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Unburnt refugia support post-fire population recovery of a threatened arboreal marsupial, Leadbeater's possum

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A R T I C L E I N F O

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A B S T R A C T

Large wildfires have the potential to create heterogeneous landscapes in forest ecosystems. Range-restricted species in fire-prone regions have evolved to persist in the face of periodic disturbance due to wildfire. However, the factors that enable them to do so are often poorly understood. Whether post-fire population recovery is driven by survival of individuals within the burnt area (*in situ* recovery) or by recolonisation from unburnt habitat outside the fire perimeter (*ex situ* recovery), and over what timeframe this occurs, is valuable knowledge for conservation management. Understanding post-fire population dynamics is important when considering whether management interventions are required to prevent local extinctions. We examined the influence of fire-derived landscape context on site occupancy by the critically endangered Leadbeater's possum *Gymnobelideus leadbeateri* in south-eastern Australia, 6–11 years after a large wildfire in 2009. Our aim was to assess whether site occupancy was influenced by fire extent in the local landscape, distance from unburnt habitat outside the fire perimeter, and/or pre-fire disturbance history. We used arboreal camera trapping to survey Leadbeater's possums within the burnt area, using 732 cameras at 245 sites. We used occupancy modelling to estimate the effects on site occupancy of (1) unburnt habitat surrounding sites (500 m radius), (2) distance from unburnt habitat at the fire perimeter, and (3) whether the site had been disturbed by either fire or timber harvesting in the decades prior to the 2009 fire. Leadbeater's possums were detected at 78 of the 245 sites (32 %). Site occupancy was positively influenced by the presence of unburnt habitat within 500 m, and was higher at sites that had experienced disturbance between the 2009 fire and the previous major wildfire in 1939. Proximity to unburnt habitat outside the fire perimeter did not influence occupancy. Our results suggest that population recovery was driven primarily by *in situ* survival and recovery, rather than via recolonisation from source populations outside the burnt area. Our findings indicate that Leadbeater's possum populations are more likely to recover from fires that are more heterogeneous in their severity, leaving relatively more unburnt patches within their perimeter. Post-fire management interventions such as translocation to facilitate population recovery are likely unnecessary for this species, provided surviving individuals have spatial continuity of habitat to enable recolonisation. Management strategies aimed at the retention of unburnt patches within the footprint of future fires will likely promote the post-fire recovery of arboreal mammal species in fire-prone forests, particularly under a changing climate with increased frequency and intensity of wildfires.

1. Introduction

Fire is a major natural disturbance influencing the distribution and abundance of species in fire-prone regions worldwide (Bowman et al., 2009; Bradstock et al., 2012b). Under predicted future climate scenarios, wildfires in many forest ecosystems are likely to become larger and more frequent (Bradstock et al., 2012a; Flannigan et al., 2013; Fasullo et al., 2018; Bowman et al., 2020; Cattau et al., 2020). These

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changes could threaten many fire-sensitive species, such as those less able to survive the direct impacts of fire, less able to recolonise burnt habitat as it recovers post-fire, or those that require fire-sensitive habitat elements that are slow to recover after major fire events (Bradstock et al., 2002, 2005; Whelan et al., 2002). With increasing extinction risk due to changing fire regimes for many forest-dependent species (Kelly et al., 2020), understanding how populations recover following major fire events is increasingly important.

Whether post-fire population recovery is driven primarily by *in situ* survival followed by population growth and expansion (*in situ* recovery), or by recolonisation by individuals dispersing from unburnt areas outside the fire perimeter (*ex situ* recovery), is a key question of interest across species and ecosystems globally (Brotons et al., 2005; Knight and Holt, 2005; Bradstock, 2008; Banks et al., 2017; Gill et al., 2022). In the case of *in situ* recovery, survival of individual animals within the broader burnt area is facilitated by fine-scale refugia in the form of habitat features (e.g., logs, hollow-bearing trees) that persist within burnt habitat (Banks et al., 2015; Berry et al., 2015). The presence of these individual habitat features, referred to as 'biological legacies', may enable persistence and recovery of populations following fire (Hutto, 1995; Franklin et al., 2000; Johnstone et al., 2016). In addition to fine-scaled legacy elements, post-fire recovery is also supported by larger patches of unburnt vegetation within the perimeter of a fire-affected area (Robinson et al., 2013; Meddens et al., 2018). For some arboreal marsupials, the amount of unburnt relative to burnt vegetation in the local landscape of a site affects post-fire occurrence (Lindenmayer et al., 2013). Where biological legacies or unburnt patches provide sufficient resources, they may enable a nucleated mode of population recovery, whereby individuals persist until habitat in the surrounding burnt landscape recovers, facilitating recolonisation from within the fire footprint (Banks et al., 2017).

Recolonisation of burnt habitat from outside the fire perimeter (*ex-situ* recovery) will be influenced by the distance to source populations and a species' reproductive and dispersal ability (Whelan et al., 2002). If *ex situ* recovery drives recolonisation, decreasing occurrence and abundance are expected with increasing distance from the fire perimeter in the short term (Knight and Holt, 2005; Banks et al., 2017). In large disturbances, distance-to-edge effects may be particularly pronounced (Turner et al., 1998). For example, some studies have found gradients in occurrence of ground-dwelling mammals (Do Rosário and Mathias, 2007) and bird assemblages (Watson et al., 2012; Morales et al., 2020), where both refuge patches and burnt habitat close to the fire perimeter are more likely to be occupied post-fire, compared with sites in the interior of the fire footprint. Distance-to-edge effects in post-fire population recovery are mediated by species vagility, with highly mobile species, such as birds and some rodents, able to rapidly recolonise the interior of disturbed areas (Lindenmayer et al., 2009; Sainz-Elipe et al., 2012; Puig-Gironès et al., 2018; Murphy et al., 2021). In contrast, less mobile species may recolonise more slowly. Spatial patterns of species occurrence in burnt landscapes can provide insights into the relative importance of *in situ* and *ex situ* recovery mechanisms.

The duration after fire until regenerating habitat becomes able to support dispersing individuals, and thus population recovery, also varies among species (Meddens et al., 2018). Most studies investigating post-fire recovery of fauna have focused on the years immediately after fire (e.g., <5 years; Banks et al., 2011; Lindenmayer et al., 2009, 2013; Diffendorfer et al., 2012; Robinson et al., 2014; Chia et al., 2015; Puig-Gironès et al., 2018; Shaw et al., 2021), when differences in structure and composition of burnt and unburnt vegetation patches are most stark (Whelan, 1995; Lentile et al., 2007). Whether these effects persist into the medium term (e.g., 5–15 years) post-fire is poorly known for many species but is critical for understanding species' resilience to fire.

