Untangling the influences of fire, habitat and introduced predators on the endangered heath mouse

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Abstract

Globally, species extinctions are driven by multiple interacting factors including altered fire regimes and introduced predators. In flammable ecosystems, there is great potential to use fire for animal conservation, but most fire-based conservation strategies do not explicitly consider interacting factors. In this study, we sought to understand the interrelationships between the endangered heath mouse (*Pseudomys shortridgei*), fire, resource availability and the introduced fox (*Vulpes vulpes*) in southeast Australia. We predicted that heath-mouse relative abundance would respond indirectly to post-fire age class (recently burnt; 0-3 years since fire, early; 4-9 years, mid; 10-33 years and late; 34 – 79 years) via the mediating effects of resources (shrub cover and plant group diversity) and fox relative abundance. We used structural equation modelling to determine the strength of hypothesised pathways between variables, and mediation analysis to detect indirect effects. Both the cover of shrubs 0-50 cm from the ground and fox relative abundance were associated with post-fire age class. Shrub cover was highest 0-9 years after fire, while fox relative abundance was highest in recently burnt vegetation (0-3 years after fire). Heath mice were positively correlated with shrub cover and plant-group diversity, and negatively correlated with fox relative abundance. We did not detect a direct relationship between heath mice and post-fire age class, but they were indirectly associated with age class via its influence on both shrub cover and fox relative abundance. Our findings suggest that heath mice will benefit from a fire regime promoting dense shrub regeneration in combination with predator control. Understanding the indirect effects of fire on animals may help to identify complementary management practices that can be applied concurrently to benefit vulnerable species. Analytical and management frameworks that include multiple drivers of species abundance and explicitly recognise the indirect effects of fire regimes will assist animal conservation.

Key words: Fire ecology, introduced predators, network analysis, small mammals, structural equation modelling

1. Introduction

Biodiversity loss is a global and expanding problem (Dirzo *et al.*, 2014). Increased rates of species extinctions are due to multiple interacting factors, including climate warming, habitat loss and fragmentation, introduced species, and inappropriate fire regimes (Doherty *et al.*, 2016, Haddad *et al.*, 2015, Stevens-Rumann *et al.*, 2018, Thomas *et al.*, 2004). For instance, fire regimes interact with climate change resulting in more frequent, larger fires (Jolly *et al.*, 2015). In turn, increased fire frequency and extent reduce the availability of ground-level vegetation, depleting food resources, and increasing the risk of post-fire predation, population decline and extinction for many species (Doherty *et al.*, 2015, Ward *et al.*, 2020). Nevertheless, fire is essential for species persistence in many ecosystems, providing an opportunity for fire-based conservation management (Kelly & Brotons, 2017, Sitters & Di Stefano, 2020).

Prescribed burning is used in flammable ecosystems to reduce the risk of wildfire to human life and property and to achieve conservation objectives (Fernandes *et al.*, 2013, Penman *et al.*, 2011, Stephens *et al.*, 2012). Fire management for animal conservation typically involves altering aspects of the fire regime (e.g., frequency, intensity and patchiness) for the benefit of species and communities (Di Stefano *et al.*, 2013, Hovick *et al.*, 2015, Kelly, Brotons & McCarthy, 2017). However, animals respond to fire-mediated change in resource availability (e.g. food and shelter) rather than fire *per se* because resources are functionally linked to species distributions (Fox, 1982, Pons *et al.*, 2012). For example, fire changes the availability of important resources such as logs, litter, ground vegetation and canopy cover (Hall, Burke & Hobbs, 2006, Haslem *et al.*, 2011), which influences the abundance and persistence of species and the composition of communities (Fuhlendorf *et al.*, 2006, Swan *et al.*, 2015).

Shelter resources, including patches of dense ground vegetation and hollow logs, are critical for many animals, helping them to avoid predation (Jacob & Brown, 2000, McGregor *et al.*, 2015). Fire often consumes shelter resources and can influence predator-prey interactions by increasing predator activity (a numerical response; Birtsas, Sokos & Exadactylos, 2012, Hradsky *et al.*, 2017a), improving predation efficiency (a functional response; McGregor *et al.*, 2015), or both. In Australia, post-fire predation by introduced foxes (*Vulpes vulpes*) and cats (*Felis catus*) can have pronounced negative consequences for native prey (Doherty *et al.*, 2015), and has contributed to continental-scale species declines and extinctions (Woinarski, Burbidge & Harrison, 2015). Understanding the inter-relationships between fire, shelter resources, predators and native prey will improve conservation management in flammable landscapes (Hradsky, 2020).

The heath mouse or dayang (*Pseudomys shortridgei*) is a 55-90 g Australian rodent currently listed as nationally endangered, and near threatened and declining by the International Union for Conservation of Nature (Department of the Environment and Energy, 2020, IUCN, 2020). Once widely distributed across southern coastal regions of Australia (Cockburn, 1978, Kemper, Medlin & Bachmann, 2010), the species' current distribution is restricted to two locations around 2000 kilometres apart, one in the south-west of Australia and the other in the south-east (Salinas *et al.*, 2009). Reasons for heath-mouse declines are uncertain, however climate change, habitat fragmentation and loss, competition with introduced rodents (e.g., house mouse *Mus musculus* or black rat *Rattus rattus*), predation (predominantly by foxes and cats) and altered fire regimes are probable causes (Cockburn, 1978, Kemper, Medlin & Bachmann, 2010).

Heath mice inhabit heathlands and woodlands with historical fire regimes of relatively high frequency and severity; fire return intervals are typically between 12 and 45 years (Cheal, 2010, Enright *et al.*, 2012). Their response to introduced predators is unknown, although foxes and cats have been implicated in the decline of many native Australian rodents (Smith & Quin, 1996). Data related to resource and fire regime preferences are minimal, inconsistent, and differ between the western and eastern populations (Cooper *et al.*, 2003, Salinas *et al.*, 2009). Early research in eastern Australia suggested that heath mice prefer dense, floristically rich, regenerating heathland which provides shelter and meets the species' broad dietary requirements (Cockburn, 1978). However, subsequent studies of the eastern population have revealed variable fire responses, including no response to fire and interactions between fire and drought (Cooper *et al.*, 2003, Di Stefano *et al.*, 2011, Hale *et al.*, 2016, Salinas *et al.*, 2009). In contrast, the western population has shown a preference for older successional vegetation (Quinlan, Moro & Lund, 2004). Despite an absence of a successional preference in the eastern population, heath mice responded to aspects of vegetation structure, indicating that fire history may be a poor proxy for their abundance (Di Stefano *et al.*, 2011).

