Biological Conservation 307 (2025) 111206

Contents lists available at ScienceDirect

Biological Conservation

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

Megafire severity, fire frequency and their interactions with habitat affect post-fire responses of small mammal and reptile species

Don A. Driscoll [a,*], Zac Walker [a], Desley A. Whisson [a], Euan G. Ritchie [a], Chloe Sato [b], Kristina J. Macdonald [a,c]

[a] *School of Life and Environmental Sciences, Deakin University, Burwood, VIC 3125, Australia*
[b] *ACT Government, Australia*
[c] *Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, NT 0810, Australia*

ARTICLE INFO

Keywords:
Bushfires of black summer
Wildfire
Reptile
Mammal
Plant
Invasive and threatened species

ABSTRACT

Climate change is driving extreme fires in many ecosystems around the world. There is an urgent need to understand how co-occurring and interacting threats compound megafire impacts on habitats and wildlife. Using repeated surveys after the 2019–20 Australian megafires, we investigated how the abundance and occupancy of five small mammal and reptile species were influenced by fire severity, fire frequency, feral herbivore impacts, three key habitat components (logs, moss, and weeds), and their interactions. We found that fire severity, fire frequency, weeds and logs were the most important factors affecting species abundance and occupancy. Increasing fire severity caused precipitous declines of the threatened broad-toothed rat *Mastacomys fuscus* and glossy grass skink *Pseudemoia rawlinsoni*. The impact of fire frequency depended on environmental covariates. High fire frequency led to low abundance of the water skink *Eulamprus tympanum* and *M. fuscus* if there were no logs. However, both species increased with fire frequency if logs were abundant, implying that logs can ameliorate negative impacts of frequent fire. The threatened *Eulamprus kosciuskoi* needed fewer than two fires in the past 80 years as well as high moss cover to achieve high abundance. Two threatened alpine skinks, *E. kosciuskoi* and *P. cryodroma*, declined with increasing weed cover. Our study highlights that elucidating interactions between fire and habitat attributes helps to characterise wildfire refuges. Countering the expected impacts of repeated megafires globally will likely require increased protection of refuges from frequent burning, supplementing shelter such as logs where scarce, and mitigating co-occurring and compounding threats.

1. Introduction

Climate change is altering fire regimes, leading to longer fire seasons and more extensive, frequent, and extreme fires in many ecosystems globally (Cunningham et al., 2024; Jones et al., 2022). Increased fire frequency and intensity threatens almost 10,000 species (IUCN, 2024), affecting species' persistence and interactions, community composition, and ecosystem structure and function (Bowman et al., 2009; He et al., 2019; Kelly et al., 2020). Understanding how to counter these escalating impacts requires new knowledge about the circumstances that worsen or limit impacts of extreme wildfires on biodiversity.

Species' responses to fire can depend on specific aspects of the fire regime such as extent, frequency and severity. Fires that burn extensive areas homogeneously can impact the survival of species that rely on unburnt habitat and reduce recolonisation opportunities (Puig-Gironès et al., 2018; Robinson et al., 2013). Frequent fires may limit the ability of populations to recover between disturbances (Fairman et al., 2016; Nolan et al., 2021) and can prevent re-establishment of ecosystem features critical to some species, such as deep moss (Turetsky et al., 2010) and logs (Collins et al., 2012). High fire severity is often associated with intense fire which can kill plants (Trouvé et al., 2021) and cause high animal mortality (Jolly et al., 2022), including in the post-fire period when there is little vegetation for shelter (Campbell-Jones et al., 2022).

The effects of fire on native fauna can be exacerbated by additional stressors such as invasive species (Kelly et al., 2020). Invasive weeds can increase fuel loads and flammability (Read et al., 2020), and alter habitat structure that impacts resources for native wildlife (Santos et al., 2022). Feral herbivores can also have profound effects on ecosystems

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* Corresponding author at: School of Life and Environmental Sciences, Deakin University, Melbourne Burwood Campus, 221 Burwood Highway, Burwood, VIC 3125, Australia.

E-mail address: d.driscoll@deakin.edu.au (D.A. Driscoll).

https://doi.org/10.1016/j.biocon.2025.111206
Received 11 November 2024; Received in revised form 10 April 2025; Accepted 26 April 2025

(Eldridge et al., 2020) by damaging vegetation, soils and waterways and increasing weed invasion (Hartley et al., 2022; King et al., 2019). Loss of habitat in fires can also increase predation risk (Doherty et al., 2022). In turn, the presence of feral herbivores could prolong this higher predation risk by slowing vegetation recovery and shifting habitats to more open understoreys.

The 2019–20 Australian megafires (hereafter; 2019–20 fires) burnt 10.3 M ha of forests, heathlands, and grasslands across south-eastern Australia (Penman et al., 2023). These fires were unprecedented in area burnt and extent of high severity fire (Collins et al., 2021), and were predicted to have substantial impacts on biodiversity (Geary et al., 2022). Feral herbivores, particularly horses and deer, are common in much of the affected area and had the potential to compound fire impacts (Geary et al., 2022).

