood of occupancy (effect size >0.7) (S3a). We also calculated the number of samples that would theoretically be needed to detect a change in occupancy under these four different effect sizes (0.2, 0.4, 0.6 and 0.8) (S3b).

2.7 | Model fitting and selection

We used single-species single-season occupancy modelling to assess the effect of grazing and fire regime attributes on the occupancy of mammals and reptiles. Statistical analysis was undertaken in the *unmarked* package (Fiske & Chandler, 2011) in R 4.3.2 (R Core Team, 2025). We included total camera trap nights per sample and time since camera deployment as detection covariates. Camera trap nights varied between samples (e.g. because cameras were retrieved from sites over several days) and other studies found small mammals declined in detection with time since camera deployment (McDonald et al., 2015).

We ran occupancy models for each species, including the two detection covariates and six occupancy covariates: season, grazing intensity, fire severity, time since fire, fire frequency and time since late-dry-season fire. We included season as a fixed effect and site

as a random effect within occupancy models to account for non-independence of repeat samples at each site.

The global model was assessed for goodness-of-fit using the Mackenzie and Bailey goodness-of-fit test run with 1000 simulations. We considered models a good fit if $p > 0.1$ and the overdispersion parameter ($\hat{c}$) was close to 1 (MacKenzie & Bailey, 2004). We used the *dredge* function in the R package *MuMIn* (Barton & Barton, 2015) to rank all models including possible combinations of covariates. Models were ranked according to their Akaike Information Criterion corrected for small sample size (AICc). If species showed overdispersion ($\hat{c} > 1$) we used the $\hat{c}$ value to adjust for overdispersion and ranked models according to Quasi-AICc (QAICc) rather than AICc (Burnham & Anderson, 2004). We considered occupancy models $<2.0 \Delta\text{AICc}/\Delta\text{QAICc}$ from the top model to be similarly plausible (Burnham & Anderson, 2002). We used model averaging across plausible models using the *AICcmodavg* package (S4), which allowed us to average estimates of effect sizes over all plausible models instead of relying on multiple individual models to make inferences (Kéry & Royle, 2016). We considered covariates to be associated with occupancy or detectability if $p < 0.05$.

3 | RESULTS

3.1 | Species detected

From August 2020 to June 2021, we surveyed a total of 16,155 camera trap nights. We recorded 29 species: 18 native mammal species, five native reptile species and six introduced mammal species (Table 1). The most captured species across all samples were the house mouse (*Mus musculus*) (96 samples), followed by the common rock rat (*Zyomys argurus*) (81 samples), the eastern grey kangaroo (*Macropus giganteus*) (42 samples) and the pig (39 samples). The least captured species were Herbert's rock wallaby (*Petrogale herberti*) and rufous bettong (*Aepyprymnus rufescens*) which were only detected in one sample, followed by northern brown bandicoot (*Isodon macrourus*), common brushtail possum (*Trichosurus vulpecula*), eastern blue tongue lizard (*Tiliqua scincoides scincoides*), fawn-footed melomys (*Melomys cervinipes*), yellow-footed antechinus (*Antechinus flavipes*) and dingo (*Canis lupus dingo*) all of which had a naïve occupancy of less than 9%. These species were omitted from occupancy analysis because of their sparse presence/absence data.

3.2 | Species detection probability

We assessed detection probability with occupancy held constant for all 29 species. Detection probability (p) varied from <0.1 to 0.97 when detection and occupancy were held constant (Table 1). Species with the lowest detection probability were the Herbert's rock wallaby, common brushtail possum, northern brown bandicoot

and blue tongue lizard ($p < 0.01$). *Planigale* species, freckled monitor (*Varanus tristis*) and cat (*Felis catus*) also had detection probabilities below 0.15, and this excluded them from further occupancy analysis. Species with the highest detection probability were the house mouse ($p = 0.97$) followed by the common rock rat ($p = 0.84$). When detection probability was not held constant, several species detection probability was influenced by the number of trap nights: delicate mouse (*Pseudomys delicatulus*), eastern bearded dragon (*Pogona barbata*), sand goanna (*Varanus gouldii*) and rabbit (*Oryctolagus cuniculus*), or time since camera deployment: common rock rat (S5).