In this study, we sought to understand the interrelationships between the endangered heath mouse, fire, the availability of important resources and foxes (*V. vulpes*), an introduced predator. Our objective was to determine whether heath mice respond (a) directly to post-fire age class (a categorical representation of time since fire), (b) indirectly to post-fire age class via its influence on resources or foxes, or (c) directly to resources or foxes independent of post-fire age class (Fig. 1A). While all plausible, these alternative response pathways reflect different underlying mechanisms and have different implications for heath-mouse conservation.

We predicted that heath mice would respond more strongly to resource availability (shrub cover and plant-group diversity) than to post-fire age class due to its demonstrated responses to similar variables (Cockburn, 1978, Di Stefano *et al.*, 2011), and a general expectation that animals will respond more strongly to the availability of important resources than to fire history (Nimmo *et al.*, 2014, Sitters *et al.*, 2014, Swan *et al.*, 2015). We also expected a negative response of heath mice to foxes and a negative response of both foxes and our two resource variables to post-fire age class (Haslem *et al.*, 2011, Hradsky, 2020). Finally, under the assumption that heath mice would respond to either foxes, resources, or both, we expected an indirect effect of heath mice to post-fire age class. Our full set of expected relationships is outlined graphically in Fig. 1B.

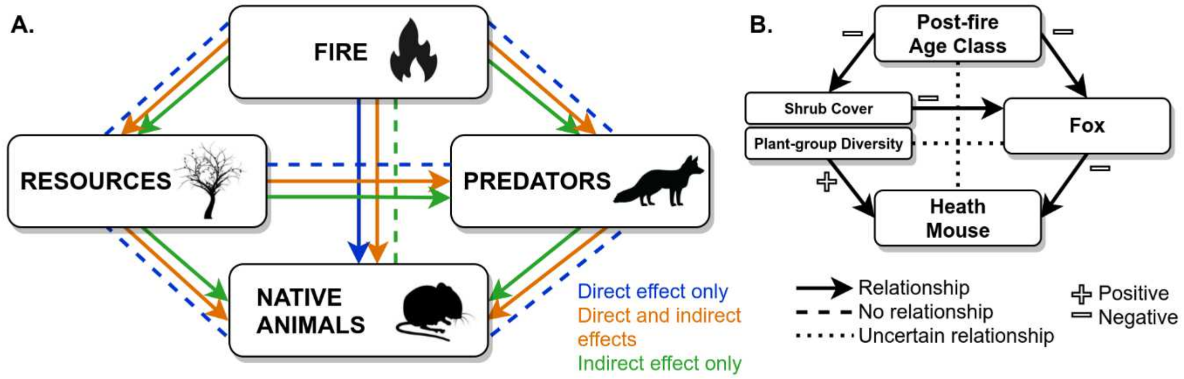

Figure 1. A. Conceptual model of the interactions between fire, resources, predators and a native animal species. Arrows represent detectible or expected relationships, dashed lines represent the absence of relationships and colours represent three ways that a native animal might respond to fire; directly only (blue), both directly and indirectly (orange) and indirectly only (green). B. Expected relationships specific to the variables in the current study. Arrows and signs represent the expected direction of relationships and dotted lined represent uncertain relationships.

2. Methods

2.1. Study area

The study area in south-west Victoria, Australia (Fig. 2A) contains large (1000 – 10 000 ha) patches of Eucalyptus woodland with an overstory dominated by *Eucalyptus baxteri* (north and central) and *E. obliqua* (south), and an understorey containing a variety of heathy shrubs and grass-trees (*Xanthorrhoea* spp.) The woodland contains small (2 – 150 ha) patches of treeless vegetation characterised by small-medium shrubs including *Sprengelia incarnata*, *Melaleuca squarrosa*, *Leptospermum continentale*, *L. myrsinoides*, *Banksia marginata*, *Dillwynia glaberrima*, *Isopogon ceratophyllus* and *Hibbertia sericea*. We sampled treeless areas in this study as evidence indicates high habitat suitability for heath mice at treeless sites (Cockburn, 1978, Cockburn, Braithwaite & Lee, 1981). The climate is temperate with mean annual rainfall of 634 mm and mean annual minimum and maximum temperatures of 8.3 °C and 20.1 °C respectively (Bureau of Meteorology, 2020; weather station 090182). The region is susceptible to wildfires and planned burns are applied every year during spring and autumn to reduce wildfire risk and promote biodiversity (Dess, 2016).

2.2 Study design and site establishment

We used aerial photographs to locate a pool of 80 treeless patches, and then selected 38 for sampling (Fig. 2B). We stratified the study area by (a) four post-fire age classes reflecting major developmental stages in vegetation succession (recently burnt; 0-3 years since fire, early; 4-9 years, mid; 10-33 years and late; 34 – 79 years; Cheal, 2010), (b) latitude (north and south), and (c) treeless vegetation patch size (0 – 9 ha, 10 – 20 ha and >20 ha) and attempted to select at least one site within each of the resulting 24 strata, choosing sites at random when there were several to choose from (Table S1). Selecting sites within these strata ensured that they were well distributed spatially, and occurred across the range of post-fire age classes, a key design variable, and treeless vegetation patch sizes, a factor we felt may influence the abundance of the focal species. Latitude and patch size (median = 11.0 ha, standard deviation = 33.0 ha) were not analysed due to inadequate replication. Each site was ≥1 km from others and contained a 200 m transect with a randomly selected start point and bearing.