We investigated the effects of the 2019–20 fires on one small mammal and four reptiles that were predicted to be negatively affected by the fires (Legge et al., 2020) or are threatened by the impacts of feral herbivores (Driscoll et al., 2019). Specifically, taking into account detection probability, we examined how the abundance and occupancy of each species was affected by fire severity, fire frequency, feral herbivores, three key habitat components (logs, moss and weeds), and two-way interactions of these variables. These interactions may help define areas with conditions that act as population refuges and would be priority states for which to manage. Understanding which factors can modify the impacts of megafires on small vertebrates could thereby prove important for planning countermeasures to the globally worsening fire outlook. Our findings provide timely insight with relevance for increasingly fire-affected ecosystems globally.

2. Methods

2.1. Sites

Sites were stratified across two regions; 82 sites in the Australian Alps (mountain series) and 80 sites in lowland forests and heathland (lowland series). The mountain series encompassed subalpine and alpine vegetation above 1200 m (Fig. 1) with annual precipitation averaged across sites of 1460 mm (SD = 305 mm) (BOM, 2020). Historically, mega-fires occurred every 50–100 years (Williams et al., 2008), but recent mega-fires have had shorter intervals (2003, 2006–7, 2013 and 2019–20). In this region, feral horses and deer have increased in abundance and range over the past 20 years (Cairns, 2020; Davis et al., 2016). The lowland sites were below 1200 m (Fig. 1), with average rainfall of 960 mm (SD = 157 mm) (BOM, 2020) including eucalypt forests and coastal heathland. The coastal heathland sites had shrubby, seasonally wet vegetation containing *Xanthorrhoea resinosa;* key habitat for *Pseudemoia rawlinsoni* (Farquhar et al., 2023). In this region there are feral sambar *Cervus unicolor* and hog deer *Axis porcinus* (Davis et al., 2016), but no feral horses.

Sites were surveyed across a range of 2019–20 fire severity classes (unburnt, low-moderate, high, very high; DCCEEW, 2020) from November 2020 to April 2021, between seven and 13 months after the