In this study, we report on post-fire site occupancy of a threatened arboreal marsupial, Leadbeater's possum *Gymnobelideus leadbeateri*, in a forested landscape burnt by a large wildfire 6–11 years prior. Leadbeater's possum (~120 g) has a colonial social structure, with family groups defending territories of approximately 1–3 ha from conspecifics (Smith, 1980). Individuals typically forage within 100 m (and up to 600–700 m) from den sites (Lindenmayer et al., 2018b; McBurney, 2019). Colonies consist of a breeding pair and several younger non-breeding individuals; breeding females typically reproduce twice per year, with each litter containing on average 1.5 young (Smith, 1984). Dispersal occurs prior to reproductive maturity (Harley and Lill, 2007) at 10 months old in females and 15 months in males (Smith, 1984), with dispersal distances of approximately 1 km reported (Harley, 2005). The possums are dependent both on *Acacia* spp. (a key foraging resource), and on cavities in hollow-bearing trees, where they den and breed, requiring multiple den sites per colony territory (Lindenmayer et al., 1991a). Peak densities of Leadbeater's possum occur in younger forest stands 15–50 years old (Smith and Lindenmayer, 1992; Banks et al., 2013), conditional on the presence of den sites. Hollow-bearing trees are a declining resource across the possum's range, particularly dead hollow-bearing trees that are decaying and collapsing at accelerating rates (Lindenmayer et al., 1997; Lindenmayer et al., 2020; Lindenmayer et al., 2023) with loss and deterioration positively associated with disturbance (fire and/or timber harvesting) (Lindenmayer et al., 2018a). The extent of disturbance due to timber harvesting in the landscape surrounding a site has been shown to negatively affect Leadbeater's possum occurrence (Lindenmayer et al., 2020).

Leadbeater's possum has declined from a historically broader range in south-eastern Australia, indicated by sub-fossil and historical records (pre-1920) (Bilney et al., 2010), likely linked to changes in climate and vegetation (Lindenmayer et al., 1991c). The possum is now largely restricted to montane ash forest and sub-alpine woodlands in a 70 × 95 km area of the Victorian Central Highlands region, south-eastern Australia (Department of Environment, Land, Water and Planning, 2022). In the 'Black Saturday' fires of February 2009, the Kilmore East-Murrindindi fire complex burned through approximately 400,000 ha, including 78,300 ha of montane ash forest, and 36 % of the potential montane ash habitat within the contemporary distribution of Leadbeater's possum (Lumsden et al., 2013). The severe impact of the fire on this species, based on an inferred decline in area of occupancy, contributed to a change in conservation status from 'Endangered' to 'Critically Endangered' (Australian Government Department of Agriculture, Water and the Environment, 2015). Post-fire surveys at sites or in areas occupied by Leadbeater's possum pre-fire found that the species was absent or extremely rare on burned sites within the first three years post-fire (Harley, 2016; Lindenmayer et al., 2013; Lumsden et al., 2013), even in areas of low fire severity. Some individuals were recorded persisting in unburnt refuges within the fire footprint (Lumsden et al., 2013), but post-fire survival rates of these animals are unknown.

The relative importance of unburnt habitat within the burnt area and distance to the fire perimeter in driving the recolonisation process of Leadbeater's possums is not well understood. Previous studies have found no relationship between distance to fire perimeter and occurrence or abundance of Leadbeater's possum 11 years after the 1983 fire that affected the southern part of the possum's range (van der Ree and Loyn, 2002), or 55 years post-fire (Nelson et al., 1996). However, these studies were limited to locations <2 km from the fire perimeter. Wildfires in montane ash forest are usually of large extent (McCarthy et al., 1999), and in some locations within the footprint of the 2009 fire, the nearest unburnt Leadbeater's possum habitat at the fire perimeter was ~14 km distant. The 2009 fire event has thus provided an opportunity to examine post-fire population recovery by Leadbeater's possum at a large spatial scale, enabling insights into how this arboreal marsupial responds to the impacts of large wildfires. An improved understanding of post-fire population recovery dynamics is required to determine if management interventions, such as re-introductions or translocations, are required to re-establish Leadbeater's possum populations in fire-impacted areas.

The primary objective of this study was to understand how the presence of unburnt habitat surrounding sites, and distance to habitat outside the fire perimeter, affect site-level occupancy by Leadbeater's possum in the medium term (6–11 years) post-fire. Specifically, we wanted to determine if post-fire occurrence of this species suggests an *in situ* or *ex situ* mode of population recovery in this threatened species. If post-fire population recovery is influenced by unburnt refugia in the local landscape (*in situ* recovery), we would expect a positive relationship between site occupancy and the presence of unburnt habitat surrounding a site. If, alternatively, recolonisation occurs from unburnt habitat outside the fire perimeter (*ex situ* recovery), we would expect decreasing occurrence with increasing distance from the fire perimeter.

2. Methods

2.1. Study area

Our study was undertaken in the montane ash forests of the Victorian Central Highlands, approximately 80 km north-east of the city of Melbourne, in south-eastern Australia (Fig. 1). Montane ash forests in this area are dominated by Mountain Ash *Eucalyptus regnans* stands, with Alpine Ash *E. delegatensis* and Shining Gum *E. nitens* occurring at lower frequencies. These tree species are readily killed by fire, regenerating from seed after stand-replacing disturbance events. Such disturbance events occur naturally as high-intensity wildfires or are human-induced through clearfell timber harvesting followed by regeneration burning and re-seeding (Ashton, 1976). Large, intense wildfires occur periodically in this ecosystem, with an estimated return interval of ~ 75–150 years in any location (McCarthy et al., 1999), but may occur more or less frequently than this in some areas of the Central Highlands (Todd et al., 2016). Prior to the 2009 fire, the last large wildfires affecting the entirety of our study area occurred in 1939, 70 years prior (there were also fires in 1983, with minimal overlap with the 2009 fire). Timber harvesting is restricted to areas of State Forest where clearfell harvesting has typically been practiced on a rotation length of 70–80 years, as well as other silvicultural activity such as thinning which has been practiced at approximately 30-year intervals (VEAC, 2017). The study area also incorporates a system of National Parks, closed water catchments and other reserves, from which timber harvesting is excluded, which comprised 18 % of sites in the final dataset. The remaining 82 % of sites sampled State Forest where timber harvesting and other silvicultural practices have occurred since the stand-replacing wildfires of 1939.