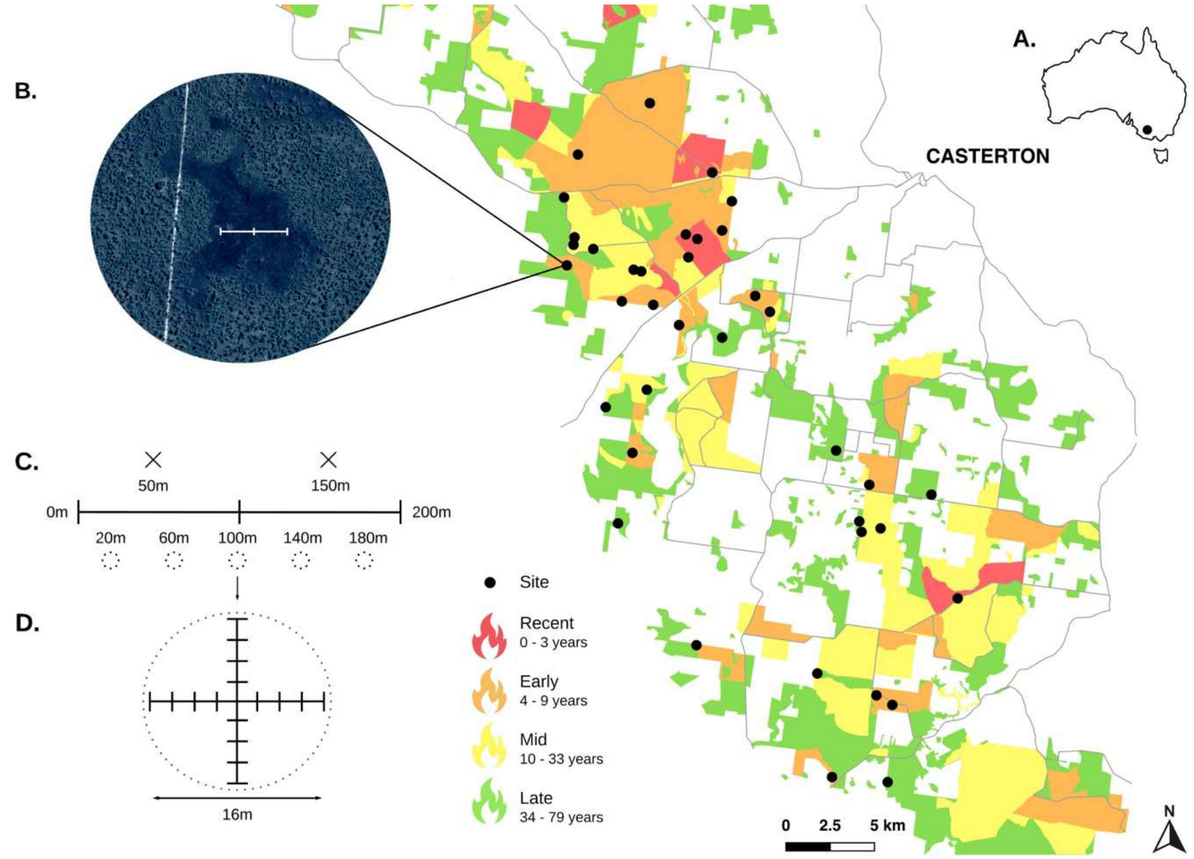

Figure 2. Map of the study area in south-western Victoria, Australia - colours represent post-fire age classes. The study area location in south-eastern Australia (A), a patch of treeless vegetation surrounded by woodland (B), the location of cameras (crosses) and vegetation sampling plots (circles) along a transect (C) and a blowout of a vegetation sampling plot (D).

2.3 Species detection

We detected heath mice and foxes using motion-sensing cameras set for 30 days per site in three deployment rounds between December 2018 to April 2019 (summer and autumn). To prevent bias associated with seasonal changes we deployed cameras in the north, centre and south of the study area during each round. We also ensured that sampling across post-fire age classes was unbiased. At each site, we deployed one infrared (Reconyx HC500) and one white-flash (Reconyx HC550) camera at the 50-m and 150-m mark of the transect, randomly allocating camera type to these locations (Fig. 2C). White-flash cameras result in colour images, making it easier to differentiate heath mice from similar looking species such as bush rats (*Rattus fuscipes*), but we had insufficient white-flash cameras to deploy two at each site.

Cameras were set to high sensitivity with five photographs per trigger event and no delay between triggers. They were attached 30 cm above the ground to PVC pipe (100-cm high by 20-cm diameter) held between two steel posts, angled down towards a bait station positioned 1.5 m away. The bait consisted of oats, peanut butter, golden syrup and pistachio essence in a perforated PVC canister (15-cm long by 4-cm diameter) attached to a wooden stake and suspended 20 cm from the ground. We used these camera set-up parameters (Fig. S1 A) as previous research in south-western Victoria has shown that they result in high detectability estimates for both small mammals and introduced predators such as cats and foxes (Delaney, Di Stefano & Sitters, 2021, Hradsky *et al.*, 2017a). Eight cameras (3 white-flash and 5 infrared) malfunctioned and at these sites we redeployed both cameras, resulting in a data set from 76 fully functional cameras.

Species were identified using a reference guide (Knight & Menkhorst, 2010) and a collection of images from previous studies. Images were labelled using digiKam v. 6.2.0 (https://www.digikam.org/) and we extracted and summarised the metadata in R v 3.6.3 (R Core Team, 2020) using camtrapR (Niedballa *et al.*, 2016). Positive identifications of heath mice and foxes (Fig. S1 B and C) from the 50-m and 150-m locations at each site were treated as sub-samples and pooled to generate a site-level relative abundance index, defined as the number of days out of 30 each species was detected (Palmer *et al.*, 2018). We considered detections that occurred on consecutive days at the same site independent if they were at least one hour apart and found no violations of this rule – the minimum time between detections on consecutive days was 8.1 hours for foxes and 1.1 hours for heath mice.

We checked for false absences in our species data, using unmarked (Fiske & Chandler, 2011) in R v 3.6.3 (R Core Team, 2020) to calculate daily detection probability p for both heath mice and foxes. We then used $1-(1-p)^n$ where *n* is deployment days (30) to calculate the probability of detection if present (Kéry, 2002). Heath mice were detected at 28 sites (74%) and foxes at 8 sites (21%). The mean (95% CL) probability of detection if present was 1.0 (1.0, 1.0) for heath mice and 0.92 (0.77, 0.98) for foxes.

2.4 Habitat structure and plant-group diversity

Habitat structure was measured at five plots per site, positioned at the 20-m, 60-m, 100-m, 140-m and 180-m marks of the transect (Fig. 2C). At each plot we established a 32-m cross (four 8-m arms) containing 16 sampling points spaced at 2-m intervals, totalling 80 sampling points per site (Fig. 2C, D). At each point habitat structure was measured by holding a 2-m pole vertically and recording the presence or absence of seven plant groups (*Xanthorrhoea* species, shrubs, rushes, sedges, ferns, grasses and herbs) within six vertical strata: 0–10 cm, 10–25 cm, 25–50 cm, 50–100 cm, 100–200 cm and 200–400 cm. The frequency of presences (n/80) was used to estimate the cover of each plant group in each height class at each site.

We used these data to derive two variables for modelling; plant-group diversity and shrub cover. We chose plant-group diversity to represent floristic diversity because heath mice have been found to occur in floristically rich areas (Braithwaite, Cockburn & Lee, 1978, Cockburn, 1978, Cockburn, Braithwaite & Lee, 1981). Shrubs were included because they dominated the understory at our sites and understorey cover is of known importance to heath mice and related species (Di Stefano *et al.*, 2011). We calculated plant-group diversity using Shannon's Diversity Index applied to cover estimates of the plant groups in the five vertical strata from 0–100 cm, excluding data from 100–400 cm as it was sparse. We represented shrub cover as the mean of cover estimates between 0–50 cm because estimates from many of the individual strata were highly correlated and exploratory analysis showed that shrub cover 0–50 cm was strongly correlated with heath-mouse relative abundance.

