Patchy prescribed fire has variable effects on invasive predators and their native prey

Darcy Watchorn[1], Tim S. Doherty[2], Barbara Wilson[1], Mark Garkaklis[3], and Don Driscoll[1]

[1]Deakin University
[2]The University of Sydney
[3]State of the Environment Pty Ltd

October 17, 2023

Abstract

In many parts of the world, climate change is increasing the likelihood of severe wildfire in protected areas, while planned burns are occurring more frequently in an attempt to manage risk. These fires shape animal communities by altering resource availability and species interactions, including between predators and prey. In Australia, there is particular concern that native prey species may experience elevated post-fire predation by introduced feral cats (Felis catus) and European red foxes (Vulpes vulpes). We tested how a prescribed fire, vegetation, and other habitat variables affected the activity of cats, foxes, and the native mammal community in southeastern Australia. We used camera traps to quantify mammal activity before and after a prescribed burn, and statistically tested how the fire interacted with key habitat variables to affect mammal activity. We found little evidence that the prescribed fire influenced the activity of cats and foxes and no evidence of an effect on macropod or small mammal (<800 g) activity. Medium-sized mammals (800–2,000 g) were negatively associated with prescribed fire extent. The lack of response of cats and foxes to the prescribed burn is a positive outcome from a fire management perspective. Nonetheless, we recommend future experiments use GPS trackers to record fine-scale movements of cats, foxes, and their native prey in temperate ecosystems immediately following prescribed fires the best inform effective management within protected areas.

Ecology and Evolution, Research Article

Darcy J. Watchorn [1, 4], Tim S. Doherty[2], Barbara A. Wilson [1], Mark J. Garkaklis [3], Don A. Driscoll [1]

[1] School of Life and Environmental Sciences (Burwood Campus), Deakin University, Geelong, Victoria, Australia

[2] School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW, Australia

[3] State of the Environment Pty Ltd, Aireys Inlet, Australia

[4] Corresponding author: dwatchorn@deakin.edu.au

Abstract

In many parts of the world, climate change is increasing the likelihood of severe wildfire in protected areas, while planned burns are occurring more frequently in an attempt to manage risk. These fires shape animal

communities by altering resource availability and species interactions, including between predators and prey. In Australia, there is particular concern that native prey species may experience elevated post-fire predation by introduced feral cats (*Felis catus*) and European red foxes (*Vulpes vulpes*). We tested how a prescribed fire, vegetation, and other habitat variables affected the activity of cats, foxes, and the native mammal community in southeastern Australia. We used camera traps to quantify mammal activity before and after a prescribed burn, and statistically tested how the fire interacted with key habitat variables to affect mammal activity. We found little evidence that the prescribed fire influenced the activity of cats and foxes and no evidence of an effect on macropod or small mammal (<800 g) activity. Medium-sized mammals (800–2,000 g) were negatively associated with prescribed fire extent. The lack of response of cats and foxes to the prescribed burn is a positive outcome from a fire management perspective. Nonetheless, we recommend future experiments use GPS trackers to record fine-scale movements of cats, foxes, and their native prey in temperate ecosystems immediately following prescribed fires the best inform effective management within protected areas.

Open Research Statement

The data that supports the findings of this study is permanently archived in OSF (https://osf.io/vgae8/?view_only=8f3be5d46dd0414186dce2616cc466c6) and will be made publicly available immediately following publication.

Introduction

Native terrestrial mammal species are experiencing rapid and significant declines across the globe (Di Marco *et al.* 2014; Woinarski*et al.* 2015; Brodie *et al.* 2021). In many cases, protected areas are providing the last population strongholds (Geldmann *et al.* 2013; Pacifici *et al.* 2020). However, altered fire regimes and invasive species, amongst other disturbances, continue to result in mammal decline even within protected areas (Lawes *et al.* 2015; McCain 2019; Rija *et al.* 2020; Tedeschi *et al.* 2022). Therefore, understanding which habitat attributes are important for mammal persistence and how disturbances, like invasive species and fire, affect mammal activity and habitat use is critical for developing effective management strategies to facilitate their persistence within protected areas (Driscoll *et al.* 2010; Maxwell *et al.*2020).

Topography and vegetation productivity are important attributes influencing terrestrial mammal occurrence and diversity (Dorph *et al.* 2021). Topographic variation can create heterogeneous habitats varying in microclimate and resource availability, providing habitat for mammals with diverse niches (Dormann *et al.* 2010). Similarly, areas with high vegetation complexity and productivity offer more food and shelter than less productive areas and support larger and more diverse mammal communities (Sukma *et al.* 2019). Small mammals, in particular, favour these productive habitats due to food availability—such as invertebrates, seeds, and fungi—as well as shelter from terrestrial and aerial predators (Hanser *et al.*2011; McCain *et al.* 2018; Swan *et al.* 2020).

Invasive mammalian predators, such as the feral cat (*Felis catus*), stoat (*Mustela erminea*), small Indian mongoose (*Urva auropunctata*), and European red fox (*Vulpes vulpes*) are major threats to native mammals globally (Doherty *et al.*2016; GISD 2023). These species are highly adaptable and opportunistic, and can thrive across a range of landscapes, including within large remnant forests, along edges of fragmented forests, in agricultural and urban environments, and many other ecosystems (Nichols *et al.*2019; Alexandre *et al.* 2020; Louppe *et al.* 2020). Activity of these predators can increase in response to prey abundance (Scroggie*et al.* 2018), anthropogenic features—like tracks and farms—that provide efficient movement and foraging opportunities in structurally complex environments like forests (May and Norton 1996; Colón 2020; Schwemmer *et al.* 2021), and time since fire (Nalliah*et al.* 2022; Doherty *et al.* 2023). Understanding how invasive predators respond to these factors can assist land managers in developing more targeted strategies to effectively mitigate their impacts (e.g., McGregor *et al.* 2020).