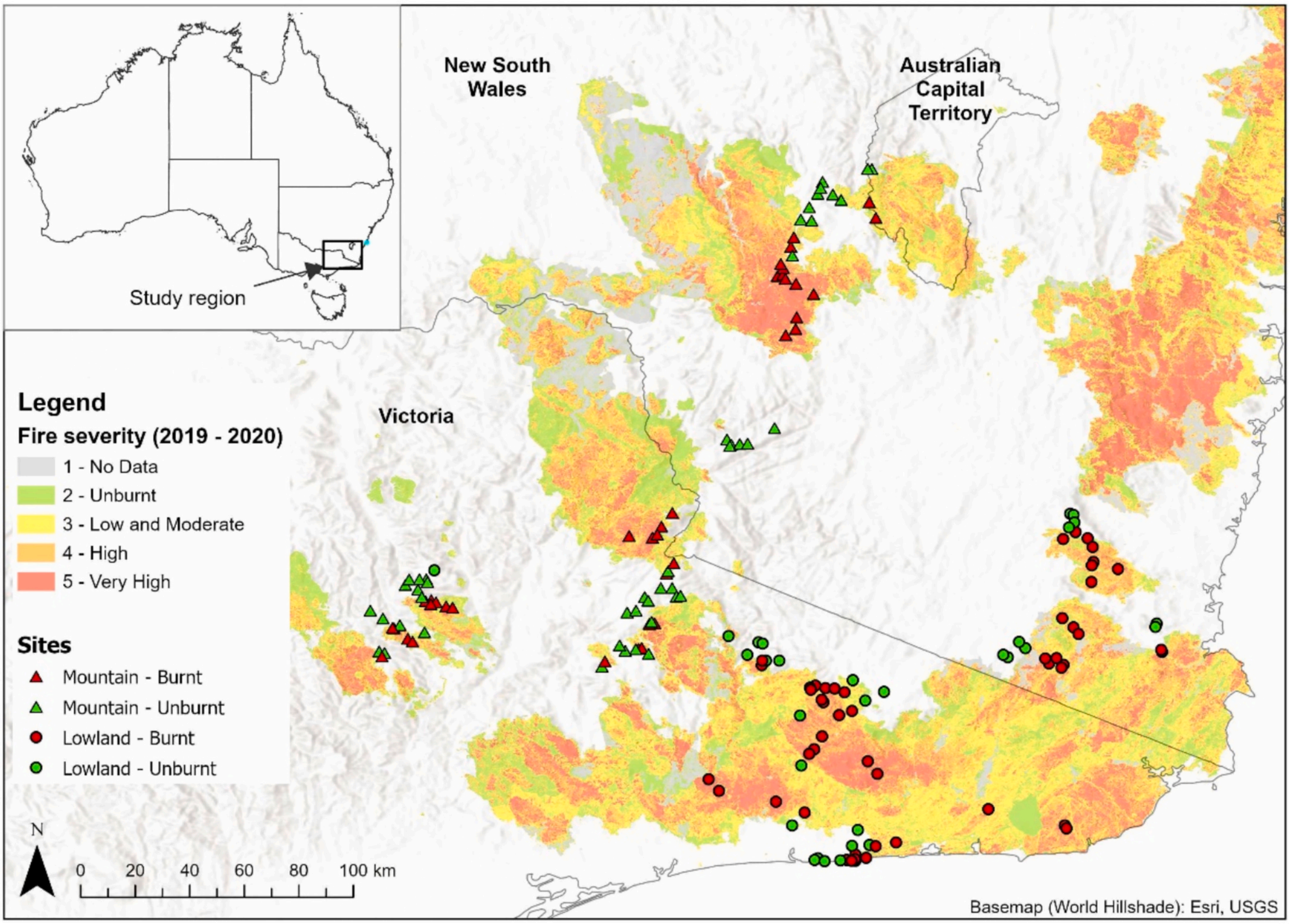

Fig. 1. The location of 162 survey sites across South-eastern Australia, with 82 sites in the alpine region (Mountain series) and 80 sites in lowland eucalypt forests and coastal heathlands (Lowland series). Stratification across burnt and unburnt areas is indicated on a background map of fire severity in the 2019–20 fires (DCCEEW, 2020).

fires ended. For mountain and lowland series respectively, there were 37 and 50 burnt sites, and 45 and 30 sites that were unburnt, with number of sites contingent on availability. Sites were located beside drainage lines and were on average 2.9 km (SD = 2.5 km) from their nearest neighbour (range 0.5 km – 23 km). These distances exceed home ranges of the small vertebrates we sampled, which are on the order of meters to tens of meters (Blomberg and Shine, 2000; Gorissen et al., 2018a; Whisson et al., 2015) giving us confidence that response variables are independent across sites. Treatment variables were unavoidably less independent across sites. Feral horse density was spatially clustered (Moran's $I = 0.51$, Z = 11.7, $P < 0.001$), reflecting densities of these wide-ranging animals, although there remains substantial interspersion of high and low horse damage values (Supplementary Information Fig. S1). Burnt and unburnt sites were well interspersed across the study region at a coarse grain (Fig. 1) while effects were inevitably spatially clustered at a finer grain because wildfire is a contagious process (Moran's $I = 0.35$, Z = 7.77, $P < 0.001$).

At each site, sample points were spaced at 2 m intervals along a 100 m transect. At each point we recorded the presence or absence of moss and exotic plant species (weeds) within 1 m, and the presence of logs or herbivore damage intersecting a 4 m line centred perpendicular to the transect. Moss and logs were measured as covariates because they are expected to influence *Eulamprus* (Brown and Nelson, 1993; Irvin et al., 2003), while we specifically sought to investigate the impacts of exotic plants and herbivores. We used presence/absence measures in 50, four meter transects because this was faster than attempting to measure area covered within quadrats, while still providing quantitative estimates. Herbivore damage (trampling, pugging, tracks, herbivory, or wallows) was attributed to either horses, deer, or pigs based on type of damage, and identification of hoof prints and scat. Our horse and deer impact variables were the proportion of points along the transect with damage attributed to those species. Fire severity was based on an on-ground assessment of the extent to which plants had been burnt (Supplementary Information Table S1) and ranged from 0 (unburnt) to 5 (highest severity).

At the centre of each transect we obtained elevation, years since the fire before 2019–20 and fire frequency (number of fires since 1939) within a GIS. We used a Digital Elevation Model (Geoscience Australia, 2018) to determine elevation. We used spatial databases of fire history for Victoria (DELWP, 2020) and New South Wales (DPIE, 2021) to determine the number of years since the last fire and fire frequency since 1939. In addition, within a buffer of 500 m, 1000 m and 2000 m, we estimated the proportion of the area burnt by the 2019–20 fires (DPIE, 2020).

2.2. Study species

We targeted five species. The endangered (DCCEEW, 2023a) *Mastacomys fuscus* (broad-toothed rat) is a small, herbivorous rodent using grassy-shrubby vegetation of upland wetlands (Green et al., 2014). The threatened *Eulamprus kosciuskoi* (alpine water skink) is restricted to sphagnum moss wetlands and drainage lines within the Australian Alps (Meredith et al., 2003). *Eulamprus tympanum* (southern water skink) is widely distributed throughout south-eastern Australia, often near streams and disturbed areas (Robertson and Coventry, 2019), and can use logs as refuges from fire (Irvin et al., 2003). The endangered (DCCEEW, 2023b) *Pseudemoia cryodroma* (alpine grass skink) has a fragmented distribution above 1000 m in dense wetland vegetation, alpine grasslands and heathlands (Robertson and Coventry, 2019). The data-deficient or threatened (Farquhar et al., 2023) *Pseudemoia rawlinsoni* (glossy grass skink) is largely restricted to wetlands and swampy habitats across south-eastern Australia (Robertson and Coventry, 2019). Four of these species (*M. fuscus, E. tympanum, P. cryodroma and P. rawlinsoni*) were identified as priorities for urgent management intervention following the 2019–20 wildfires (Legge et al., 2020), and two (*E. kosciuskoi* and *M. fuscus*) have suffered declines related to feral horse impacts (Cherubin et al., 2019; Schulz et al., 2019).