2.5 Data Analysis

All analyses were conducted using R v 3.6.3 (R Core Team, 2020) and included two main components; structural equation modelling and mediation analysis. First we used piecewise structural equation modelling (piecewiseSEM; Lefcheck, 2016) to determine the strength of the hypothesised pathways linking post-fire age class, shrub cover, plant-group diversity, fox relative abundance and heath-mouse relative abundance. Structural equation modelling (hereafter SEM) is a form of network analysis that enables the simultaneous calculation of multiple relationships, including both direct and indirect pathways. Piecewise SEM uses local estimation so that individual pathways in the network can be estimated using different statistical models (Lefcheck, 2016).

Initially we built a SEM that incorporated all pathways of primary interest; the response of shrub cover and plant-group diversity to post-fire age class, the response of fox relative abundance to post fire-age class and shrub cover, and the response of heath-mouse relative abundance to post-fire age class, fox relative abundance and the two habitat variables (Fig. 3A). We included shrub cover but not plant-group diversity as a predictor of fox relative abundance because research shows that foxes respond negatively to shrub cover (Hradsky *et al.*, 2017a) but there is no clear expectation regarding their response to floristic diversity. Prior to modelling we converted our raw fire data (years since the last fire) to four post-fire age classes (recent; 0-3 years since fire, early; 4-9 years, mid; 10-33 years and late; 34-79 years) as this was the most effective way to represent the sharp increase in heath-mouse relative abundance 5-9 years after fire (Figure S2); for example, a model using age class to predict heath-mouse relative abundance was a substantially better fit than a cubic polynomial applied to the continuous years since fire variable (likelihood ratio test, $p < 0.001$). In addition, representing years since fire as a categorical variable enabled a consistent treatment of fire in the SEM and in the subsequent mediation analysis (described below), because categorical variables can be incorporated and clearly interpreted in both cases. Further, land managers often use categorical representations of years since fire for ecosystem management (Cheal, 2010, Sitters *et al.*, 2018), thus it was hoped that using post-fire age class in our modelling would increase the practical relevance of our findings.

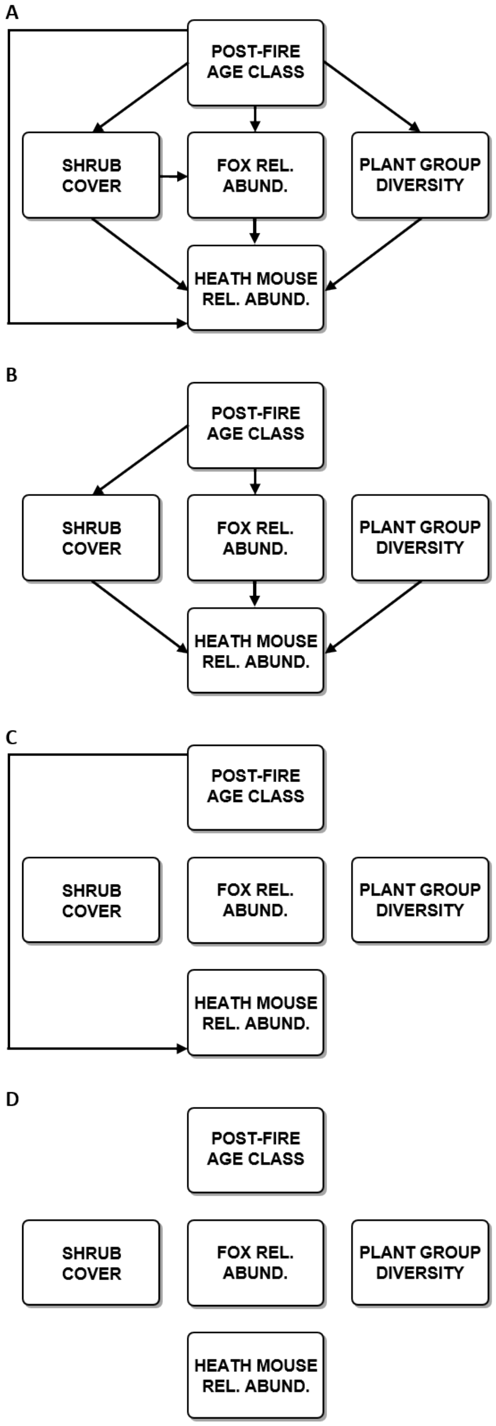

Figure 3. Diagrams of the four structural equation models compared using Akaike's Information Criteria corrected for small sample size. Black arrows represent included relationships. A model including all the relationships of primary interest (A), a reduced model produced by removing three unimportant pathways in model A (B), a model including only the direct effect of post-fire age class on heath-mouse relative abundance (C) and a null model (D).

The SEM incorporated four local models:

1. Plant-group diversity ~ age class
2. Shrub diversity ~ age class
3. Fox relative abundance ~ age class + shrub cover
4. Heath-mouse relative abundance ~ age class + fox relative abundance + shrub cover + plant-group diversity

The first two were fit as linear models and the last two were fit using the MASS package (Venables & Ripley, 2002) as generalised linear models with negative binomial errors to model the count-based fox and heath-mouse relative abundance indices while accounting for overdispersion. For models one and two we checked assumptions of equal variance and normally distributed residuals using graphical methods and detected no notable problems. For model four we checked the influence of collinearity among the predictors using generalised variance inflation factors (GVIF) calculated in the car package (Fox & Weisberg, 2019). Variance inflation values for age class, fox relative abundance, shrub cover and plant-group diversity were 1.10, 1.06, 1.25 and 1.13 respectively, indicating an acceptable degree of variance inflation due to collinearity. Finally, we checked for spatial autocorrelation in the residuals of each model by constructing spline correlograms using the package ncf (Bjornstad, 2020). In all cases we inferred spatial independence as 95% confidence limits around the estimated correlation coefficients overlapped 0 along the full range of distances between sites (0 – 40 km).