3.3 | Comparison of study results and hypotheses from literature

We hypothesized a total of 31 responses of species to fire or grazing regime attributes based on literature. Six hypotheses drawn from the literature matched results in our study, while 25 hypotheses did not (Figures 2 and 3). All six of the matching hypotheses and results were for a non-significant response. There was no apparent spatial pattern with the literature-based hypotheses that matched results found in our study; hypotheses based on studies conducted far from

TABLE 1 Species recorded during 6-week camera trapping deployments in the Carnarvon Ranges, along with the number of samples ($n = 96$) where they were detected, *naïve occupancy* (proportion of samples with at least one detection), detection probability (the probability of detecting a species in a sample during the 6-week period given that it is occupied) and inclusion in occupancy analysis (yes/no).

Species	Scientific name	Samples	Naïve occupancy	Detection probability	Included
Native large mammals					
Dingo	<i>Canis lupus dingo</i>	7	0.07	0.24	No
Eastern grey kangaroo	<i>Macropus giganteus</i>	42	0.44	0.42	Yes
Herbert's rock wallaby	<i>Petrogale herberti</i>	1	0.01	<0.01	No
Red-necked wallaby	<i>Notamacropus rufogriseus</i>	12	0.13	0.29	Yes
Swamp wallaby	<i>Wallabia bicolor</i>	14	0.15	0.24	Yes
Native small mammals					
Central short-tailed mouse	<i>Leggadina forresti</i>	11	0.11	0.22	Yes
Common brushtail possum	<i>Trichosurus vulpecula</i>	3	0.03	<0.01	No
Common dunnart	<i>Sminthopsis murina</i>	22	0.23	0.28	Yes
Common rock rat	<i>Zyomys argurus</i>	81	0.84	0.67	Yes
Delicate mouse	<i>Pseudomys delicatulus</i>	37	0.39	0.49	Yes
Eastern chestnut mouse	<i>Pseudomys gracilicaudatus</i>	24	0.25	0.33	Yes
Eastern pebble-mound mouse	<i>Pseudomys patrius</i>	28	0.29	0.4	Yes
Fawn-footed melomys	<i>Melomys cervinipes</i>	5	0.05	0.13	No
Northern brown bandicoot	<i>Isodon macrourus</i>	2	0.02	<0.01	No
Pale field rat	<i>Rattus tunneyi</i>	12	0.13	0.27	Yes
<i>Planigale</i> spp.	<i>Planigale</i>	15	0.16	0.07	No
Rufous bettong	<i>Aepyprymnus rufescens</i>	1	0.01	0.48	No
Yellow-footed antechinus	<i>Antechinus flavipes</i>	6	0.06	0.06	No
Native reptiles					
Blue tongue lizard	<i>Tiliqua scincoides scincoides</i>	4	0.04	<0.01	No
Eastern bearded dragon	<i>Pogona barbata</i>	36	0.38	0.24	Yes
Freckled monitor	<i>Varanus tristis</i>	9	0.09	0.11	No
Lace monitor	<i>Varanus varius</i>	26	0.27	0.24	Yes
Sand goanna	<i>Varanus gouldii</i>	17	0.18	0.2	Yes
Introduced mammals					
Feral cat	<i>Felis catus</i>	33	0.34	0.11	No
Cattle	<i>Bos taurus</i>	38	0.4	0.63	No
Horse	<i>Equus caballus</i>	14	0.15	0.17	No
House mouse	<i>Mus musculus</i>	96	1	0.97	No
Feral pig	<i>Sus scrofa</i>	39	0.41	0.26	Yes
Rabbit	<i>Oryctolagus cuniculus</i>	27	0.28	0.27	Yes

our study site were just as likely to be supported as those based on studies from nearby. Hypotheses and results were more aligned for reptiles compared with mammals, with all three reptile species having at least one hypothesized relationship supported. In contrast, only two of nine species of mammal did.