The response of mammals to fire is commonly driven by how fire alters their food and shelter resources

(Morris *et al.* 2011; Griffiths and Brook 2014; Lees *et al.* 2022), rather than direct mortality (Hale *et al.* 2021; Shaw *et al.* 2021). Some small mammals, like the Trowbridge's shrew (*Sorex trowbridgii*) in North America, decline after fire in response to a loss of food or an increased predation risk (Greenberg *et al.* 2007; Culhane *et al.*2022), while other more generalist species, like the cliff chipmunk (*Tamias dorsalis*), can be largely unaffected by fire (Morandini*et al.* 2023). The abundance of large herbivores, such as the red-flanked duiker (*Cephalophus rufilatus*) in Cameroon, can increase in recently burnt areas, as the regenerating vegetation is typically more palatable (Klop *et al.* 2007; Reid *et al.*2023). Fire can also create preferable hunting habitat for meso- and apex predators, such as the coyote (*Canis latrans*) and Florida panther (*Puma concolor coryi*) in the U.S.A, which benefit from the increased exposure of their prey (Dees *et al.* 2001; Cherry*et al.* 2017).

Fire-driven changes in predator-prey interactions are especially likely to be detrimental to native fauna when they benefit invasive mammalian predators (Geary *et al.* 2020; Doherty *et al.* 2022). Fire can increase the activity invasive predators, such as feral cats (hereafter 'cat') and European red foxes (hereafter 'fox'), by removing vegetation which normally provides prey with refuge (McGregor *et al.* 2015; Leahy *et al.* 2016; Hradsky 2020; Miritis *et al.*2023). Climate change is increasing the occurrence of fire in many parts of the world (Canadell et al., 2021; van Oldenborgh et al., 2020; Jones et al. 2022) and may facilitate range expansions for both cats and foxes (Aguilar *et al.* 2015; Elmhagen *et al.* 2017), thus increasing the likelihood of negative impacts on native fauna. This highlights the need for well-informed management strategies that account for the effects of fire, vegetation, and anthropogenic features on the activity of cats, foxes, and native mammals, so the effectiveness of protected areas for conservation can be optimised.

Australia serves as one of the most prominent global examples where the potential for the interaction between fire and invasive predators carries a great risk for native mammals (Doherty *et al.* 2023). Since European colonisation, many overlapping threats have contributed towards the decline of Australia's mammal community (Woinarski *et al.* 2019a; Ashman *et al.* 2021; Legge *et al.* 2023). The cat and fox have played a particularly damaging role, contributing to the extinction of >25 mammal species and killing an estimated 556 million native mammals each year (Kearney *et al.*2019; Woinarski *et al.* 2019b; Stobo-Wilson *et al.* 2022). Not all studies have found that cat and fox activity increases after fire (e.g., Hradsky *et al.* 2017b; Bliege Bird *et al.* 2018; Lothian *et al.* 2022), and a quantitative review found that—should this phenomenon be observed—it was most likely to occur shortly after fire (e.g., weeks to months; Doherty *et al* . 2023). This indicates that there may be a critical period immediately post-fire when prey is most vulnerable to an elevated risk of predation, although Doherty *et al.* (2023) emphasised that further studies that begin sampling shortly after fire (i.e., <1 month) are necessary to better understand the generality of this response.

In this study, we tested whether the activity of cats, foxes, and the native mammal community could be predicted by fire, vegetation, topography, and proximity to anthropogenic features within a high-value conservation reserve. We used camera traps to quantify mammal activity across 30 sites, both before and immediately after a prescribed burn at burnt and unburnt sites. We fitted generalised linear mixed models to test the following predictions:

1. Cats and foxes will be more active at sites burnt by the prescribed fire (McGregor *et al.* 2016b; Hradsky *et al.* 2017a), near anthropogenic features (Hradsky *et al.* 2017c; Schwemmer*et al.* 2021), and where mammalian prey activity is higher (Geary *et al.* 2022).
2. The macropod community (large herbivorous marsupials) will show increased activity in areas burnt by the prescribed fire, due to the availability of regenerating vegetation preferred for grazing (Klop*et al.* 2007; Reid *et al.* 2023).
3. The activity of the small mammal (<2 kg) community will be negatively influenced by the prescribed fire due to fewer resources and an increased predation risk and be positively influenced in riparian and highly productive areas (Lawes *et al.* 2015; Swan*et al.* 2015; Mariani *et al.* 2022).

Methods

Study area

Our study was conducted in the northeast Otway Ranges in Victoria, Australia (38°24'S, 144deg1'E). The 2,471-hectare study area comprises eucalypt woodlands, heathlands, and wet shrublands (Figure 1). This part of the Otway Ranges has a mean maximum temperature of 18.4degC and an average annual rainfall of 627 mm (BoM 2021). The dominant overstory vegetation includes messmate (*Eucalyptus obliqua*) and brown stringybark (*E. baxteri*), with common mid-storey and ground cover species including the myrtle wattle (*Acacia myrtifolia*), prickly tea tree (*Leptospermum continentale*), and austral grass tree (*Xanthorrhoea australis*). The Traditional Owners of this land are the Wadawurrung People.