2.2. Study design

We collated camera trapping data from three survey programs undertaken within the footprint of the 2009 fire, spanning a time period from 6 to 11 years post-fire. The first program was targeted surveys for Leadbeater's possum with random (43 sites) and non-random site selection (18 sites). Randomly selected sites were at least 1 km apart, within 200 m of roads, and stratified across two land tenures: State Forest available for timber harvesting, and Parks and Conservation Reserves where harvesting is prohibited. Non-random site selection was in State Forest and aimed to maximise Leadbeater's possum detections, with sites selected based on the presence of habitat features known to be associated with possum presence (e.g., high density of *Acacia* spp., dense mid-story strata, Nelson et al., 2017). Survey cameras at non-randomly selected sites were installed at least 400 m from existing Leadbeater's

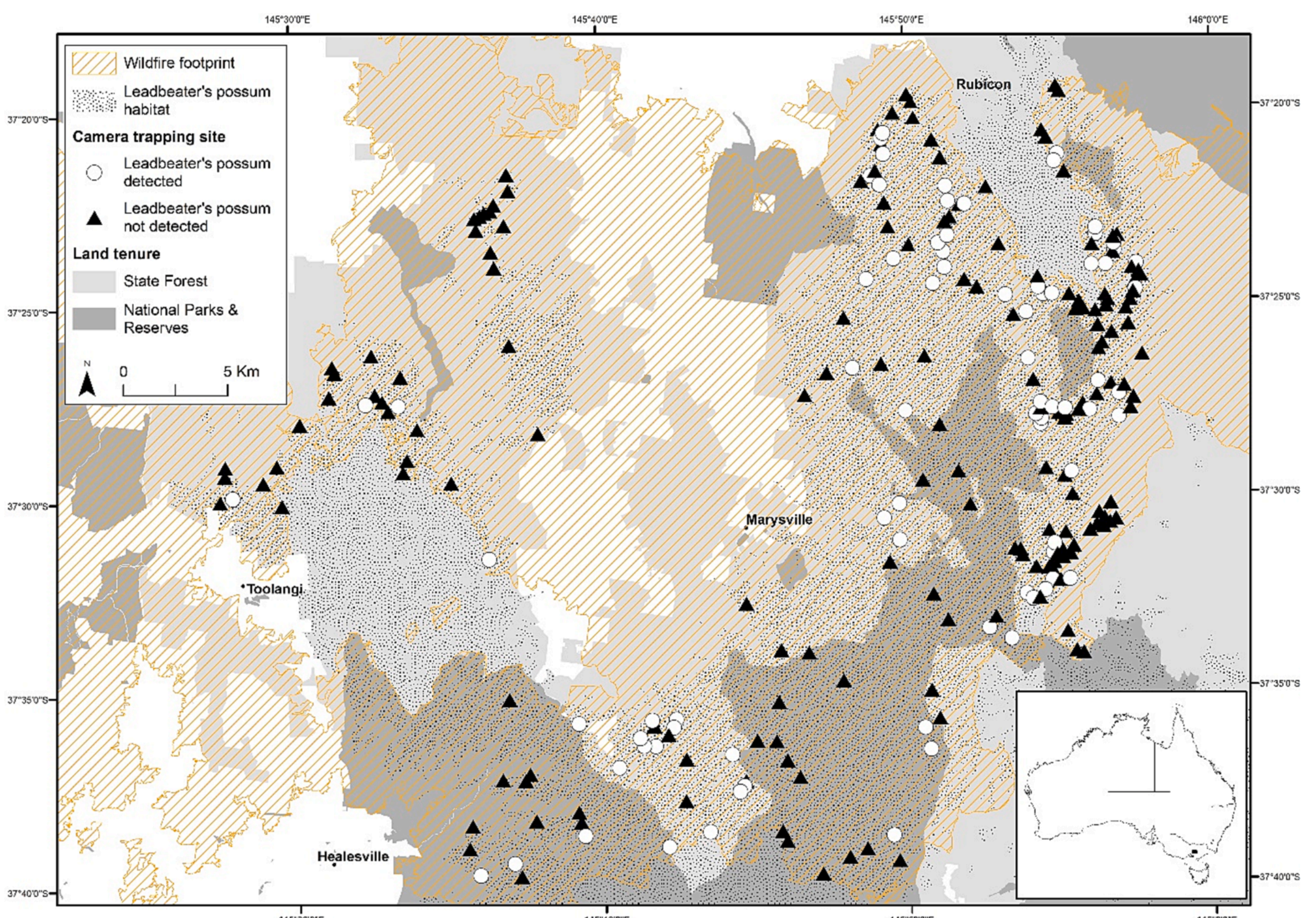

Fig. 1. Locations of surveyed sites within the area burnt by the 2009 Kilmore-Murrindindi fire complex, south-east Australia.

possum records. The second program undertook pre-harvest surveys in areas planned for timber harvesting (123 sites). All cameras during pre-harvest surveys were placed within planned harvest areas ('coupes') or within 100 m of coupe boundaries. Cameras of neighbouring sites during this program were at least 200 m apart with multiple sites within each coupe. The third program undertook additional surveys specifically for this investigation (61 sites). These surveys aimed to fill sampling gaps along two continuous gradients: the extent of unburnt forest in the landscape surrounding sites (500 m radius) and distance to unburnt Leadbeater's possum habitat at the fire perimeter. These sites were at least 350 m apart.

The final dataset was made up of 245 sites. A site consisted of three baited camera traps, each set 50–100 m apart, with 200 m – 4.5 km between sites (Fig. 1). The minimum spacing between sites of 200 m was based on current knowledge of the home range of Leadbeater's possum: 1–3 ha (Smith, 1980). A circular area of 3 ha has a radius of 97.5 m. Possum detections by cameras at neighbouring sites were assumed to be independent observations. That is, assuming a possum detected by a camera is at the core of a 3 ha circular home range, we considered another possum detection by a camera of a neighbouring site > 200 m away to be an independent observation (i.e., a different individual). We excluded sites that had been salvage harvested following the 2009 fire, to avoid confounding factors related to additional post-fire disturbance (Lindenmayer and Ough, 2006).