3.4 | Species occupancy

We examined how fire and livestock grazing covariates affected the occupancy of 15 species, after excluding 14 species that were either domestic livestock, present in fewer than 8 samples, or had a detection probability <0.15 . We found the occupancy of four small mammals changed in response to a fire regime attribute. The pale field rat (*Rattus tunneyi*) had lower occupancy at samples with a longer time since fire, estimate = -1.56 (95% CI $-2.97, -0.14$) (Figure 4a), the eastern chestnut mouse (*Pseudomys gracilicaudatus*) had lower occupancy at samples with longer time since late-dry-season fire, estimate = -0.75 (95% CI $-1.37, -0.13$) (Figure 4b), the delicate mouse had lower occupancy for samples with lower fire severity, estimate = -2.14 (95% CI $-3.79, -1.01$) (Figure 4c) and the central short-tailed mouse had lower occupancy for samples with longer time since fire, estimate = -1.04 (95% CI $-1.93, -0.15$) (Figure 4d). The red-necked wallaby (*Macropus rufogriseus*) had lower occupancy with more frequent fire, estimate = -0.87 (95% CI $-1.68, -0.06$) (Figure 4e) while the eastern grey kangaroo (*Macropus giganteus*) had lower occupancy probability with longer time since late-dry-season fire, estimate = -0.79 (95% CI $-1.36, 0.22$) (Figure 4f). The occupancy probability of pigs increased significantly in response to higher livestock grazing intensity, estimate = 3.71 (95% CI $0.33, 7.1$) (Figure 4g). The occupancy and detection probability of the swamp wallaby (*Wallabia bicolor*), common dunnart (*Sminthopsis murina*), eastern pebble-mound mouse and lace monitor (*Varanus varius*) were not significantly affected by any variables (S5).

4 | DISCUSSION

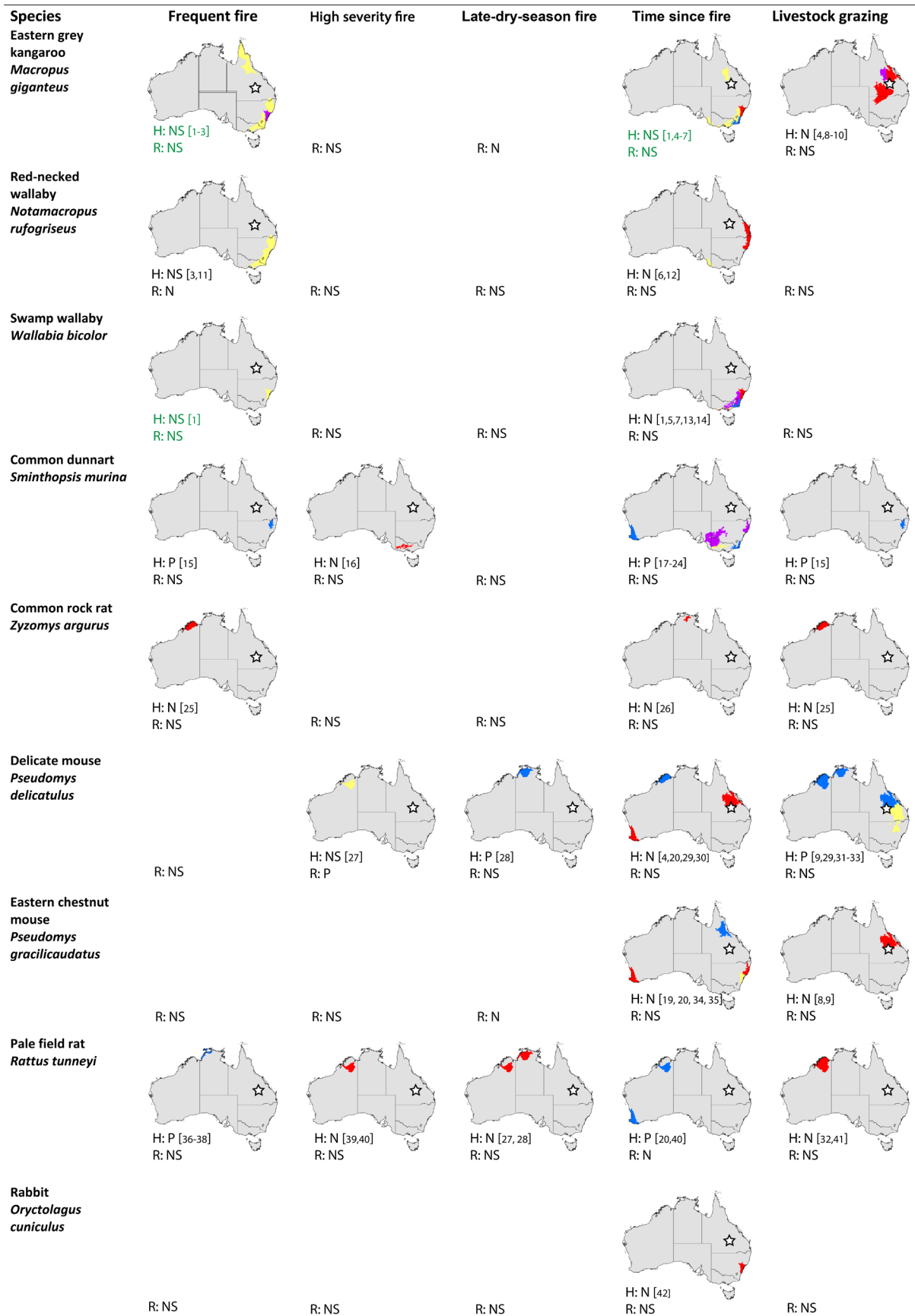
Finding clarity on species' responses to fire regimes is a complex task, hampered by the many contributing and confounding factors. Yet despite the importance of fire to most Australian ecosystems, our literature search revealed very few studies examining species responses to specific fire regime attributes across their broad ranges; and even fewer were able to determine the influence of these attributes. Given the likelihood of species' responses to fire