The region supports a diverse terrestrial mammal community which has suffered considerable decline in recent decades, including the near-threatened long-nosed potoroo (*Potorous tridactylus*), the vulnerable swamp antechinus (*Antechinus minimus maritimus*) and white-footed dunnart (Sminthopsis leucopus), and the endangered southern brown bandicoot (*Isoodon obesulus*) (Wayne et al., 2017; Wilson & Aberton, 2006; Wilson et al., 2001; Wilson et al., 2017; Wilson & Garkaklis, 2020). Foxes and cats are the largest terrestrial predators in the region. Fox control, using baits containing 1080 poison (sodium fluoroacetate), is regularly undertaken by land managers, although the impact on fox occurrence is likely modest (Robley *et al.* 2019). There is no broadscale management of cats.

There are multiple townships in the region which experience significant seasonal increases in population during the summer months (ODBPC 2021), therefore the risk posed by wildfire to people and assets is considerable. Major wildfires burnt the study area in 1939 (Black Friday; 240,000 ha) and 1983 (Ash Wednesday; 40,000 ha). Prescribed fire is regularly applied to minimise this risk (Gazzard *et al.* 2020). Much of the area within our study site experienced 1–2 prescribed burns between 1988 and 2018 (DEECA 2020), and there were 110 prescribed fires (covering approximately 70,800 ha) planned for the region between 2021 to 2024 (ODBPC 2021).
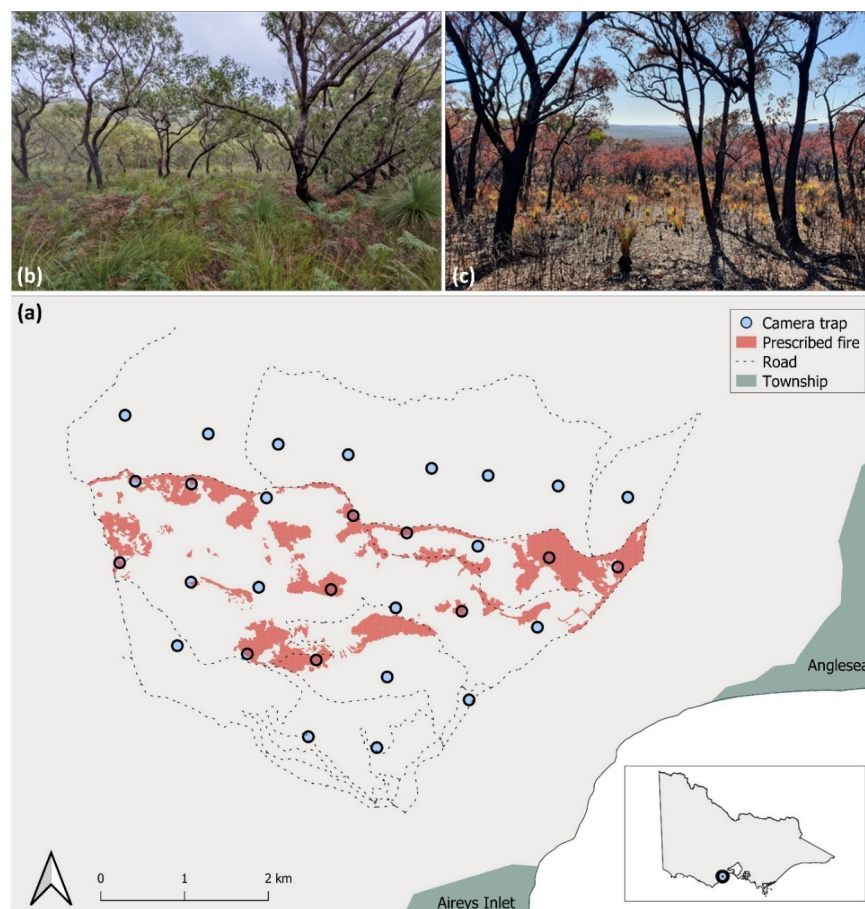
Figure 1. (a) A map of the study area in the north-eastern Otway Ranges, showing the placement of the camera trap (N=30) grid and the extent of the prescribed burn across the site and within the 100 m radius of each of the affected camera traps (N=12). The prescribed burn occurred in May 2019. (b) a photograph of one of the heathy woodland sites from the study area before the prescribed fire. (c) a photograph of the same heathy woodland site approximately four weeks after the prescribed fire.

Study design

Forest Fire Management Victoria conducted a prescribed burn within our study area in mid-May 2019. The fire affected 292 ha, of which 246 ha was forested and 46 ha was heathland (DEECA 2020). The majority of the fire (66%) burned at low-medium severity (DELWP, 2020), although severity was not quantified for heathland areas. We conducted five repeated mammal surveys using camera traps with infrared flash (Reconyx HF2X) across 30 sites (Figure 1) over a 12-month period. Surveys were conducted at six- and two months pre-fire and two weeks, three months, and six months post-fire, with each survey period being approximately two months in length (Appendix S1: Table A1). Using a Geographic Information System, we determined camera trap locations by positioning a 900 m grid over the study area and placing 30 survey points at grid intersections (ESRI 2014). During deployment, some camera traps were moved up to 150 m from grid points to account for access issues or to target nearby game trails or old vehicle/walking tracks, as feral cat and fox detectability is generally higher on trails compared to off trails (Geyle et al., 2020). We did not place cameras on public roads or heavily-used walking trails to reduce the risk of theft.