2.3. Camera trapping surveys

All surveys followed identical survey protocols: passive infra-red survey cameras (Reconyx HC500, HC600, PC900, HP2X, SC950, Reconyx, Holmen, WI, USA) were installed 1.5–3 m opposite a bait station containing creamed honey, an effective attractant for Leadbeater's possums (Smith, 1984; Harley et al., 2014; Nelson et al., 2017). Cameras were set to high sensitivity, taking five images per trigger with a 'RapidFire' image interval and no delay between successive triggers. Cameras and bait stations were placed at heights 1–24 m above ground (median height 3.6 m), depending on the structure of the forest stand. These positions targeted laterally-connected vegetation strata where Leadbeater's possums were most likely to be traversing or foraging within that stand. Cameras were left in place for 21–45 nights (mean 30, SD 3.9). This survey protocol has a high probability of detecting Leadbeater's possums on occupied sites (0.87 – 0.95 for three cameras set for at least 28 nights, Nelson et al., 2017).

Camera trapping data were available from 732 cameras at 245 sites. All sites had data from three cameras each, except two sites with either one or two cameras due to malfunction or camera theft. Surveyed sites were distributed throughout Leadbeater's possum habitat that had been burnt in the 2009 fire, from 0.2 to 11.9 km from the nearest unburnt habitat immediately adjacent to the fire perimeter (Fig. 1). Of the 245 sites surveyed, 38 (16 %) had the surrounding area (500 m radius) entirely burnt by the 2009 fire (i.e., no local unburnt refugia), with the remainder containing at least some unburnt forest (>0.04 ha in size). 101 sites (41 %) had experienced additional disturbance between the 1939 and 2009 fires.

All survey images were reviewed, photographed animals were identified to species and images were assigned metadata species tags using the image-tagging software DigiKam (https://www.digikam.org). Nightly detection histories for Leadbeater's possum were compiled for each camera using the package *camtrapR* (Niedballa et al., 2016) in the statistical program R (R Core Team, 2020).

2.4. Environmental covariates

The two primary gradients of interest were: (1) distance to unburnt Leadbeater's possum habitat at the fire perimeter (i.e., *ex situ* recolonisation source), and (2) the proportion of forest surrounding each site (500 m radius) that was unburnt by the 2009 fire (i.e., *in situ* population recovery source). Leadbeater's possum habitat was defined as either montane ash eucalypt forest or sub-alpine woodland (the latter dominated by Snow Gum *E. pauciflora*). These forest types constitute the core habitat for the possum, which rarely occurs in adjacent drier 'mixed species' eucalypt forests (Smith and Lindenmayer, 1988; McBride et al., 2019; Macak et al., 2023). Distance to unburnt habitat outside the fire footprint was measured for all sites, to the closest Leadbeater's possum habitat abutting the fire perimeter. Suitable habitat beyond the fire footprint, separated from the fire perimeter by mixed species forest or non-forest, was not considered. Fire severity mapping of the 2009 fire was used to determine the presence and area of unburnt patches within a 500 m radius of each site's centrepoint. Classified fire severity maps (20 m resolution) of the 2009 fires were obtained from the Victorian Department of Environment, Land, Water and Planning (https://discover.data.vic.gov.au/dataset/victorian-bushfires-severity-map-2009-polygons1). These maps were derived using the pre- and post-fire differenced Normalised Burn Ratio (Key and Benson, 2006) from a combination of SPOT 4/5 and Landsat 5 imagery captured shortly before and after the wildfire. The differenced Normalised Burn Ratio was then categorised into five fire severity classes for forested vegetation using thresholds derived from groundtruthed data (https://discover.data.vic.gov.au/dataset/victorian-bushfires-severity-map-2009-polygons1). The classes were: crown burn (70–100 % of tree crowns burnt); crown scorch (60–100 % of tree crowns scorched); moderate crown scorch (30–60 % of tree crowns scorched); light to no crown scorch and understorey burnt (<30 % of tree crowns scorched and >1 % of understorey burnt); and, unburnt (100 % of understorey unburnt). All burnt pixels were lumped as 'burnt', irrespective of fire severity.

Additionally, we included two other covariates that may influence site occupancy by Leadbeater's possum. First, disturbance history of each surveyed site, as previous studies have found the occurrence of Leadbeater's possum is negatively associated with the extent of logging disturbance in the surrounding landscape (Lindenmayer et al., 2020). However, this relationship is complex as occupancy rates are higher in young forest, including timber harvesting regrowth, if hollows are present or nearby (Nelson et al., 2017). We classified sites as having 'some disturbance' if at least one of the three cameras at the site intersected any area mapped as fire- or timber harvesting-affected, at any time between the 1939 and 2009 fires. All other sites, which had no additional disturbance between the 1939 and 2009 fires, were classed as 'no disturbance'. Second, we included a terrain wetness index, which is positively associated with habitat features known to be important for Leadbeater's possum, such as abundance of large old hollow-bearing trees (Lindenmayer et al., 2016) and the basal area of some *Acacia* spp. (Lindenmayer et al., 2021c). We determined area burnt in the surrounding landscape of all sites, distance to unburnt habitat at the fire perimeter, and pre-2009 disturbance history in ArcGIS (ArcMap v.10.5) using spatial data on forest types (e.g., Hamilton et al., 1999), fire severity, and timber harvesting and fire history derived from Victorian Government spatial data layers (State Government of Victoria, 2021). We extracted terrain wetness index values for the centrepoint of each site from a raster layer with a 250 m resolution.

2.5. Statistical analyses

A single season occupancy model was used to estimate occupancy (ψ) and detection (p) (MacKenzie et al., 2002). This model allows for imperfect detection at sites that are occupied. The model was constructed in a Bayesian framework, using a space-state formulation (Royle and Kéry, 2007). The model incorporates potential effects on the occupancy rate from: (1) the distance to the nearest Leadbeater's possum habitat outside the fire perimeter (univariate spline smoother (Wood, 2017)); (2) the availability of unburnt refugia within 500 m of a site; (3) site-level disturbance (by fire or timber harvesting) at any time between the 1939 and 2009 fires (indicator variable); and (4) site-level terrain wetness.