regimes is strongly influenced by spatially (e.g. soil) and temporally (e.g. recent rainfall) specific factors, it is not surprising that our data only corroborated six of the 31 literature-based hypotheses, suggesting a high variability in intraspecies responses of mammals and reptiles to fire and livestock grazing regimes. There was a lack of consistency in which fire regime attributes most invoked species' responses, revealing the importance of including multiple regime attributes and individual species to best understand fauna responses to fire and grazing. Only seven of 15 species analysed were affected by either fire or livestock grazing regime attributes. Possible explanations for this include that the species with sufficient abundance to detect and analyse are less sensitive to fire and grazing, the effect size of species responses was too small to detect, or the effect was masked by interactions with above-average rainfall during this study.

With only 23% of literature-based hypotheses supported, we conclude that these species' responses to fire and grazing regimes in subtropical woodlands generally differ from those elsewhere. We also hypothesized that findings from bioregions in closer proximity might be more like ours, but this was not the case. The Brigalow Belt bioregion is uniquely situated between coastal and semi-arid zones and between tropical and temperate climates (Ponce Reyes et al., 2016). This may make the fire and livestock grazing regimes, and the response of species to these regimes within the Brigalow Belt, different to those further east, west, north or south. Fire and grazing regimes show substantial variation across Australia: for example, fire return intervals for our study area are slightly longer (3–10 years) than further north in tropical savanna (1–5 years), but still much shorter than further south in temperate woodlands and forests (14–40 years) (Enright et al., 2012). Therefore, definitions of regime attributes such as 'frequent fire' will vary according to the region's prevailing fire regimes. Similarly, aspects of livestock grazing regimes such as stocking rates, duration, type of livestock and method (e.g. rotational, set-stocking or seasonal grazing) differ, as will species' responses to these across environmental gradients. This makes comparisons of a species' response to aspects of fire or grazing regimes very difficult among studies done in different regions, which could help explain inconsistencies in results.