Of the 30 camera trap sites, 40% (12/30) were burnt during the prescribed burn (Appendix S1: Table A1: Figure 1), and the mean area burnt within a 100 m radius (i.e., Fire extent, Table 1) for these sites was 54%

5

(range 34–95%); highlighting the patchy burning style that is common of prescribed fires in our study region (e.g., Sitters *et al.* 2015; Hradsky *et al.* 2017a). The burnt and unburnt sites were not spaced far enough apart to be considered independent for all of our study species (i.e., they were within the feasible movement range of some species). Therefore, our study design would be more appropriately described as a quasi-BACI (before-after, control-impact) design, acknowledging this potential for spatial dependence between the sites.

At each site, cameras were attached to a tree at a height of approximately 40 cm facing a lure station two metres away. Each lure station was comprised of wadding soaked in tuna oil encased in a polyvinyl chloride (PVC) vent cowl. Lure stations were pegged securely into the ground, and vegetation in each camera's line of sight was cleared to prevent false triggers and to ensure animals were clearly visible. Cameras were set to record three images per trigger at medium-high sensitivity, with no delay between trigger events.

Statistical analyses

Images were processed using CPW Photo Warehouses (Ivan and Newkirk 2016). Animals were identified to species level where possible, otherwise, they were categorised according to the finest taxonomic/functional group possible (e.g., 'unknown small mammal species'). Each photo sequence was treated as a single point in time and a detection event was defined as images of the same species on the same camera that were separated by at least 60 minutes. Species detection matrices were created using the camtrapR package (Niedballa *et al.* 2016) in R version 4.2.2 (R Core Team 2022).

To test the influence of the fire, habitat, anthropogenic, and prey variables (Table 1) on mammal activity, we fitted generalised linear mixed models (GLMMs) to each species/group with sufficient data (Appendix S1: Table A2). There were many zeros (i.e., days in which a species was not detected) in the detection matrices due to long intervals between detection events. To account for this, we defined the response variable as the number of days a species was detected in each survey period relative to the number of days it was not detected. There were four species included in our analyses: the red fox, feral cat, swamp wallaby, and eastern grey kangaroo. To fit models and test our predictions on smaller mammals (<2,000 g), we pooled detections from small mammals (<800 g) and medium-sized mammals (800 – 2,000 g). The species comprising these two groups (see Appendix S1: Table A2) were recorded too infrequently to fit models to individual species, and many detections were not identifiable to species level. We conducted all model fitting and verification using the glmmTMB (Brooks *et al.* 2017), MUMIn (Barton 2022), and DHARMa (Hartig 2022) packages in program R version 4.2.2 (R Core Team 2022).

Before testing the covariates for each species/species group, we constructed models to test the effect of two possible detection covariates, namely camera placement (on or off trail) and age of lure (Table 1) on each response variable. Camera placement can influence the detectability of cats and foxes (Geyle et al., 2020), while the age of a lure might impact mammal activity either through reduced potency over time or behavioural alterations (Frey *et al.* 2017; McHugh *et al.* 2019). While the five survey periods were similar in length (refer to Appendix S1: Table A1), there was inconsistency in the timing of lure replacement. Lures for surveys four and five were replaced part-way through the survey periods, unlike those in surveys one, two, and three, which were replaced at the beginning. These detection models incorporated the main effects of both camera placement and lure age, along with random effects of Survey period and Site, allowing us to account for repeat sampling over time and any camera-level variability. We assessed the output of these models and included camera placement and/or lure age as fixed effects in subsequent analyses if the 95% confidence intervals did not cross zero.

To test the effect of our remaining variables on mammal activity, we fitted binomial GLMMs containing three-way interactions between Treatment (CI), Before-After (BA) and each of the remaining non-detection covariates (Table 1). These models included a total of 14 variables: two Fire History variables, three variables relating to the 2019 Prescribed Fire, two Vegetation variables, one Topography variable, two variables representing proximity to Anthropogenic Features, and potentially one or both of the Detection variables if they influenced the activity of the species/group (Table 1). We included both the Large mammal

6

and Small mammal Prey Activity variables (Table 1) for the fox, and the Small mammal Prey Activity variable for the cat. We used the 'dredge' function from the MuMIn package for model selection. This function only allows a maximum of 31 variables in the global model, including interaction terms. Due to the complexity arising from fitting three-way interaction between BA, CI, and most of the aforementioned variables, we fitted two unique 'sub-global' models containing different sets of variables, each with <31 terms. We then used the 'merge.model.selection' to combine the two model selection tables per species/group and reranked the models by AICc. The selection criteria for well-supported models were based on a delta Akaike Information Criterion (ΔAICc) of less than 2 (Burnham and Anderson 2004).

For the Fire extent variable, we fitted a simplified two-way interaction with BA. This is because all unburnt sites had a Fire extent of 0%, making it redundant to include the CI variable. We did not fit an interaction between BA or CI and Vegetation Type, Time Since Fire, or Fire Frequency, as this resulted in model convergence issues. Moderately and highly correlated variables (i.e., Pearson's r [?]0.5) were not included in the same model, and we excluded NDVI and TPI (Pearson's $r = 0.49$) from appearing in the same model because preliminary analyses showed that well-supported models containing both variables reported influential interactions that were not supported by the underlying data. We included the random effects of Site and Survey Period as per the initial detection models, and we scaled and centred each of the continuous variables prior to modelling. We limited the maximum number of variables per model to 10 to avoid issues associated with overfitting, which meant that only one three-way interaction could feature in any given model.

Table 1. Descriptions of the predictor variables included in our generalized linear mixed models of mammal activity in the eastern Otway Ranges, Victoria. The spatial data from the 2019 prescribed fire was sourced from DELWP (2020).