The initial SEM (Fig. 3A) revealed three unimportant pathways (heath-mouse relative abundance ~ age class; $p = 0.13$, fox relative abundance ~ shrub cover; $p = 0.21$ and plant-group diversity ~ age class; $p = 0.23$) so we built a second model with these pathways removed (Fig. 3B). In addition, we built a model including only the effect of post-fire age class on heath-mouse relative abundance and a null model with no paths (Fig. 3C and D), and compared all four models using Akaike's Information Criteria corrected for small sample size (Shipley, 2013). In addition, we calculated Akaike weights representing the probability that each model was the best in the set of models. We used the top-ranked SEM for inference after re-checking model assumptions and spatial autocorrelation in the altered sub-models. The fit of the final SEM was assessed using a test of directed separation; in this test a p-value > 0.05 indicates that the included pathways adequately reflect the data.

We present the core results as a path diagram, representing the strength of each detectible pathway using Bayes factor bounds (BFB; Benjamin & Berger, 2019) to summarise the diverse outputs from linear and generalised linear models incorporating both categorical and continuous predictors. BFBs can be calculated from p-values as $1/-e \times p \times \log(p)$ and represent the maximum odds of an alternative hypothesis relative to a null hypothesis. For example, in the context of regression with a continuous predictor, a BFB of 2 means that the estimated regression slope is, at most, twice as likely as a regression slope of 0.

We used mediation analysis (mediation; Tingley *et al.*, 2014) to quantify the indirect effect of post-fire age class on heath-mouse relative abundance. We sought to determine the indirect effect of post-fire age class on heath-mouse relative abundance via the mediating influence of (a) shrub cover and (b) fox relative abundance. This process involved the following steps (see Imai, Keele & Tingley, 2010 for details):

Step 1: Fit separate response and mediator models. In our case the response model described the influence of post-fire age class and all other covariates of interest on heath-mouse relative abundance and was specified as heath-mouse relative abundance ~ age class + fox relative abundance + shrub cover + plant-group diversity. We fitted two mediator models, one for each of the two potentially mediating variables, shrub cover and fox relative abundance. The mediator models described the influence of post-fire age class and other relevant covariates on the focal mediator. The shrub mediator model was specified as shrub cover ~ age class + plant-group diversity + fox relative abundance and the fox mediator model was specified as fox relative abundance ~ age class + plant-group diversity + shrub cover. We fitted the response model using a negative binomial distribution, the shrub mediator model using a gaussian distribution and the fox mediator model using a Poisson distribution after checking for overdispersion (residual deviance / df = 1.09) as the mediation package does not accept negative binomial mediation models.

Step 2: Simulate model parameters from the sample data. We used n = 1000 iterations.

Step 3: Using the outputs from Step 2 (a) simulate values of the mediator, (b) simulate values of the response given the simulated values of the mediator and for each iteration (c) calculate the average mediation effect. Because post-fire age class was a categorical variable, these sub-steps were applied separately to each age class contrast; recent v. early, recent v. mid, recent v. late, early v. mid, early v. late and mid v. late.

Step 4. Compute point estimates and 95% confidence limits from the distribution of average mediation effects for each age class contrast.

3 Results

The simplified SEM including the response of heath-mouse relative abundance to fox relative abundance, shrub cover and plant-group diversity, and the responses of both shrub cover and fox relative abundance to post-fire age class was substantially better than its alternatives (Table 1, Fig. 4). Heath-mouse relative abundance was positively correlated with shrub cover and plant-group diversity and negatively correlated with fox relative abundance, but we did not detect a direct relationship between heath-mouse relative abundance and post-fire age class (Fig. 4, Fig. 5A - C, Table S2). Based on Bayes factor bounds, heath-mouse relative abundance was most strongly associated with shrub cover followed closely by fox relative abundance. The SEM provided an adequate fit to the data (Fisher's C = 15.20, p = 0.13).

Table 1. Comparison of four structural equation models using Akaike's Information Criteria corrected for small sample size (AICc). The Akaike weight is the probability that the associated model is the best in the set of models. The initial model and simplified model are described in section 2.5 and shown in Figure 3A and B. The model including the direct association between post-fire age class and heath mice contains no other paths. A null model with no paths is included as a reference.

Model description	ΔAICc	Akaike weight
Simplified model – used for inference	0	1
Null	18.45	0
Direct association between post-fire age class and heath mice	26.16	0
Initial model – containing all paths of primary interest	49.15	0

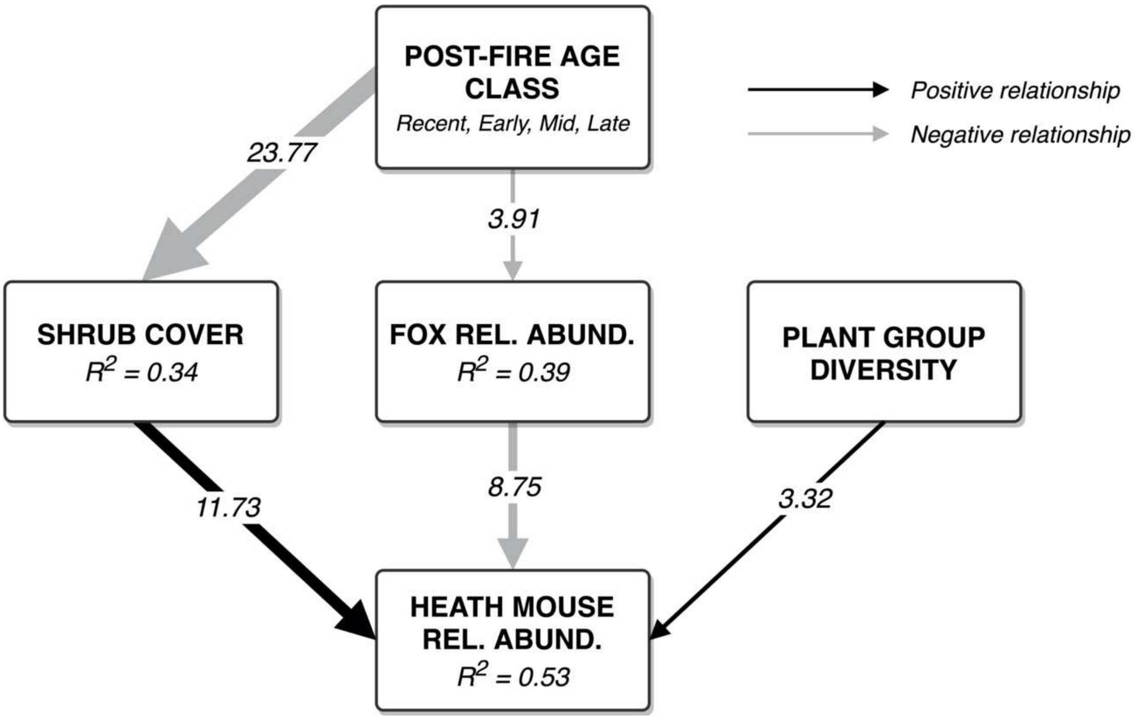

Figure 4. Path diagram showing relationships between post-fire age class, shrub cover, plant-group diversity, fox relative abundance and heath-mouse relative abundance. Arrows represent detectible relationships between variables and arrow thickness reflects the strength of each relationship. Values over the arrows are Bayes factor bounds (BFB), representing the maximum odds of the effect relative to a null hypothesis of no effect (see text for details). BFB values between 1-3, 3-10 and >10 represent weak, moderate and strong evidence for an effect (Wasserman, 2000). R^2 values represent variance explained for the three response variables.