We tested models representing local refugia as either a continuous variable (i.e., proportion unburnt) or indicator variable (i.e., whether the surrounding area was entirely burnt or not entirely burnt). We report the indicator (i.e., categorical) view of this covariate here, as it performed better during analyses (with a more consistent posterior distribution). A fire severity covariate was not included as it showed signs of collinearity with the area unburnt surrounding sites (*U*). Time-since-fire (i.e., the time elapsed between the 2009 fire and the commencement of camera trap surveys at a site) also showed signs of collinearity with other terms, including the area unburnt surrounding the site, disturbance history and the wetness index, and was excluded from the analysis.

Disturbance history (fire or timber harvesting) between the 1939 and 2009 fires was used as an indicator variable (*H*). The (standardised) terrain wetness index (*W*) was used as a linear predictor. The square root of the distance to Leadbeater's possum habitat outside the fire perimeter (*D*) was included as a univariate smoother (Wood, 2017). The area unburnt surrounding the sites (*U*) was included as a univariate spline smoother (Wood, 2017). Univariate smoothers were used for variables where the effect was nonlinear over the range of values surveyed, based on initial viewing of the data.

Detection on a given night (*P*) was calculated at the site level across all cameras. There was an array of between 1 and 3 operational cameras at each site. These were combined for a single detection indicator across the camera array, at the site level, for each night, accounting for the number of active cameras as formulated in equation (1) below. The model assumes that the detection rate per camera per night (ρ) for the cameras was constant across sites and time given temporal variables like temperature were not recorded on all nights at all locations. Combined, this results in a model given below:

$$\begin{gathered} Z_i \sim Bern(\mu_i) \\ logit(\mu_i) = \beta_0 + \beta_1 \times F_i + \beta_2 \times H_i + \beta_3 \times W_i + sm(D_i) + sm(U_i) \\ P_i = 1 - (1-\rho)^{nCam} \\ X_{i,j} \sim Bern(Z_i \times P_i) \end{gathered} \tag{1}$$

where Z_i is 1 when the site is occupied and 0 otherwise; μ_i is the expected occupancy probability for site i; $X_{i,j}$ is 1 when the camera array at site i detected a Leadbeater's possum on night j and 0 if the camera array was operational, but no Leadbeater's possums were detected; and *sm* denotes that a spline smoother was used on that explanatory variable.

The model was constructed in JAGS (Plummer, 2003) using the package *R2jags* (Su and Yajima, 2020) in the statistical program R (R Core Team, 2020). All priors were naïve/uninformative to avoid any introduced assumptions affecting the results of the analysis. Five chains were run for 60,000 iterations with the first 20,000 discarded. Convergence was assessed visually and where all Gelman and Rubin's convergence diagnostic potential scale reduction factors were less than 1.05 (Gelman et al., 2004). The smoother was constructed using a penalized spline regression (Crainiceanu et al., 2005).

3. Results

Leadbeater's possums were detected at 78 of the 245 sites surveyed (32 %), up to 10.6 km from the nearest unburnt habitat outside the fire perimeter. Sixty-three percent of sites with detections had experienced disturbance by either timber harvesting or fire in between the 1939 and 2009 wildfires, with only 41 % of survey sites in this category. The occupancy model gave an estimated detection rate per camera per night of 0.1 (95 % credible interval (CI): 0.09 to 0.1) at occupied sites. Thus, at a standard array with three cameras, the nightly detection rate was 0.26 (95 % CI: 0.25 to 0.28) at occupied sites when using the equation for P_i from equation (1) above.

Leadbeater's possum occupancy was higher at sites that had experienced a disturbance between the 1939 fire and the 2009 fire, and/or when the local landscape was not entirely burnt by the 2009 fire (Table 1 and Fig. 2). When the surrounding 500 m radius of a site had been entirely burnt (i.e., no local unburnt refugia), the odds the site was occupied decreased by 83 % (95 % CI: 40 to 96) compared to sites with only partially burnt 500 m radii. At disturbed sites, the odds that the site was occupied increased by a factor of 3.7 (95 % CI: 2.1 to 6.7) compared to sites that had no disturbance between the 1939 and 2009 fires. There was insufficient evidence that the distance to Leadbeater's possum habitat outside the fire perimeter (Fig. 3) or the wetness index impacted the occupancy rate during the timeframe of our study (Table 1). The 95 % CI for each of those parameters was relatively wide and incorporated zero (no significant effect). The effect of the smoothing spline is shown in Fig. 3.

Table 1
Parameter estimates (posterior medians and 95% credible intervals) from the final model of Leadbeater's possum occupancy. The detection intercept term gives the probability of a single camera detecting a Leadbeater's possum on a given night at an occupied site. The occupancy parameters are given on the logit scale.

Component	Parameter	Median	Lower bound	Upper bound
Detection	Intercept	0.097	0.090	0.104
Occupancy	Intercept	−1.129	−1.674	−0.587
Occupancy	Entirely burnt	−1.757	−3.167	−0.512
Occupancy	Disturbed	1.303	0.730	1.904
Occupancy	Terrain wetness	0.027	−0.333	0.420

4. Discussion

Understanding population- and species-level responses to fire is an integral step towards informed conservation management in fire-prone ecosystems. We utilised a large arboreal camera trapping dataset to reveal patterns of site occupancy by the range-restricted, critically endangered Leadbeater's possum after a major wildfire. To our knowledge this is the largest arboreal camera trapping study yet reported in the published literature from Australia (Moore et al., 2021). We demonstrate that Leadbeater's possum occurrence in the medium-term post-fire (6–11 years) is positively influenced by the presence of unburnt refugia surrounding sites, rather than proximity to unburnt habitat outside the fire perimeter.