Variable (*abbr.*)	Description
Detection	Detection
Camera placement (CP)	Cameras were placed on trails (i.e. well-established gamepads or discontin
Age of lure (AoL)	Mean (x) number of days (per survey period) since lures were replaced. L
Fire History	Fire History
Time since fire (TSF)	Number of years since the site was last burnt by prescribed or wildfire (i.e
Number of fires (NoF)	Number of fires (incl. prescribed and wildfire) that have affected each site
2019 Prescribed Fire	2019 Prescribed Fire
Before-after (BA)	Before *cf.* after prescribed fire. Two surveys pre-fire, three surveys post-fi
Treatment (CI)	Burnt *cf.* unburnt. 12/30 sites were burnt by the prescribed fire.
Fire extent (FireExt)	The percentage of burnt area at each site within a 100 m radius of the ca
Vegetation	
Vegetation type (VT)	One of four categories: lowland forest, heathy woodland, swampy riparian
Normalized difference vegetation index (NDVI)	NDVI is a remotely sensed measure of vegetation productivity that is posi
Topography	
Topographic position index (TPI)	A measure of the relative height of each camera site (i.e., topographic rug
Anthropogenic Features	Anthropogenic Features
Distance nearest township (DNT)	The Euclidean distance (m) from each site to the nearest mapped townshi
Distance nearest farm (DNF)	
Prey Activity	
Small mammal (SM)	Detections of SM (<2 kg) and LM (>2 kg) per site, standardised for surv
Large mammal (LM)	

Results

Detection summary

We recorded 4,476 mammal detections events, of which 132 (2.95%) were feral cats, 286 (6.39%) were red foxes, and 4,058 (90.66%) were native animals comprising 17 species (Table A1). The most frequently detected native species was the swamp wallaby (*Wallabia bicolor*) (3,231 detections, 72.19%), followed by the eastern grey kangaroo (*Macropus giganteus*) (290 detections, 6.48%), and bush rat (*Rattus fuscipes*) (93 detections, 2.08%; Table A1).

Predictors of invasive predator activity

There were six well-supported models for the feral cat (Appendix S2). Cat activity was higher on trails compared to off trails (β [95% CI] = 1.86 [1.37, 2.34]; 6/6 models), negatively associated with time since fire (-0.70 [-1.09, -0.30]; 6/6 models), and higher in swampy riparian woodland vegetation type (0.50 [0.01, 1.00], 2/6 models) (Figure 2). There were also two interactions present; cat activity was negatively associated with NDVI before the prescribed fire (-0.86 [-1.41, -0.32]; 6/6 models) and in unburnt areas (-0.71 [-1.39, -0.03]; 2/6 models) (Figure 2). There was no evidence that cat activity was influenced by prey activity.

There were eight well-supported models for the red fox (Appendix S2). Fox activity was higher on trails compared to off trails (1.24 [0.82, 1.67]; 8/8 models), higher after the prescribed fire (-0.50 [-0.90, -0.10]; 8/8 models), higher at treatment compared to control sites (0.57 [0.13, 1.02]; 8/8 models), and negatively associated with distance from farmland (-0.35 [-0.55, -0.15]; 5/8 models) (Figure 3). There was no evidence that fox activity was influenced by prey activity (Appendix S2).
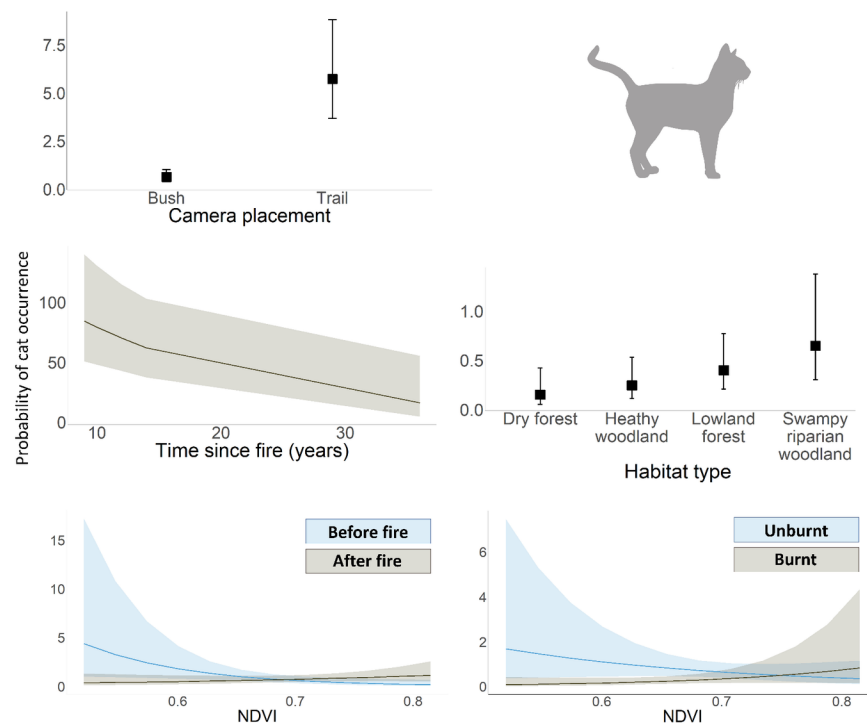