Both shrub cover and fox relative abundance were correlated with post-fire age class. Shrub cover was highest in the recent and early age classes before declining (Fig. 5D, Table S2). Fox relative abundance was highest at recently-burnt sites and very low elsewhere (Fig. 5E, Table S2).

We detected an indirect association between heath-mouse relative abundance and post-fire age class via the mediating effect of both shrub cover and fox relative abundance (Figure 6). The mediating effect of shrub cover was driven by the contrasts between younger age classes (recent and early) and older age classes (mid and late) (Fig. 6A). This effect resulted from the strong correlation between shrub cover and age class (Fig. 5D, Table S2) and the corresponding positive relationship between heath-mouse relative abundance and shrub cover (Fig. 5B, Table S2). The mediating effect of fox relative abundance was driven by the contrasts between the recent age class and the other three age classes (Fig. 6B). This effect resulted from the attraction of foxes to recently burnt sites (Fig. 5E, Table S2) and the corresponding negative association between heath-mouse relative abundance and fox relative abundance (Fig. 5C, Table S2).

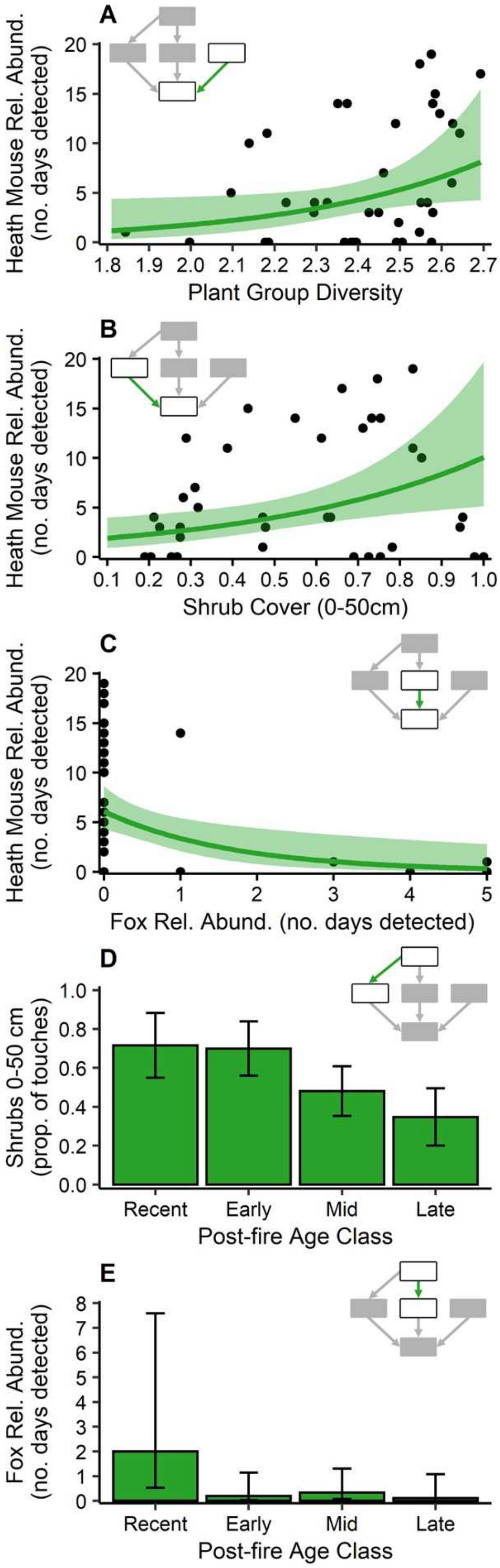

Figure 5. Model predictions corresponding to the detectible relationships identified in Figure 4 (see inset). In A to C shaded regions are 95% confidence limits and dots represent the raw data. In D and E error bars are 95% confidence limits.