2.3. Fauna surveys

Trained observers surveyed each 100 m transect three times between 8:00 h and 19:00 h from November 2020 to April 2021. For *M. fuscus*, two observers searched for faecal pellets and runways in 1 m radius plots at 2 m intervals along the transect (50 plots/transect) to estimate relative abundance as the proportion of plots occupied. For skinks, we had two observers conduct a visual search for up to 20 min. However, practical constraints meant survey effort varied (mean 18.5 min, SD = 2.7) so in analyses, survey duration was included as a variable influencing detection probability. To aid identification, photographs were taken when possible, using a digital SLR camera with a telescopic zoom lens. Identification of *Pseudemoia* species followed Robertson and Coventry (2019) and advice from experts (M. Haines, pers. comms). Temperature, cloud cover, wind, and rainfall were recorded at the beginning of each survey.

2.4. Statistical analyses

There was high collinearity between fire severity and the proportion of burnt area (Pearson's $r = 0.84$, 0.83, 0.82 for burnt area based on 500 m, 1000 m and 2000 m buffers respectively). We therefore excluded proportion burnt from analyses. Other pairs of continuous covariates had $r < 0.33$.

Feral herbivore damage was frequent in the mountain sites (horse impacts: 45 % of sites, deer impacts: 40 %), but rare in the lowlands (horse impacts: 0 %, deer impacts: 15 %). There were few instances of feral pig impacts, and these were excluded from the analyses. For the two species *(E. tympanum* and *P. rawlinsoni*) that occurred in both regions, we completed one series of analysis using the mountain sites only, to investigate the impacts of feral herbivores along with other covariates, and a second series of analysis using the full set of sites, which excluded feral herbivore impacts. For each of our target species, sites were only included if they were within the species' expected distribution and habitat type (Table 1).

We fit N-mixture models with the unmarked package in R (Kellner et al., 2023) to identify variables influencing detection, occupancy (presence/absence), and abundance for most species (Table 1). We used the secondary candidate set strategy to identify the most plausible models (Morin et al., 2020). In the first phase, we identified the best detection covariates (with a null occupancy or abundance model), and

Table 1
Number of sites used for analysis, number of occupied sites, number of animal detections, and model types for each species. Series: Mt. = mountain sites; All = mountain and lowland sites. Model type: det-occ = detection and occupancy; det-abund detection and abundance; bin.glm-occ = binomial generalised linear model used to model occupancy; beta-binom – abund = beta binomial generalised linear model used to model abundance.

Species	Series	Model types	No. sites	No. occ. sites	No. animals
Mastacomys fuscus	Mt	det-occ, beta-binom - abund	81	47	NA
Eulamprus kosciuskoi	Mt	det-occ, det-abund	78	27	125
Eulamprus tympanum	All	det-occ, det-abund	162	66	314
Eulamprus tympanum	Mt	det-occ, det-abund	82	39	170
Pseudemoia cryodroma	Mt	det-occ, det-abund	51	24	78
Pseudemoia rawlinsoni	All	bin. glm-occ	74	29	51
Pseudemoia rawlinsoni	Mt	bin. glm-occ	56	21	32

the best occupancy or abundance covariates (with a null detection model). In each case, we retained models within six Akaike's Information Criterion for small samples (AICc) of the best model (Burnham and Anderson, 2002), as recommended by Morin et al. (2020) to limit the risk of excluding plausible models in the next step. We then fitted all combinations of the best detection models and the best occupancy or abundance models.

Because *M. fuscus* data were the proportion of plots occupied, they were modelled using an over-dispersed beta-binomial generalised linear model with the aod R package (Lesnoff and Lancelot, 2012) (Table 1). There were not enough data to use N-mixture models for *P. rawlinsoni* so we used presence-absence data and fitted binomial generalised linear models (R Core Team, 2024).

We ranked models using AICc, and further considered models within two AICc of the best model (Burnham and Anderson, 2002). We used conditional model averaging with the package MuMIn (Barton, 2020) to obtain predicted values when there was more than one model among the best models. We plotted results for variables with significant ($P < 0.05$) effects.

All mountain series analyses included the potential explanatory variables: fire severity, number of fires 1939–2019, and number of quadrats with moss, logs, weeds, horse impact and deer impact. For the two series of analyses using the whole set of sites (Table 1), we used the same first five variables, plus elevation because the sites spanned a broad elevational range (10–1914 m). We included all combinations of up to four main-effect variables in the same model and no more than one two-way interaction. Detection covariates were air temperature during the survey, percentage cloud cover, wind (calm, light wind, windy),