Leadbeater's possum occupancy was significantly higher at sites with unburnt refugia in the surrounding area, compared to sites that were within entirely burnt landscapes. This result concurs with previous work on this species, where animals were more likely to be found in areas with more intact surrounding forest. For example, from stagwatching surveys in the first three years after the same fire event, Lindenmayer et al. (2013) reported decreased abundance of Leadbeater's possum with increased amounts of burned forest in the surrounding landscape. Other studies have shown that several arboreal mammal species, including Leadbeater's possum, declined in abundance with increased amounts of burnt forest surrounding a site (Chia et al., 2015; Lindenmayer et al., 2020; May-Stubbles et al., 2022). The higher occupancy rates we observed at sites where the surrounding area had *not* been entirely burnt by the 2009 fire suggests that Leadbeater's possums may persist in unburnt patches within the fire footprint into the medium term, enabling *in situ* population recovery from residual possum colonies once the surrounding habitat becomes suitable. This *in situ* survival followed by population recovery from within has also been found in ground-dwelling, small mammal communities in montane forest (Banks et al., 2017), heathy woodland (Hale et al., 2022) and tropical savannah woodland (Shaw et al., 2021). For arboreal, cavity-dependent fauna, within-patch habitat attributes important for persistence include biological legacies that are less likely to persist in the surrounding burnt forest, such as both living and dead hollow-bearing trees (Franklin et al., 2000; Lindenmayer et al., 2012; Lindenmayer et al., 2018a; Lindenmayer et al., 2020). These features are critical habitat elements for Leadbeater's possum (Lindenmayer et al., 1991a), with possums more

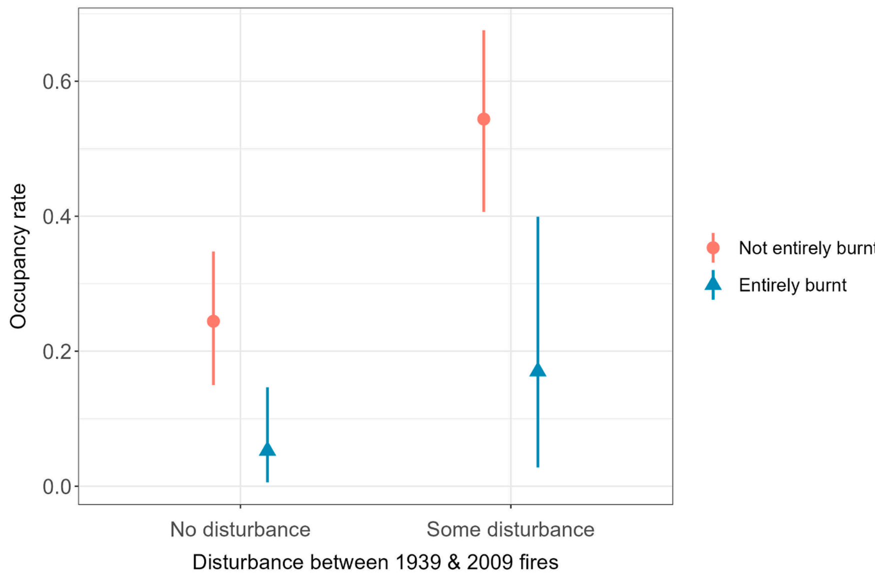

Fig. 2. Estimated probabilities of Leadbeater's possum occupancy under different disturbance scenarios, given the other covariates (terrain wetness, burnt) are all held at their means. Colours refer to whether the surrounding landscape (500 m radius) of a site was entirely burnt by the 2009 fire or not. 'Disturbance' refers to any site-level timber harvesting or fire.

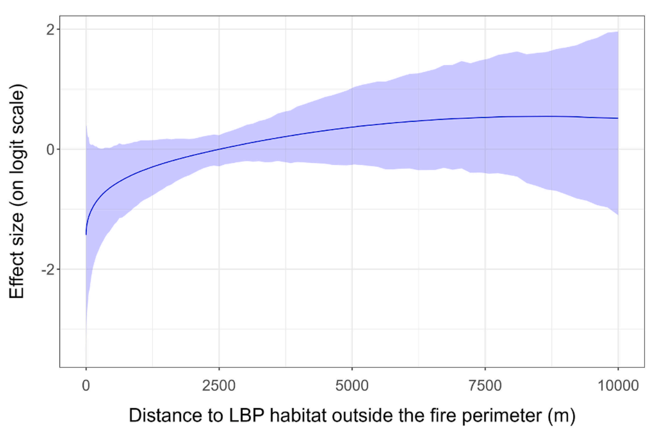

Fig. 3. Estimated effect of distance to Leadbeater's possum (LBP) habitat outside the fire perimeter on the log-odds of site occupancy. The fitted curve is a smoothing spline. The shaded area is the 95% credible interval.

likely to occur at sites with more hollow-bearing trees (Lindenmayer et al., 2020). The post-fire distribution and abundance of hollow-bearing trees is likely an important factor in the persistence of surviving possum colonies in unburnt refuge patches.

Unburnt patches exist at different scales (e.g., individual trees to forest stands; Turner et al., 1994), and whether minimum patch size thresholds exist, supporting persistence of species post-fire, is of interest for conservation management following large wildfires. The occurrence of fine-scaled biological legacies in post-fire forest landscapes is linked to site- and landscape-scale disturbance regimes. These include factors such as the pre-fire age of a forest stand (i.e., the time elapsed since the previous fire) and the site-level disturbance history, where the structure and composition of early successional forest stands differ markedly between sites where the prior disturbance was wildfire and sites where the prior disturbance was human-induced such as clearcut timber harvesting, which typically removes a greater proportion of above-ground biomass (Lindenmayer et al., 2019). Refugia during and after a fire may exist as large contiguous patches of unburnt habitat, or as fine-scaled elements such as riparian vegetation corridors associated with streams, or at a very fine-scale, e.g., as individual hollow-bearing trees that may escape burning due to topographic position (Berry et al., 2015) or fire behaviour (Collins et al., 2019). Unburnt refugia important for post-fire persistence of Leadbeater's possum may exist at finer scales than we considered, however we did not consider unburnt patch size in our study, and our class 'some unburnt refugia within 500 m' included both aggregated and dispersed unburnt pixels, from 0 to 100 % of the surrounding landscape. Unburnt patches larger than 1 ha were rare within the Kilmore-Murrindindi fires, occupying less than 1 % of the area within this fire complex (Leonard et al., 2014). Leadbeater's possums were present in a small proportion (16 %) of unburnt patches surveyed 3.5 years after the 2009 fire, with the smallest occupied patch ~ 10 ha in size (Lumsden et al., 2013). At that time, it was unknown whether possums would survive in these patches until the surrounding forest became suitable, or if they would be unable to persist due to patch size (Lindenmayer and Possingham, 1995), lack of resources or predation. Our results suggest that Leadbeater's possum colonies survived within the fire footprint, likely due to resources available in unburnt patches. Closely monitoring the fate of surviving possum colonies after a large fire event would yield valuable insights into patch size thresholds for persistence until the surrounding habitat recovers. Furthermore, extending this work to investigate the impact of fire severity, rather than a binary view of whether habitat was burnt or not burnt, would likely increase our understanding of post-fire population recovery in Leadbeater's possum.