Our study also revealed important knowledge gaps in the response of many species to fire and livestock grazing regime attributes across Australia. Even for relatively common species, responses were often unknown, or knowledge was limited to one or two bioregions. An important reason for this is likely to be the practical challenge of identifying such relationships. Our power analyses showed that a relatively large change (>3.56 change) in species

FIGURE 2 The response of mammals to fire regime attributes and livestock grazing across different Australian bioregions from a literature search of peer-reviewed studies, with a hypothesized response for our study region (H) and result from our study (R) below each map. Within each map literature-based non-significant responses are shaded in yellow, positive responses in blue, negative responses in red and mixed responses in purple. Hypothesized responses were based on the majority finding across studies or if there was none, the study with closest geographic proximity to our study. N, negative response; NS, non-significant response; P, positive response; star, study site. Matching literature-based hypotheses and results from our study are written in green. Fire and grazing regime attributes that did not have a hypothesis were left blank.



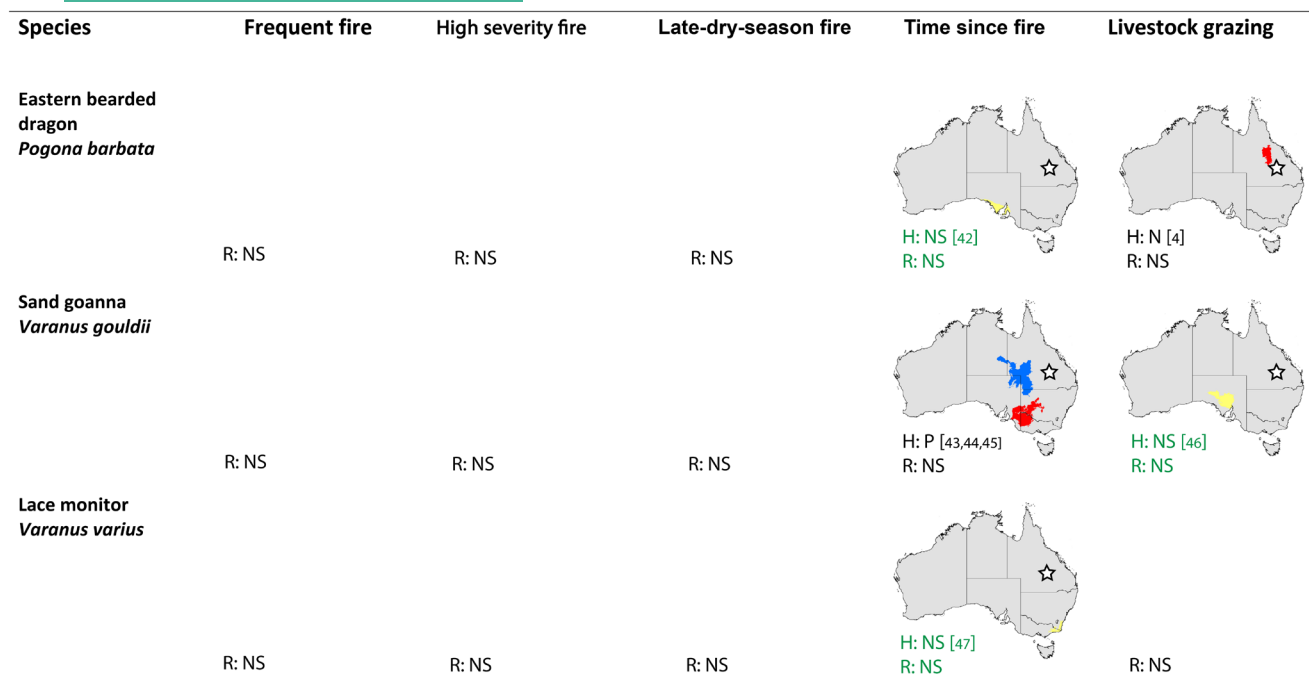


FIGURE 3 The response of reptiles to fire regime attributes and livestock grazing across different Australian bioregions from a literature search of peer-reviewed studies, with a hypothesized response for our study region (H) and result from our study (R) below each map. Within each map literature-based non-significant responses are shaded in yellow, positive responses in blue, negative responses in red and mixed responses in purple. Hypothesized responses were based on the majority finding across studies or if there was none, the study with closest geographic proximity to our study. N, negative response; NS, non-significant response; P, positive response; star, study site. Matching literature-based hypotheses and results from our study are written in green. Fire and grazing regime attributes that did not have a hypothesis were left blank.