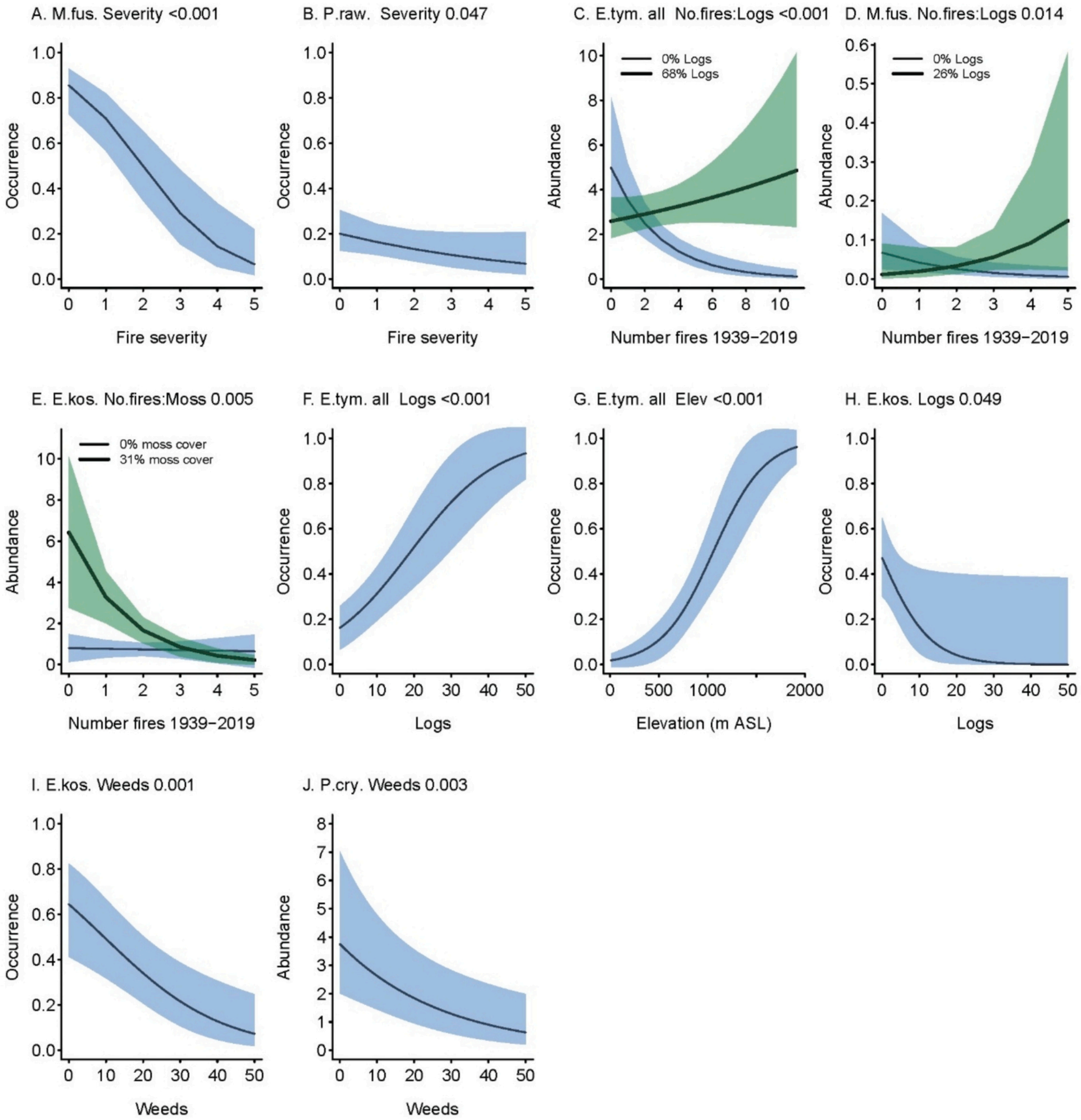

Fig. 2. Predicted values and 95 % CIs illustrating how species were affected by fire, logs, moss and weeds. Panel headers include the species, predictor, and *P* value. Datasets using mountain and lowland sites are headed 'all', while all others use the mountain series only. M.fus. = Broad-toothed rat *Mastacomys fuscus*. E.tym = Southern water skink *Eulamprus tympanum*. E.kos = Alpine water skink *Eulamprus kosciuskoi*. P.cry = Alpine bog skink, *Pseudemoia cryodroma*. P.raw = Glossy grass skink *Pseudemoia rawlinsoni*. Elev = elevation. Colons indicate an interaction. Values for legends (panels C, D, E) are mean ± SD, truncated at 0. X-axis values for logs and weeds are the number of quadrats occupied out of 50.

Julian day to assess seasonal changes in detectability, and survey effort (minutes). The dataset for *E. tympanum* (all sites) was large enough to include ‘rain during the survey’ as an additional detection covariate. Rain was rarely recorded during the mountain series surveys so could not be used as a covariate. All combinations of up to three detection covariates at a time were included in the candidate models. We limited the number of variables used in individual models to avoid overfitting.

3. Results

3.1. Fire covariates

Increasing fire severity was associated with declines of occurrence in *M. fuscus* and *P. rawlinsoni* (Fig. 2 A, B) (see Supplementary InformationTables S2 and S3 for model selection and model averaging tables). In contrast, fire severity was not a good predictor of *E. kosicuskoi*, *E. tympanum* or *P. cryodroma* occurrence, nor the abundance of any species (Supplementary Information Table S2).