We found no relationship between the distance to unburnt habitat at the fire perimeter and the occurrence of Leadbeater's possum, suggesting that recolonisation from source populations outside the burnt area (*ex situ* recovery) was not a dominant factor in the possum's population recovery after the 2009 fire. Similar conclusions have been reached in other studies, where distance to unburned habitat at the fire perimeter had no apparent influence on post-fire occurrence of small mammal and bird species (Banks et al., 2011; Diffendorfer et al., 2012; Hale et al., 2022), with few exceptions (e.g., Do Rosário and Mathias, 2007; Puig-Gironès et al., 2018; Puig-Gironès et al., 2022). These studies all examined post-fire occupancy 0–3 years after a wildfire. Our data were collected between 6 and 11 years post-fire, and while this timeframe addresses a temporal knowledge gap in the occurrence of this species in early successional forest, we cannot exclude the possibility that recolonisation via emigration of individuals from outside the burnt area could already have occurred *prior* to our sampling. Furthermore, some authors have pointed out that *in situ* and *ex situ* recovery mechanisms for post-fire recolonisation are not mutually exclusive (Watson et al., 2012; Puig-Gironès et al., 2018). Unburnt 'islands' of habitat in burnt landscapes can act as 'stepping stones' for dispersing animals (Longland and Bateman, 2002), whether the dispersers originate from within or outside of a fire-affected area. Given this, we acknowledge that the design of our study did not allow us to exclude the possibility of a co-occurring model of recovery, with both *in situ* and *ex situ* pathways contributing to population recovery. However, some factors suggest that *in situ* recovery was the main driver of post-fire recolonisation, and that rapid *ex situ* recovery did not occur prior to our sampling. First, Leadbeater's possum was virtually absent from previously-occupied burnt sites in the first three years after the 2009 fire (Lindenmayer et al., 2013), and populations within the burnt area were likely decimated. Second, we detected the possum throughout the entire burnt area from as early as six years after the fire, with no effect of time-since-fire across the five-year spread of our dataset (data not shown). This indicates rapid, broadscale recolonisation across a large area. If this pattern was driven by *ex situ* recovery, our temporal sampling window should have been sufficient to capture it, particularly given the large size of the fire, with regenerating Leadbeater's possum habitat in the interior up to 12 km distant from the perimeter, and the modest dispersal capacity (~1 km) of Leadbeater's possum (Harley, 2005). Instead, we found the probability of site occupancy did not decrease with increased distance from the fire perimeter. These results concur with those of van der Ree and Loyn (2002) who found that Leadbeater's possum recolonised burnt forest within the southern part of the species' range within 11 years of the 1983 fire, discerning no influence of distance to the fire boundary on site occupancy. That study investigated post-fire Leadbeater's possum occurrence up to a maximum distance of 2 km from a fire edge, and the earliest time-since-fire assessed was 11 years. Here, we detected Leadbeater's possum in the interior of the fire footprint, up to 10.6 km from the nearest unburnt habitat at the fire perimeter, a detection which occurred seven years and nine months post-fire. The lack of a relationship between site occupancy and distance to the fire perimeter suggests that post-fire recolonisation more likely occurred from within the burnt area.

Sites that had experienced disturbance from either timber harvesting or fire between the 1939 and 2009 fires were more likely to be occupied by Leadbeater's possum. This was an unexpected result, as disturbance generally results in fewer biological legacies such as hollow-bearing trees (Smith et al., 2008; Haslem et al., 2012). This finding contrasts with previous studies that have identified negative relationships between the occurrence of this species and the amount of harvested (Lindenmayer et al., 2020) or burnt (Lindenmayer et al., 2013) forest in the surrounding landscape. However, in those studies, disturbance was quantified at the landscape level whereas in our study, disturbance between 1939 and 2009 was only considered at the site level. Our finding that sites were more likely to be occupied by the possum after the 2009 fire if they had experienced a disturbance between the 1939 and 2009 fires may reflect the tendency of Leadbeater's possum to inhabit young forest (Banks et al., 2013) as well as ecotones between younger and older forest stands (Nelson et al., 1996). In a study of hollow-bearing tree occupancy, the highest emergence rates of Leadbeater's possums were observed from trees in relatively young stands regenerating from timber harvesting during the 1960s–1990s, compared to stands of 1939 fire regrowth, old growth or mixed age stands (Lindenmayer et al., 2017). When the 2009 fire occurred, Leadbeater's possums may therefore have been more abundant in these relatively younger stands, provided hollow-bearing trees were present within the stand or nearby. If this was the case, it may have influenced the 'starting point' for population recovery (Banks et al., 2011), especially if more individuals were present in these areas to potentially survive the 2009 fire and persist locally, and critical resources (food and denning sites) were available post-fire.