Figure 2. Plots of the GLMMs showing the influential effects of the two well-supported models (∆AIC<2) on the activity of feral cats (*Felis catus*) in the eastern Otway Ranges, Victoria. Full model summaries are provided in Appendix S2 (separate document).
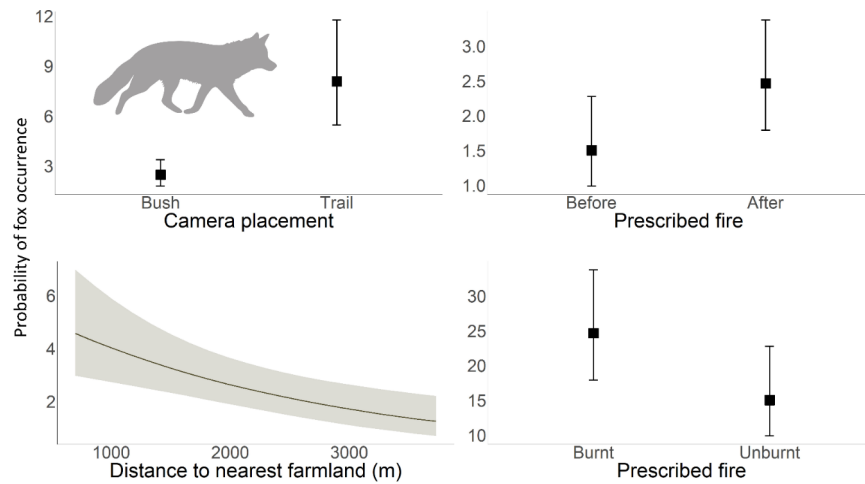
Figure 3. Plots of the GLMMs showing the influential effects from the two well-supported models (ΔAIC<2) on the activity of the European red fox (*Vulpes vulpes*) in the eastern Otway Ranges, Victoria. Full model summaries are provided in Appendix S2 (separate document).

Predictors of macropod activity

There were six well-supported models for the eastern grey kangaroo (Appendix S2). Kangaroo activity was higher on trails (1.09 [0.43, 1.74]; 6/6 models), positively associated with lure age (0.48 [0.34, 0.61]; 6/6 models), and negatively associated with both NDVI (-0.45 [-0.70, -0.21]; 6/6 models) and distance from farmland (-0.34 [-0.64, -0.04]; 5/6 models) (Figure 4). There was no evidence that kangaroo activity was influenced by the prescribed fire (Appendix S2). There were two well-supported models for the swamp wallaby, both of which indicated that activity declined with time since fire (-0.32 [-0.47, -0.16] and was higher before the prescribed fire (0.42 [0.10, 0.74]) (Figure 4).
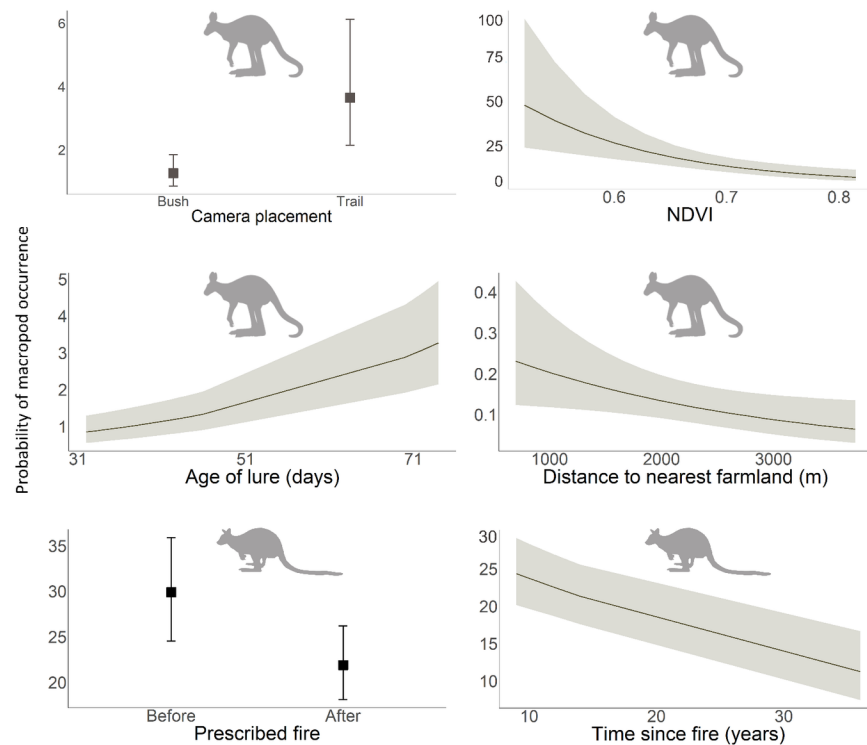
Figure 4. Plots of the GLMMs showing the influential effects from the single, well-supported models (ΔAIC<2) for both the eastern grey kangaroo (*Macropus giganteus*) (top four) and the swamp wallaby (*Wallabia bicolor*) (bottom two) in the eastern Otway Ranges, Victoria. Full model summaries are provided in Appendix S2 (separate document).