Using the full set of sites, *E. tympanum* abundance increased with fire frequency, but only when there was high log cover, with the opposite response when there were no logs (Fig. 2 C). *Mastacomys fuscus* showed a similar relationship (Fig. 2 D), increasing with fire frequency when there were many logs, but declining when logs were absent. In addition, we found that fire frequency interacted with moss cover to influence *E. kosciuskoi* abundance (Fig. 2 E). When moss cover was high, fire frequency had a negative effect on *E. kosciuskoi* abundance. In contrast, at sites with low moss cover, *E. kosciuskoi* abundance was low across all frequencies (Fig. 2 E). Fire frequency had no effect on the abundance of the *Pseudemoia* species, or the occurrence of any species.

3.2. Habitat covariates

Eulamprus tympanum occurred more frequently at sites with a higher proportion of logs and at higher elevations using data from all 162 sites (Fig. 2 F, G). The occurrence of this species showed a similar, but non-significant ($p = 0.062$) relationship with logs when analysing just the mountain series (Supplementary Information Table 3). In contrast, *E. kosciuskoi* occurrence was significantly lower at sites with more logs (Fig. 2 H). We also found that weed cover had a significant negative effect on the occurrence of *E. kosciuskoi* and the abundance of *P. cryodroma* (Fig. 2 I, J).

3.3. Detection

Detection probability depended on environmental covariates, including expected positive relationships with temperature (*E. tympanum*), survey effort (*E. tympanum*, *E. kosciuskoi*) and julian date (*E. kosciuskoi*, *P. cryodroma*), and a negative relationship with cloud cover (*E. tympanum*) (Supplementary Information Fig. S2).

4. Discussion

Our results demonstrate that severe wildfires and more frequent fire can cause large declines of wildlife, but impacts are moderated by habitat attributes. Fire severity affected two of our five focal species, whereas three species were affected by the number of fires in the last 80 years. Our findings provide insight into why fire impacts can vary and can be used to help identify refuges where animals are most likely to persist through otherwise challenging fire regimes or fire events.

4.1. Fire severity

Complete loss of vegetation during high severity fires is expected to drive declines in species that depend on vegetation for food and shelter. We found that high fire severity caused dramatic declines in the occurrence of *M. fuscus* and *P. rawlinsoni. Mastacomys fuscus* habitats typically have substantial cover of grass, sedges and forbs which provide food for this obligate herbivore (Green et al., 2014). Further, structural components such as shrubs or dense grass tussocks provide shelter from harsh weather and predators (Whisson et al., 2015). Little is known about *P. rawlinsoni* (Farquhar et al., 2023), although it lives in low, swampy vegetation (Robertson and Coventry, 2019) and so would be vulnerable if all plants are incinerated.

If these species have time to completely recover between fires, they may persist in the landscape. *Mastacomys fuscus* had recovered from occupying 8 % of burnt sites in the first year after the 2019–20 fires to occupying 66 % of sites by the third year (Schulz et al., 2024). Key to understanding the likelihood of persistence will be knowledge of where populations occur in the landscape, rates of in-situ survival and the probability of recolonisation after local extinction (Puig-Gironès et al., 2018). The 2019–20 fires were characterized by extensive high severity fire (Collins et al., 2021). Such fires could drive localised extinctions over large areas, which may disrupt metapopulation dynamics. It is therefore critical to model fire extent and severity as the climate continues to change, to better understand the spatial challenges of recolonisation. Assisted recolonisation could be needed to accelerate recovery of dispersal-limited species killed by extensive high severity fire (Backus et al., 2022).

In contrast with the decline of *P. rawlinsoni* and *M. fuscus* with high severity fire, the abundance and occurrence of the two *Eulamprus* skinks and *P. cryodroma* appeared to be unaffected by fire severity, despite occurring in the same habitats. Animal behaviour has a critical influence on population responses to fire (Nimmo et al., 2021), with access to protective shelter during a fire being essential for limiting mortality (Webb et al., 2023). *Eulamprus* species, the water skinks, use water and crayfish burrows for shelter (Turner, 2014), and have higher abundance after fire when there are more invertebrate burrows (Gorissen et al., 2018b). We suggest *P. cryodroma* also uses burrows and water to avoid fire and to shelter post-fire, while its congener *P. rawlinsoni* does not, making it vulnerable to decline when fire is severe. Burrowing and burrow-using reptiles are generally more robust to fire impacts (Driscoll and Henderson, 2008; Friend, 1993), explaining some of the contrasting fire responses among species. Unexplained however, is why congeneric species using similar habitat would not all use burrows to escape fire, a question that awaits future behavioural research.

Conflicting with our findings, Letnic et al. (2023) found *E. tympanum* was less abundant in sites burnt at high severity on a high elevation plateau in the northern part of its range. Their sites were similar to our mountain sites but had experienced more severe pre-fire drought. Using the Standardised Precipitation Index (SPI) (Gallagher et al., 2022) of the 12 months prior to December 2019, our mountain sites had a mean SPI of −4.8 (SD = 7.9), whereas Letnic et al.’s (2023) sites had a mean SPI of −17.1 (SD = 14.4). These observations are consistent with Driscoll et al.’s (2024) synthesis demonstrating that high pre-fire drought generally increased the impact of the 2019–20 bushfires on plant and animal species. If *E. tympanum* uses water and burrows to survive through fire, the implication is that in severe drought, water is less available, and burrows may be less effective because the peaty swamp soils can be incinerated.