Post-fire population dynamics are governed primarily by the availability of resources, which themselves are affected by interactions between time-since-fire (Monamy and Fox, 2000), climate, aridity gradients (Puig-Gironès et al., 2017) and antecedent disturbance regimes (Lindenmayer et al., 2019). Fire-induced changes to vegetation structure are ephemeral, in that burnt areas may be impermeable to certain species for a period after a fire, then become highly permeable once fire-affected habitat reaches some threshold of suitability (Borchert and Borchert, 2013; Parkins et al., 2018). Leadbeater's possums are arboreal and forest-dependent, requiring stands with adequate foraging and denning resources, and can most easily traverse vegetation in dense stands (Lindenmayer et al., 1991a). In montane ash forests, the time between a stand-replacing fire and canopy closure of the regrowth is only 2–3 years (Blair et al., 2017). Regenerating forest, characterised by a high density of *Acacia* spp. (Lindenmayer et al., 2021b), an important foraging resource for Leadbeater's possum, would likely become permeable to dispersing individuals within 3–6 years post-fire. The key limiting habitat feature for the possum in such landscapes is likely the availability of suitable hollow-bearing trees for denning, with cavities with small entrance sizes but internal dimensions large enough to accommodate the nests built by this colonial species (Lindenmayer et al., 1991b). Notably, the dominant cohort of fire-killed trees were re-growth from a previous fire in 1939, and were 70 years old when burnt in 2009. In montane ash forest, cavities do not typically begin developing until trees are at least 120 years old (Ambrose, 1982), and the 70-year old fire-killed trees are unlikely to provide hollows suitable for most arboreal species in this landscape (Lindenmayer et al., 2023). Hollow-bearing trees in these forests (including dead and decaying trees) are generally biological legacies from older cohorts, and are deteriorating and collapsing faster than they can be replaced by natural accumulation in forests that are now 84 years old (i.e., the 1939 fire regrowth) or much younger (i.e., the 14 year old 2009 fire regrowth) (Lindenmayer et al., 2018a). Our finding that Leadbeater's possums recolonised much of the fire-affected forest within 6–11 years seems surprising in the context of this species' requirement for larger hollow-bearing trees, which were destroyed in large numbers by the 2009 fires. Hollow-bearing trees in forest burned in 2009 have deteriorated more than those in unburned areas (Lindenmayer et al., 2012; Lindenmayer et al., 2021a). One potential factor that may have aided the rapid recolonisation of a large area of regenerating forest with few hollow-bearing trees is the possibility that recolonising Leadbeater's possums may use atypical den sites, such as fallen logs, burnt stumps of collapsed trees or ground debris more frequently than currently appreciated. Emergence from such features by dispersing individuals has been directly observed (Smith and Lindenmayer, 1988). However, this behaviour is unlikely to explain the majority of the population recovery, particularly given the well-known importance of large cavities in large old trees for this species (Smith and Lindenmayer, 1988; Lindenmayer et al., 1991a; Lindenmayer et al., 2013; Lindenmayer et al., 2017). Alternatively, individual possums could be foraging further than usual from increasingly scarce den trees, which may have subsequent consequences for individual's energy budgets, as well as the maximum carrying capacity of a regenerating forest largely devoid of den trees. Further, population recovery following future fires in this landscape may differ from what we observed after the 2009 fires. That is, after successive further fires the set of biological legacies available to support post-fire persistence will have changed, with a key factor being the ongoing decline of hollow-bearing trees in this ecosystem (Lindenmayer et al., 2020). Targeted research directed at these knowledge gaps, as well as ongoing monitoring of the possum in these areas, including time series data (e.g., Blair et al., 2017), is required to provide critical information for understanding longer-term population dynamics post-fire.

A potentially confounding factor in our study design that may limit our ability to infer the effects of disturbance on occupancy of Leadbeater's possum, is that we measured disturbance at the site level, not the landscape level. Detected possums may have travelled from locations distant from the cameras, either drawn by the bait lures or during their usual overnight activity. This possibility underscores an inherent drawback of camera trapping surveys to assess occupancy if sites are close together – the potential to double-count individual animals that may travel between sites we assume to be independent. The effective survey radius of a baited camera trap for Leadbeater's possum is uncertain but could be at least 80 m (Holland et al., 2011). Previous work has shown that Leadbeater's possums are detected by arboreal cameras even on 1 ha plots with no hollow-bearing trees (Nelson et al., 2017), suggesting that individuals may travel from den sites located >100 m from camera traps. Although most movements between den trees are less than 200 m (Smith, 1984; Lindenmayer and Meggs, 1996), movement up to 600 m between dens within one night has also been documented (Lindenmayer et al., 2018b). Therefore, if possums were travelling several hundred metres before encountering the camera traps, they may be persisting in the landscape due to habitat features beyond the 500 m radius of our survey sites, such as hollow-bearing trees in unburnt patches located far from the cameras. An important limitation of arboreal camera trapping for Leadbeater's possum is the unknown distance that an individual has travelled to reach a camera, and uncertainty of where detected possums are denning. Nevertheless, that the possums were detected by cameras stationed in apparently hollow-free patches of forest, and areas subject to disturbance pre-fire, demonstrates that these habitats are still used by this species in burnt landscapes.

5. Conclusions

We present evidence that the post-fire recovery of Leadbeater's possum populations is positively associated with the presence of nearby unburnt habitat, as well as additional site disturbance between the large wildfire events of 1939 and 2009. Post-fire occurrence of the possum in the medium term (6–11 years following fire) was not influenced by proximity to unburnt habitat outside the fire, and we conclude that population recovery likely occurred via an *in situ* survival and recovery model, rather than via recolonisation from source populations outside the burnt area. However, our surveys did not commence until six years post-fire, and we cannot entirely exclude supplementation via *ex situ* recovery because recolonisation by individuals from outside the burnt area may have occurred prior to or during our sampling period. Further work to address post-fire recovery dynamics should incorporate the years immediately following fire, and track change in occupancy over time. Population genetics approaches comparing animals inside and outside the burned area could also provide useful information on the origin of post-fire recolonisers (e.g., Lindenmayer et al. 2005).

We present evidence that Leadbeater's possum occurrence within burnt areas is associated with whether unburnt forest remains locally, and that populations are more likely to recover from fires that are spatially heterogeneous, with more unburnt patches in the fire footprint. The optimum scale and distribution of unburnt refugia, and minimum thresholds of critical habitat features within them, is an important area for future research to support the persistence of this critically endangered species in post-fire landscapes. Whether post-disturbance management interventions such as reintroductions or translocations might be required to re-establish populations of threatened species first requires an improved understanding of post-fire population recovery dynamics. For Leadbeater's possum, such interventions are likely unnecessary, provided surviving individuals have spatial continuity of habitat to enable recolonisation.

This study builds on a body of research pointing to the importance of unburnt refugia within fire extents for supporting residual populations and subsequent population expansion (Robinson et al., 2013). Management strategies aimed at promoting the occurrence of unburnt patches within the footprint of future forest fires will be important for the conservation of arboreal mammal species in fire-prone landscapes, particularly under a changing climate with increased frequency and intensity of wildfires (Bowman et al., 2020).

CRediT authorship contribution statement

Louise K. Durkin: Conceptualization, Validation, Investigation, Data curation, Visualization, Writing – original draft, Writing – review & editing. **Paul Moloney:** Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Jemma K. Cripps:** Validation, Investigation, Data curation, Writing – review & editing. **Jenny L. Nelson:** Conceptualization, Investigation, Writing – review & editing, Supervision, Funding acquisition. **Phoebe V. Macak:** Validation, Investigation, Writing – review & editing. **Michael P. Scroggie:** Conceptualization, Methodology, Writing – review & editing. **Luke Collins:** Conceptualization, Methodology, Writing – review & editing. **Luke Emerson:** Investigation, Data curation, Writing – review & editing. **Jamie Molloy:** Writing – review & editing, Funding acquisition. **Lindy F. Lumsden:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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