Predictors of small and medium-sized mammal activity

There were four well-supported models for the medium-sized mammal group (Appendix S2). Activity was negatively associated with Fire extent (-1.17, [-1.92, -0.42]; 4/4 models) and NDVI before the prescribed fire (-1.42 [-2.11, -0.74]; 4/4 models) (Figure 5). Activity was also positively associated with the main effect of NDVI (0.55 [0.03, 1.06]; 2/4 models) (Figure 5). There were nine well-supported models for the small mammal group, however, none of these contained influential effects of the predictor variables. The null model was the second highest ranked model (ΔAIC = 0.32).
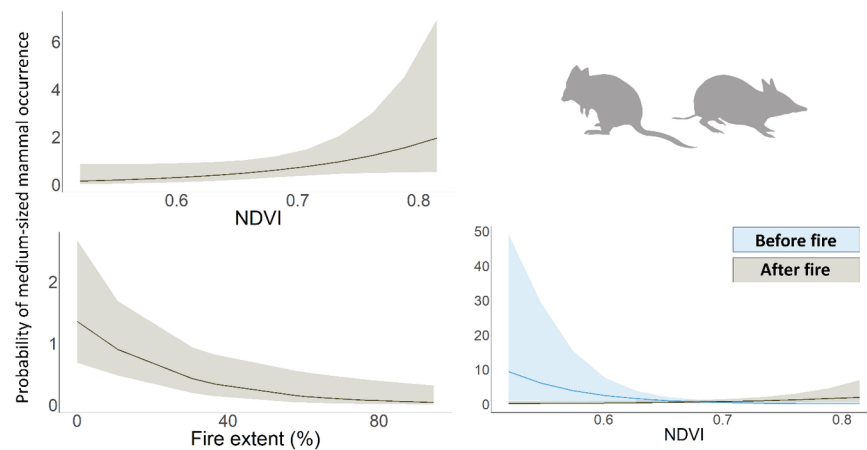

10

Figure 5. Plots of the GLMMs showing the influential effects from the single, well-supported models (ΔAIC<2) for the medium-sized mammals in the eastern Otway Ranges, Victoria. Full model summaries are provided in Appendix S2 (separate document).

Discussion

Cats and foxes

We predicted that cat and fox activity would be higher in areas burnt by the prescribed fire, however, we did not find any evidence in support of this. Whilst some studies have found strong evidence of cat or fox activity increasing after fire (McGregor *et al.* 2016a; Miritis*et al.* 2023), others have found a negative response (Bliege Bird*et al.* 2018; Lothian *et al.* 2022), no response (Hradsky*et al.* 2017c; Moore *et al.* 2018; Senior *et al.*2022), or a context-dependent response. For instance, in the USA, swift foxes (*V. velox*), which are closely related to red foxes, only used burnt areas more frequently if their existing core home ranges were burnt (Thompson *et al.* 2008). Indeed, a recent analysis of existing evidence found that there was a high likelihood of neutral responses to fire being recorded for both cats and foxes in Australia (55% and 67%, respectively; Doherty *et al.* [2023]). One explanation for our result could be that the prescribed fire in this study was too mild to illicit an increase in cat or fox activity. A GPS study of feral cats in northern Australia found that, whilst cats strongly selected for areas recently burnt by severe fires, they did not select for areas recently burnt by mild fire—despite these areas having a high abundance of small mammal prey (McGregor *et al.*2014). The authors suggested that cats did not benefit from mildly burnt areas due to unburnt patches likely providing refuge for prey, making hunting less profitable compared to severely burnt areas (McGregor*et al.* 2014).

While cats did not increase their activity following the prescribed fire, they were more active in areas with a shorter time since fire and lower NDVI—both indicators of simpler vegetation structure (Haslem*et al.* 2016). Cats also favoured swampy riparian woodlands, which is typically the most structurally complex vegetation type in our study area. The seemingly conflicting habitat complexity preferences may be explained by resource availability. Feral cats are capable of exploiting a diverse range of habitats, and it is generally considered that they prefer dense habitats for shelter—such as riparian woodlands—and more open habitats for hunting (Lozano *et al.* 2003; Doherty*et al.* 2015; Stobo-Wilson *et al.* 2020). Whilst foraging efficiency may theoretically be highest in recently burnt areas, these areas may be sub-optimal, and thus avoided, if prey availability is low (Pyke *et al.* 1977). The small mammal population in the eastern Otway Ranges has been declining for several decades and is now depauperate (Wayne et al., 2017; Wilson & Aberton, 2006; Wilson et al., 2001; Wilson et al., 2017; Wilson & Garkaklis, 2020). While we did not find a relationship between fire and small mammal activity (discussed below under *Small and medium-sized mammals*), the most frequently detected small mammal species, the bush rat, almost completely avoids recently burnt areas (Lees *et al.* 2022). Further, during a separate, concurrent small mammal study in the eastern Otways, we found that detections of other small mammal species in burnt areas were very uncommon (Watchorn, unpublished data). These factors may partially explain why neither cats nor foxes increased their activity in burnt areas, and why cat activity was higher in relatively open areas that likely supported higher prey availability.

We did, however, find that fox activity increased across the study area after the fire, although due to the proximity of our control and treatment sites, we cannot be sure if the prescribed fire drove this change. Juvenile foxes typically disperse in winter (April to June in this region; Baker *et al.* 2001), and Hradsky *et al.* (2017) also observed an increase in fox activity at their control sites following a prescribed fire, which was thought to be driven by dispersing foxes. Spatially independent control sites would have better isolated the impact of the fire from other factors like seasonal fox dispersal, however, equipment limitations made such an approach unfeasible for this study.