Dispersal and predation are two other potential mechanisms affecting species’ responses to fire severity. In our study, fire severity was highly correlated with fire extent. If a species is eliminated by fire, the time it takes to re-establish depends on the distance to unburnt areas and the species’ dispersal ability (Lindenmayer et al., 2014). The dispersal capabilities of the skink species have not been studied. Genetic evidence suggests *P. cryodroma* is unlikely to be a strong disperser (Haines et al., 2017), yet did not decline with high severity, extensive fire. Further, although predation-risk can change after fire (Doherty et al., 2022), this probably does not account for the decline of *P. rawlinsoni* because the similar sized *P. cryodroma* was not affected by fire severity, but would likely be affected by generalist predators. Therefore, it seems unlikely that dispersal or predation account for the differences in species' responses to fire severity, rather differential use of burrows and water remains the most likely explanation.

While the impact of fire severity often depends on site condition (Driscoll et al., 2024), none of our habitat components, including moss, logs and weeds, substantively modified fire severity impacts. Understanding the effects of fire-regime components depends on identifying such interactions (Driscoll et al., 2010) and future research should include among their survey covariates, variables most likely to alter a species' resistance to high severity fire.

4.2. *Fire frequency and interactions*

Fire frequency influenced the abundance of three species, but in all cases these effects were moderated by environmental covariates. While increasing fire frequency led to declines of both the non-threatened skink *E. tympanum*, and the broad-toothed rat *M. fuscus*, this trend was reversed if log density was high. Logs or coarse woody debris are associated with increased densities of many taxonomic groups (Croft et al., 2010) including reptiles (Evans et al., 2019). Irvin et al. (2003) suggested that logs help *E. tympanum* survive fire by providing shelter inside hollows. While fallen logs have been inferred to aid species' resistance to fire (Driscoll et al., 2024; Irvin et al., 2003), this is not always the case (Hale et al., 2021) and there is very little direct evidence. In one study, added coarse woody debris increased reptile richness and abundance, but Evans et al. (2019) found that adding fire nullified the benefits of the added timber, possibly because habitat quality of burnt timber is reduced (Croft et al., 2010). Our results show that logs have potential to reverse the negative impacts of frequent fire for some species, and experimental work (e.g. Croft et al., 2010) is now needed to confirm this relationship and better understand the mechanism.

For *M. fuscus*, the mechanism could be related to shrub growth caused by fire every few decades (Camac et al., 2017), because shrubs provide important shelter and protection from feral predators (Green et al., 2014). Sheltered space beneath the winter snow can be absent after fire (Green and Sanecki, 2006), but logs could help create those subnivean spaces, as well as possible refuge during fire (Hale et al., 2021) and protection from predators. The combination of shrub cover with logs could be increasing habitat suitability for *M. fuscus* when there is frequent fire. However, this relationship is tenuous. Logs can be destroyed when fire is frequent (Collins et al., 2012) so *M. fuscus* may decline under a predicted regime of increasing fire frequency.

Eulamprus kosciuskoi, the threatened water skink, had consistent low abundance across fire frequencies when moss cover was low, but at high moss cover, had a strong negative relationship with fire frequency. Further, this threatened species had a negative relationship with the number of logs, whereas the common *E. tympanum* had a positive relationship. It seems unlikely that *E. kosciuskoi* would be disadvantaged by having logs in their habitat. It is more likely that *E. tympanum* is outcompeting *E. kosciuskoi* in disturbed sites (Meredith et al., 2003) characterized by low moss cover or frequent fire and high log cover. High log cover tended to occur at sites where trees had fallen after being killed in major fires in 2003. *Eulamprus tympanum* was previously reported to have low abundance when moss cover was high (Brown and Nelson, 1993), so mossy sites appear to provide refuges for *E. kosciuskoi* if fire frequency is low, with less than two fires over 80 years (Fig. 2 F). Critical to determining the extent of likely declines of *E. kosciuscoi* will be to understand the distribution of, and threats to, mossy, rarely burnt habitats.

Other fire-competition studies of animals report competitive release after fire, followed by intensifying competition (e.g. Allen et al., 2022; Higgs and Fox, 1993). In contrast, for *Eulamprus*, we suggest that frequent fire favours the competitively dominant species, provided that logs are present. Further, we suggest the dominant species is less successful in undisturbed sites, potentially due to foliage or moss shading basking sites (Kutt, 1993), creating space for the competitively inferior species. Direct evaluation of competition, survival, and reproduction of these species is needed, along with experimental manipulations (Higgs and Fox, 1993), to explore our hypothesised mechanisms.