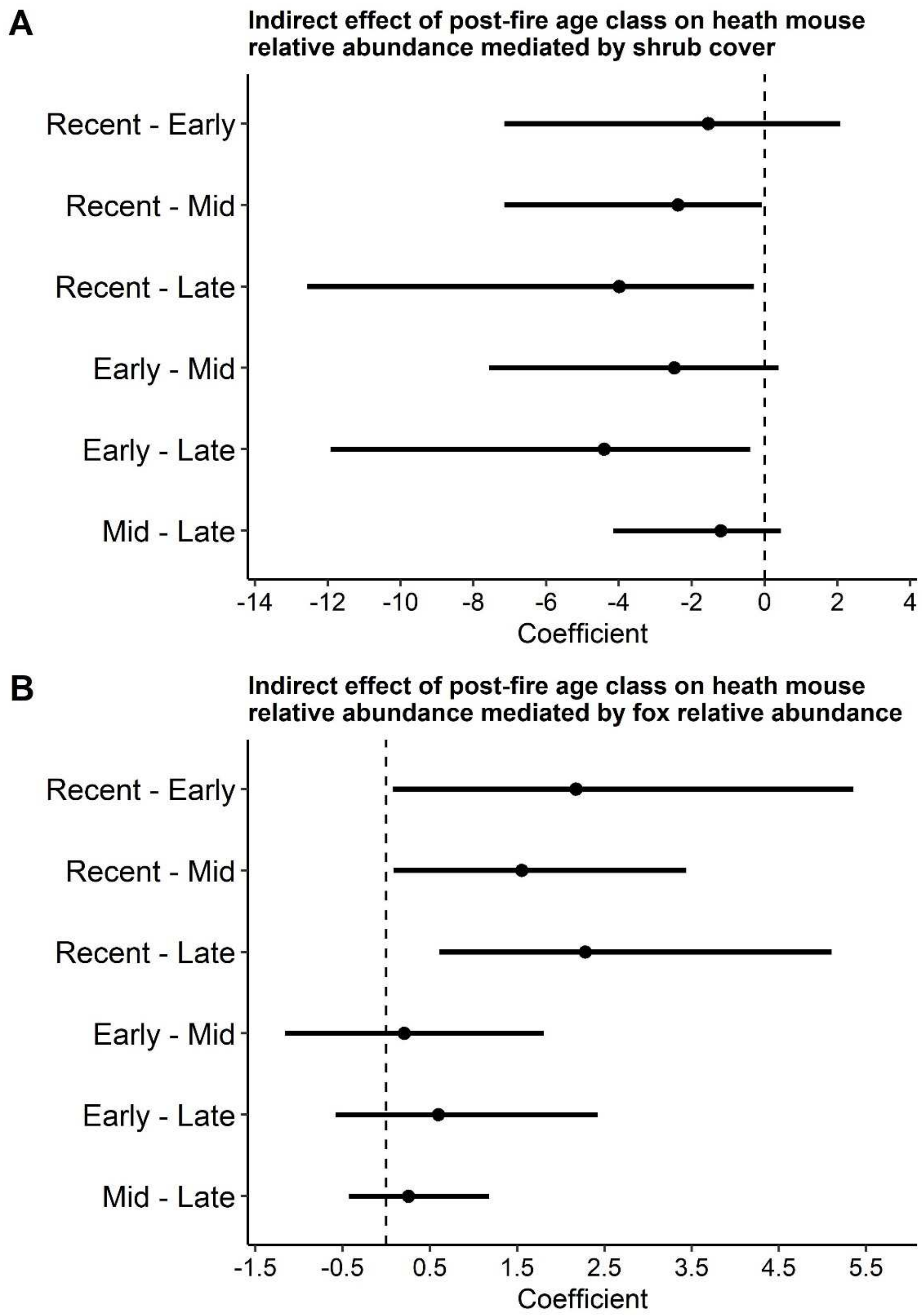

Figure 6. Indirect effect of post-fire age class on heath mouse relative abundance mediated by shrub cover (A) and fox relative abundance (B). Dots represent estimated coefficients for each of six growth stage contrasts. Indirect effects are considered detectible if 95% confidence limits (solid horizontal lines) do not overlap 0 (dashed vertical line).

4 Discussion

Conserving species in flammable ecosystems is a key component of the global conservation effort because fire regimes interact with climate warming and introduced predators to increase the likelihood of extinction (Doherty *et al.*, 2015, Jolly *et al.*, 2015, Ward *et al.*, 2020). In cases where species do not respond strongly to fire-regime variables, new knowledge of indirect and interactive effects of fire with other drivers is needed to inform species conservation (Driscoll *et al.*, 2010, Fernandes *et al.*, 2013). We sought to disentangle the interrelationships between the endangered heath mouse, fire, the availability of important resources and the introduced fox. Heath mice did not respond to post-fire age class directly, but age class was correlated with them indirectly via its influence on shrub cover and fox relative abundance. We discuss how fire, resource availability and predators may influence heath-mouse persistence, and we consider the implications of our results for conservation management.

4.1 Relationships between heath mice, fire, resource availability and foxes

Consistent with our expectations, we found that heath mice were positively associated with shrub cover and plant-group diversity, and they were negatively associated with fox relative abundance. Further, because both shrub cover and fox relative abundance were related to post-fire age class, we detected an indirect relationship between heath mice and age class via the influence of age class on shrubs and foxes.

Increased heath-mouse relative abundance at sites with high plant-group diversity may be related to diet and reproductive behaviour. Heath mice are generalist feeders (Braithwaite, Cockburn & Lee, 1978, Di Stefano, Ashton & York, 2014) and floristically diverse sites likely provide a stable food source throughout the year (Cockburn, 1978). In addition, nutritional stability may promote high reproductive effort, rapid juvenile growth and early reproduction, a strategy previously observed at floristically diverse sites, but not at sites supporting a simplified plant community (Cockburn, Braithwaite & Lee, 1981).

Many small mammal species have been positively associated with ground vegetation (Fordyce *et al.*, 2016, Jacob & Brown, 2000) and the heath mouse is no exception (Di Stefano *et al.*, 2011). The positive correlation with shrub cover in our study could reflect increased food resources at shrubby sites, anti-predator behaviour, or both. Selection of dense vegetation is a common anti-predator strategy for ground-dwelling mammals (Jacob &

Brown, 2000, McGregor *et al.*, 2015) and although predation of heath mice has not previously been studied, it is likely that both native birds of prey and introduced species exert some influence on its behaviour. For example, foxes and cats have been identified as a key threat to native mammals globally and have contributed to the decline and extinction of many Australian species (Doherty *et al.*, 2016, Woinarski, Burbidge & Harrison, 2015). Indeed, the negative association we detected between heath mice and fox relative abundance may indicate predation by foxes; there is evidence that small (<150 g) native mammals can form a substantial portion of the fox's diet in forests and woodland habitats (Davis *et al.*, 2015, Hradsky *et al.*, 2017a). Nevertheless, foxes have a flexible diet and consume a wide variety of food items (Davis *et al.*, 2015), and the extent to which they predate heath mice requires confirmation.

Conceptually, associations between fire, important resources, predators and native mammals include indirect fire effects, where native species respond to fire via the effect that fire has on resource availability or predators (Geary *et al.*, 2018, Hradsky *et al.*, 2017a, Parkins, York & Di Stefano, 2018, Puig-Gironès & Pons, 2020). Nevertheless, we are aware of only two other studies that have quantified an indirect fire effect. In a flammable region of Australia containing both dingoes (*Canis dingo*) and foxes, dingoes both suppressed foxes and were attracted to recently-burnt areas. Although foxes were not affected by fire directly, they responded indirectly to fire via the mediating effect of dingoes (Geary *et al.*, 2018). Similarly, in Spain, the occurrence of carnivore signs (mainly faeces of foxes and stone martens (*Martes foina*)) was influenced indirectly by fire via the mediating effect of plant cover (Puig-Gironès & Pons, 2020). The fact that indirect fire effects involving foxes have been identified in systems where they are both introduced (Australia) and native (Spain) suggests the underlying mechanisms are insensitive to predator origin, and that interactions between fire, resource availability and predators may influence species conservation in a diverse range of settings. Under climate warming fires are becoming larger and more intense (van Oldenborgh *et al.*, 2021), resulting in reduced ground vegetation and increased predation risk for many species (Jolly *et al.*, 2015, Leahy *et al.*, 2015, Ward *et al.*, 2020). In this context, understanding how vulnerable species are influenced by the interacting effects of fire, resources and predators will have important implications for conservation management.