occupancy was required to confidently detect an effect of management variables across our 96 samples (48 unique sites); to detect smaller changes in species occupancy (<1.44 change), over 800 samples would have been needed. This highlights a common issue faced in conservation, whereby a large amount of effort is needed to truly determine whether a species is unaffected by a given disturbance, given the variability of ecosystems (Smith et al., 2013). Often, a combination of survey methods is needed to detect cryptic and rare species in the landscape (Vine et al., 2009), and this comes with higher effort and costs. Perhaps because of these challenges, many government agencies, particularly in Australia, rely heavily on expert elicitation to underpin management decisions (Legge et al., 2022). However, our results suggest species responses to large disturbance regimes are highly nuanced and localized, making expert elicitations based on limited geographic extents unrepresentative and suboptimal.

Attributes of the fire regime can vary in their effect on different species, even within broad taxonomic groups. Species-specific responses to fire regime attributes are likely a reflection of different mobility, body size, predation risk, diet and life history between species. For example, we found the delicate mouse's occupancy increased in areas burnt by higher severity fire, likely because it is a small (<12g) rodent noted as a disturbance specialist well-adapted to post-fire conditions (Braithwaite & Brady, 1993; Kutt & Woinarski, 2007) and too small to be a target prey-size for cats

(Woolley et al., 2019). Other small rodents, the eastern chestnut mouse, pale field rat and central short-tailed mouse preferred areas burnt more recently by fire or late-dry season fire. These species are closer to or within the 'critical weight range' known to be particularly affected by cat depredation (24–200g) (Woolley et al., 2019). Yet, despite being a potential post-fire prey target for cats, these species were found to have greater occupancy in these burnt areas. This may indicate that vegetative cover and food availability was greater or recovered quickly post-fire. The response of larger herbivores to time since late-dry-season fire and fire frequency is likely to be at least partially mediated by the quality of forage available (Allred et al., 2011). In our study region eastern grey kangaroos favoured areas recently burnt by late-dry-season fire, indicating that they may be attracted to these areas to feed on high-quality growth post-fire. The red necked wallaby preferred areas that burnt less frequently, perhaps because this species has a comparatively smaller home range and needs denser vegetation or gullies for shelter that are close to more open areas where it feeds (Johnson, 1987).

Rainfall can have a large influence on the response of fauna after disturbances (Yarnell et al., 2007), likely because the response is driven indirectly through the vegetation response (Schieltz & Rubenstein, 2016; Yarnell et al., 2007). When fire or livestock grazing is followed by higher than average rainfall, vegetation regenerates faster, mitigating the overall impact (Yarnell et al., 2007). In contrast, when these disturbances are followed by lower than average