4.3. *Weeds*

High weed cover had negative effects on the two threatened alpine skink species (*E. kosciuskoi* occurrence and *P. cryodroma* abundance). Invasive weeds can negatively impact reptiles and reduce habitat quality by altering the structure and distribution of vegetation (Martin and Murray, 2011). Invasion-driven reptile declines can also arise from altered food availability (Martin and Murray, 2011), altered thermoregulation (Hacking et al., 2014) and potential increased predation (Hawlena et al., 2010). Expert opinion on Australian reptiles suggested weeds were likely to interact with fire to affect more species than other interacting threats (Santos et al., 2022). Our study highlights a clear threat of weeds to these alpine skinks. Recent research in the Australian alps demonstrates that weeds increase with total herbivore pressure, a pressure driven largely by feral horses, deer, and lagomorphs (Hartley et al., 2022). This evidence highlights a potential indirect way that feral herbivores could influence reptiles.

4.4. *Feral herbivores*

Detrimental impacts of feral herbivores on ecosystems, plants and animals are well established, both for the Australian alps (Driscoll et al., 2019; Hartley et al., 2022; Robertson et al., 2019; Treby and Grover, 2023) (Supplementary Information Fig. S3) and in many ecosystems globally (Coates et al., 2021; Eldridge et al., 2020; Rogers, 1991; Zalba and Cozzani, 2004). It was therefore surprising not to detect an effect of feral herbivores in this study, especially given some of our target species are known to be vulnerable to feral horse impacts (Cherubin et al., 2019; Schulz et al., 2019). Impacts of mammalian herbivores may be moderated by high rainfall (Orr et al., 2022), with plant growth appearing to outstrip herbivore consumption in the high rainfall year that followed the 2019–20 fires. Future studies should also consider alternative measures of feral herbivore impacts that cover larger areas, such as drone-sourced data (Giles et al., 2023), or remotely-sensed data that capture more of the history of feral herbivore impacts.

5. Conclusions

Fire regimes have already become more extreme under climate change and these changes will worsen over time (Cunningham et al., 2024). Adapting to climate change includes limiting biodiversity loss by adopting new management strategies and priorities that use new knowledge about wildlife responses to fire (Legge et al., 2023). Our findings show that to understand the response of animals to a wildfire, it is critical to consider the fire regime including fire severity and frequency, along with interactions with environmental variables.

Like other recent megafires around the world (Ayars et al., 2023; El Garroussi et al., 2024; Parisien et al., 2023), the 2019–20 Australian fires left a large extent of recently burnt ecosystems. Given that wildfire impacts are worsened when fire intervals are short or fire is frequent, a robust management response would aim to reduce fire frequency and restrict the extent of high severity fire, including by increasing capability in rapid wildfire suppression (Driscoll et al., 2024; Lindenmayer and Zylstra, 2024).

New knowledge about factors interacting with fire make it possible to spatially prioritise management actions. Rapid wildfire suppression could be used to protect mapped critical habitat for threatened species. For example, in our case study, rapid suppression would focus on rarely burnt sites with high moss cover for the threatened skink, *E. kosciuskoi.* Such refuges would also be a high priority for protection from other threats, such as development, weeds and feral herbivores. Manipulating sites where threatened species occur to increase in-situ survival through fires is also a potential new management response. Countermeasures could include adding course woody debris (Manning et al., 2013) or other structures (Watchorn et al., 2022) and controlling invasive species. Research aimed at identifying environmental refuges for taxa that are vulnerable to frequent or severe fire must now be a priority throughout flammable regions of the world. This research would support pre-fire seeding of sites with micro-refuges and enable important spatial refuges to be incorporated into fire plans for protection when megafires return. Nevertheless, such manipulations are unlikely to be enough to prevent species declines and extinctions unless climate change is urgently reversed.

CRediT authorship contribution statement

Don A. Driscoll: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Zac Walker:** Writing – review & editing, Project administration, Investigation, Data curation. **Desley A. Whisson:** Writing – review & editing, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Euan G. Ritchie:** Writing – review & editing, Funding acquisition, Conceptualization. **Chloe Sato:** Writing – review & editing, Funding acquisition, Conceptualization. **Kristina J. Macdonald:** Writing – review & editing, Project administration, Investigation.

Declaration of competing interest

We have nothing to declare.

Acknowledgments

Kevin Rowe (Museums Victoria), Mel Schroder (NSW Parks and Wildlife Service), Cat Campbell (NSW Parks and Wildlife Service), Renee Brawata (ACT Government), Sakib Kazi (Zoos Victoria), Jerry Alexander (DELWP) and Phoebe Macak (DELWP) provided technical advice and assistance in the field. Rangers from Parks Victoria, ACT Parks and Conservation, and NSW Parks and Wildlife service assisted with site access. Maggie Haines and Ken Green assisted with skink identification. Kris Bell, Kyra Evanochko, Emma Sumner, Kim Lewendowski and Matthew Lefoe assisted in the field. This project was funded by the Australian Government Department of Agriculture, Water and Environment's Wildlife and Habitat Bushfire Recovery Program 2019–2020, GA-2000607. This research was completed under the Deakin Animal Ethics Committee project number B28-2020, National Parks Act (Victoria) permit # 10009667; Nature Conservation Act Licence (ACT) # PA20212; Scientific licence under the Biodiversity Conservation Act (NSW) # SL102483.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111206.

Data availability

Data will be made available on request.

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