4.2 Direct effects of fire

Heath-mouse relative abundance was not directly correlated with post-fire age class. Previous studies have revealed contrasting associations between heath mice and age class, with results reflecting variable responses of heath mice to age class in the eastern population, and a preference for older age classes in the western population (Cockburn, 1978, Cooper *et al.*, 2003, Di Stefano *et al.*, 2011, Quinlan, Moro & Lund, 2004, Salinas *et al.*, 2009). The spatially and temporally variable relationship between heath mice and fire is consistent with findings for other species (Nimmo *et al.*, 2014), likely reflecting interactions between fire and other processes (Hale *et al.*, 2016), and the fact that fire history variables only partially reflect changes in important resources (Swan *et al.*, 2020).

Post-fire age class was strongly correlated with shrub cover and fox relative abundance. Shrub cover was highest during recent and early growth stages (0 – 9 years since fire) which is consistent with rapid post-fire regeneration in southern Australian heathlands (Benwell, 1998). In the late growth stage (34 – 79 years) we observed shrub senescence which was reflected by reduced cover.

Fox relative abundance was greatest in the recently-burnt growth stage, a finding consistent with a growing body of evidence suggesting positive relationships between foxes and fire (Hradsky, 2020, Puig-Gironès & Pons, 2020). For example, telemetry studies have shown that foxes intensified their use of recently-burnt sites within their home ranges (Hradsky *et al.*, 2017b), and research in open forest 50-km south of our study area found that fox relative abundance was substantially higher immediately post-fire compared to pre-fire (Robley *et al.*, 2016). In Spain, fox occurrence was high near the edges of a burnt patch immediately after fire and then increased in the interior of the burn block over time (Puig-Gironès & Pons, 2020). In most cases, attraction to burnt sites appears to be brief, lasting weeks to months (Hradsky, 2020), although elevated post-fire fox relative abundance has been detected for up to two years (Robley *et al.*, 2016). Nevertheless, the attraction of foxes to recently burnt areas is not ubiquitous. For example, in the Murray Mallee region of south-eastern Australia, fox relative abundance did not respond to time since fire measured over a 0-105 year chronosequence (Payne *et al.*, 2014).

4.3 Implications for conservation management

There is great potential to use fire for animal conservation (Kelly & Brotons, 2017, Sitters & Di Stefano, 2020). However, most fire-based conservation strategies aim to manipulate spatial and temporal aspects of the fire regime without explicitly incorporating important links between fire, resource availability and the focal species (Di Stefano *et al.*, 2013, Kelly, Brotons & McCarthy, 2017, Watson *et al.*, 2012). Moreover, other drivers of species distributions that likely interact with fire, such as introduced predators, are often ignored, despite calls for the integrated management of fire and predators (Doherty *et al.*, 2015, Hradsky *et al.*, 2017a).

We argue that fire-based conservation planning will benefit from a holistic approach that considers the responses of native species to multiple interrelated factors. For example, although heath mice did not respond directly to post-fire age class, our findings suggest that a fire regime promoting dense shrub regeneration (e.g., increasing the extent of the recent and early post-fire age classes) will benefit heath-mouse populations. In other words, fire can have a positive influence on heath mice through its effect on important resources, and understanding this association provides fire managers with a resource-based goal directly linked to heath-mouse persistence. Further, the strong negative association between heath-mouse relative abundance and fox relative abundance indicates that a dual focus on habitat improvement and predator suppression may be an effective strategy to conserve this threatened species in one of its last remaining strongholds. For example, burning to increase shrub cover and reducing predation risk from foxes at shrubby sites may be more effective at protecting heath-mouse populations than either strategy on its own. Reducing fox density using poison 1080 bait (sodium fluoroacetate) is the most common form of fox control, however this practice causes animals to suffer without clear evidence that reducing fox density benefits populations of their prey (Hradsky, 2020). Strategies targeting functional responses may be an effective alternative. For instance, randomly deploying prey odour throughout the landscape altered predator perception of prey availability, reducing predation of native birds by introduced mammals and increasing hatchling success by a factor of 1.7 (Norbury *et al.*, 2021). Further experiments are needed to determine how fire and predator management can be integrated to benefit vulnerable species.

Understanding the indirect effects of fire on animals is likely to reveal options for fire-based conservation that may otherwise be overlooked. Moreover, it may help identify linked management practices (such as fire management and predator control) that can be used concurrently to benefit vulnerable species. Both analytical and management frameworks that incorporate multiple drivers of species distributions and explicitly consider the indirect effect of fire will benefit animal conservation in flammable landscapes.

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Figure Captions

Figure 1. A. Conceptual model of the interactions between fire, resources, predators and a native animal species. Arrows represent detectible or expected relationships, dashed lines represent the absence of relationships and colours represent three ways that a native animal might respond to fire; directly only (blue), both directly and indirectly (orange) and indirectly only (green). B. Expected relationships specific to the variables in the current study. Arrows and signs represent the expected direction of relationships and dotted lined represent uncertain relationships.

Figure 2. Map of the study area in south-western Victoria, Australia - colours represent post-fire age classes. The study area location in south-eastern Australia (A), a patch of treeless vegetation surrounded by woodland (B), the location of cameras (crosses) and vegetation sampling plots (circles) along a transect (C) and a blowout of a vegetation sampling plot (D).

Figure 3. Diagrams of the four structural equation models compared using Akaike's Information Criteria corrected for small sample size. Black arrows represent included relationships. A model including all the relationships of primary interest (A), a reduced model produced by removing three unimportant pathways in model A (B), a model including only the direct effect of post-fire age class on heath-mouse relative abundance (C) and a null model (D).

Figure 4. Path diagram showing relationships between post-fire age class, shrub cover, plant-group diversity, fox relative abundance and heath-mouse relative abundance. Arrows represent detectible relationships between variables and arrow thickness reflects the strength of each relationship. Values over the arrows are Bayes factor bounds (BFB), representing the maximum odds of the effect relative to a null hypothesis of no effect (see text for details). BFB values between 1-3, 3-10 and >10 represent weak, moderate and strong evidence for an effect (Wasserman, 2000). R^2 values represent variance explained for the three response variables.

Figure 5. Model predictions corresponding to the detectible relationships identified in Figure 4 (see inset). In A to C shaded regions are 95% confidence limits and dots represent the raw data. In D and E error bars are 95% confidence limits.

Figure 6. Indirect effect of post-fire age class on heath mouse relative abundance mediated by shrub cover (A) and fox relative abundance (B). Dots represent estimated coefficients for

each of six growth stage contrasts. Indirect effects are considered detectible if 95% confidence limits (solid horizontal lines) do not overlap 0 (dashed vertical line).