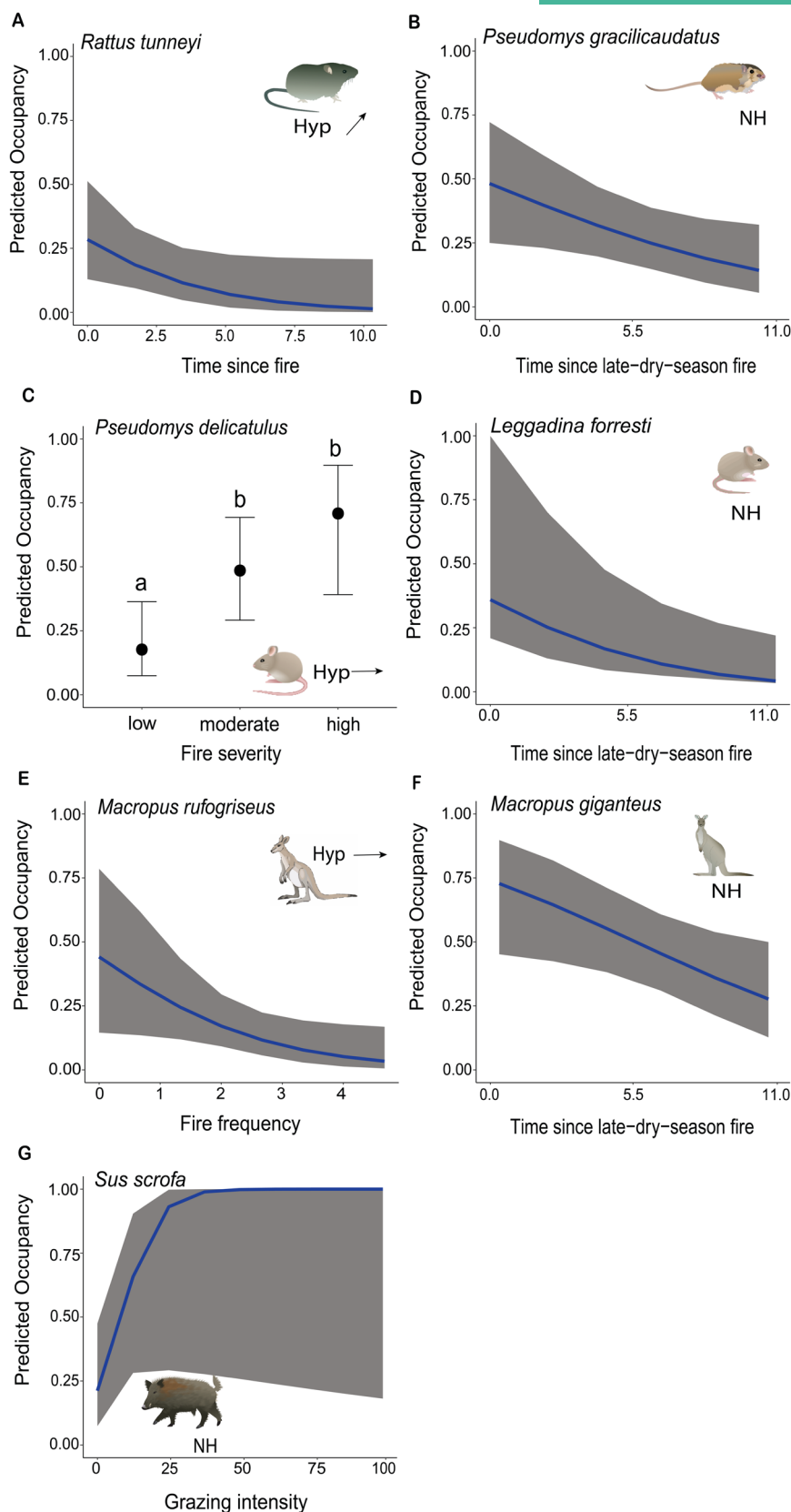


FIGURE 4 Model predictions of occupancy $\pm 95\%$ CI based on the model-averaged estimates of influential variables in top-ranking models ($\Delta AIC_c < 2$) for (A) pale field rat (*Rattus tunneyi*), (B) eastern chestnut mouse (*Pseudomys gracilicaudatus*), (C) delicate mouse (*Pseudomys delicatulus*), (D) central short-tailed mouse (*Leggadina forresti*), (E) red-necked wallaby (*Macropus rufogriseus*), (F) eastern grey kangaroo (*Macropus giganteus*) and (G) pig (*Sus scrofa*) in response to fire and grazing covariates. Black arrows = literature-based hypothesis, NH = no hypothesis could be made from literature. An 'a' symbol indicates a significantly different ($p < 0.05$) species occupancy from 'b' groups.

rainfall, species may decline or not recover because food and shelter resources are absent for an extended period (Kutt, Vanderduys, & O'Reagain, 2012). Our study took place during a La Niña year when rainfall was above average; therefore, the negative effects that can occur from fire and livestock grazing may have been masked because of greater ground cover than in drier years.

Other possible explanations for the lack of response found in this study include cats masking some of the effects of fire regime attributes and livestock grazing on smaller species via predation or changes to prey behaviour (Banks et al., 2018). Depredation could decrease overall occupancy, while avoidance behaviour in the presence of cats could potentially decrease the detectability of that species. In addition, species most affected may have already disappeared or become severely depleted in the landscape. The study area was used for livestock grazing for the previous 150 years, with private protected area status eventuating 20 years ago. This may not be enough time for sensitive species to recover in the landscape. Other studies have shown that fauna recovery after destocking is complex and can vary with rainfall and vegetation community, with species often failing to increase in abundance and richness many years later (Kutt, Vanderduys, Perry, et al., 2012; Neilly et al., 2021). The Carnarvon Ranges had experienced many years of drought prior to this study, and at least two large wildfires had burnt large areas in the last 3 years (2017 and 2020). The combination of altered fire and grazing regimes and drought may have depleted species in the landscape through time.

4.1 | Limitations

The interconnectedness between fire, grazing and vegetation makes separating their individual effects on species challenging. In particular, vegetation communities exhibit unique fire regimes, and species' responses to disturbances such as fire and grazing are often mediated through changes in vegetation structure (Schielitz & Rubenstein, 2016; Zylinski et al., 2022). We found that vegetation type was strongly correlated with fire severity, grazing intensity and time since late-dry-season fire in our study region, complicating efforts to determine whether species such as the delicate mouse, eastern chestnut mouse, eastern grey kangaroo, central short-tail mouse and pig were responding to fire and grazing regime attributes, vegetation type or both. The confounding influence of vegetation type demonstrates the importance of considering habitat characteristics when assessing species responses to disturbance. To better understand the effects of fire, grazing and vegetation type on fauna species, further research that can disentangle these interactions is needed.

5 | CONCLUSIONS

Our findings suggest that studies of faunal responses to fire and grazing regimes cannot be widely generalized across bioregions and that conservation land managers should not rely solely on peer-reviewed

studies from other bioregions to inform their fire and grazing management. Instead, local knowledge and context are needed. Further, given interspecific variation in responses to fire regime attributes, it is likely that heterogeneity in such attributes across the landscape is necessary to cater for different species' requirements (Radford et al., 2015; Smith et al., 2013). We recommend maintaining areas with low grazing pressure wherever possible, as such places are rare in central Queensland (Ponce Reyes et al., 2016) and may be the last refuges for grazing-sensitive species.

AUTHOR CONTRIBUTIONS

Miranda Rew-Duffy collected the data, conducted the analyses and led the writing of the manuscript. Martine Maron, Rebecca Diete, Luke Leung, John Hunter, Zachary Amir and April Reside contributed to the conception and development of the project, contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing or financial interests.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository via <https://doi.org/10.5061/dryad.7d7wm385p> (Rew-Duffy et al., 2025).

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SUPPORTING INFORMATION

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

Data S1: Hypothesized relationships between fauna species and fire and grazing regime attributed derived from peer-reviewed studies across Australia.

Data S2: Histograms of the fire and livestock grazing variables recorded across sites and included in analyses, (A) Time since fire, (B) Time since late-dry-season fire, (C) Fire frequency, (D) Fire severity, (E) Livestock grazing intensity.

Data S3a: A simulated power analysis for detecting changes in occupancy and detection depending on various effect sizes: 0.2, 0.4, 0.6 and 0.8. Number of samples=96, number of sampling occasions=6, Type 1 error=0.05.

Data S3b: A simulated power analysis for the approximate number of samples needed to reach a 0.8 power threshold depending on the various effect sizes: 0.2, 0.4, 0.6 and 0.8. Number of sampling occasions=6, Type 1 error=0.05.

Data S4: Species top-ranked occupancy models that were used for model-averaging ($\Delta AICc < 2$). df = degrees of freedom, LL = log-likelihood output from occupancy model, $AICc$ = Akaike's information criterion, ΔAIC = change in AIC from the top-ranked model, weight = model weight. Grey shading represents variables included in the model.

Data S5: The model-averaged effect of covariates on species detection or occupancy probability. Model = model-averaged parameters for p (detection probability) and Ψ (occupancy probability), Estimate = coefficient estimate, Std. Error = standard error, z-value, Lower CI = lower 95% confidence interval, Upper CI = Upper 95% confidence interval, p-value.

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