We predicted that cat and fox activity would be higher near farms and towns due to increased resource

availability (Hradsky *et al.*2017c). We found some support for this prediction, with foxes more active closer to farmland. Across their global range, red foxes, as well as other generalist mesopredators such as coyotes (*Canis latrans*) and golden jackals (*C. aureus*), use farmlands due to the availability of denning habitat, water and food (e.g., livestock, rodents, human food waste), as well as edge habitats which can support relatively diverse fauna communities and hunting opportunities (Gosselink *et al.* 2003; Šálek *et al.* 2014; Laux *et al.* 2022; Aikawa and Saito 2023). Indeed, we found that the eastern grey kangaroo, a common prey item of the red fox (Stobo-Wilson *et al.* 2022), was also more active near farmlands—likely due to the availability of pasture for grazing (Arnold *et al.* 1992; Maguire*et al.* 2006). In a GPS tracking study, Hradsky *et al.*(2017c) found that foxes in the Otway Ranges selected for farmland and forest-farmland interfaces at night, possibly due to livestock carcasses or prey availability. Collectively, these findings indicate that farm peripheries could provide effective fox baiting targets for land managers (Engeman and Linnell 1998; Carter and Luck 2013). Further high-resolution telemetry and resource mapping studies may provide further insight into the specific features foxes use (e.g., water dams, livestock carcasses etc.,), which may further improve bait uptake in these areas.

Macropods

Fire stimulates a short-term increase in plant nutrients, such as nitrogen (N), increasing both the nutritional availability and palatability for herbivores (Eby *et al.* 2014). This, in turn, drives temporary increases in the abundance of large herbivores after fire—a phenomenon observed around the world (Klop *et al.* 2007; Raynor *et al.* 2015; Reid *et al.* 2023). As such, we expected eastern grey kangaroos and swamp wallabies to increase their activity in recently burnt areas. Swamp wallaby activity was higher in areas with a shorter time since fire, a result consistent with studies showing this species' preference for early successional vegetation and minimal short-term impacts of fire (Styger *et al.* 2011; Swan*et al.* 2021; Chard *et al.* 2022). However, we found no evidence that macropod activity increased at sites burnt by the prescribed fire or with Fire extent. Rather, swamp wallaby activity decreased following the prescribed burn. One explanation for this may be that the willingness of macropods to forage in recently burnt areas can vary with predator abundance. For example, Banks (2001) found that eastern grey kangaroos were more active in open areas were foxes had been removed, but spent more time near forest edges when foxes were present. Di Stefano *et al.* (2009) also found that swamp wallabies favour more structurally complex vegetation to increase obscurity from predators, whilst other large herbivores, such as the white-tailed deer and caribou (*Rangifer tarandus*) in North America, also reduce their use of open areas—despite an abundance of food in those areas—to reduce the risk of predation (Joly *et al.* 2003; Cherry*et al.* 2017).

Small and medium-sized mammals

The small and medium-sized mammals in our study area typically prefer dense vegetation, where food and denning resources are greater and the risk of predation is likely lower (Catling *et al.* 2001; Dexter*et al.* 2011). We therefore predicted that the activity of these groups will be positively associated with NDVI and decrease after the prescribed fire (White *et al.* 2022). In support of this prediction, medium-sized mammal activity decreased with Fire extent, a trend also seen with medium-sized prey in Europe (Sokos *et al.*2016), North America (Zwolak and Foresman 2007), and elsewhere in Australia (Robley *et al.* 2023). Hradsky et al. (2017a) observed that fox consumption of medium-sized mammals, such as bandicoots, doubled after a patchy prescribed fire in the Otways, highlighting the increased vulnerability of these species to predation following fire, notwithstanding possible scavenging of carcasses.

Medium-sized mammals also showed a complex relationship with NDVI; while the main effect of NDVI was generally positive, activity was negatively associated with NDVI before the fire and slightly increased afterwards. This may suggest that these species increased their selection of microhabitat features associated with higher NDVI (e.g., gullies, sedges) following the fire (e.g., Swan *et al.* 2016; Fordyce*et al.* 2016; Lees *et al.* 2022). However, the high level of uncertainty with this interaction limits our ability to draw strong conclusions. Notably, while higher NDVI is typically associated with higher species richness for the mammals

comprising this species group (Youngentob *et al.* 2015b; Dorph *et al.* 2021; White*et al.* 2022), individually, these species have exhibited positive (Miritis *et al.* 2020; White *et al.* 2022), negative (Ralph 2021), and neutral (Youngentob *et al.* 2015b; Hale *et al.*2016) responses to NDVI. These varied relationships are likely due to factors such as drought, fire history, and habitat type (Youngentob*et al.* 2015a; White *et al.* 2022). Nonetheless, our findings suggest that NDVI may be a useful means of identifying and conserving productive and structurally complex areas which may facilitate mammal occurrence and diversity in this landscape (Sukma*et al.* 2019; Rivarola 2022), especially following disturbances such as drought (White *et al.* 2022), plant pathogen spread (Casey 2022), or fire (Dorph *et al.* 2021).

None of the variables predicted the activity of small mammals, a finding at odds with previous studies on these species that identified relationships with NDVI (Hale *et al.* 2016; Chadwick *et al.*2022) and changes in habitat use following fire (Swan *et al.*2016; Fordyce *et al.* 2016; Lees *et al.* 2022). One reason for this discrepancy may be that our camera arrangement, in terms of both density and spatial extent, was insufficient to reliably detect discrete patterns of microhabitat use for these species, especially considering the depauperate state of the small mammal community (Wilson and Garkaklis 2020). The incorporation of fine-scale, site-level habitat information—such as understorey vegetation structure (e.g., Hradsky*et al.* 2017a; Lees *et al.* 2022)—may have further improved our ability to detect any potential response to fire or vegetation structure.

Conclusions

We found little evidence to support our predictions that cat, fox, and macropod activity would increase following the prescribed burn, or that small mammal (<800 g) activity would decrease. Medium-sized mammals were negatively associated with Fire extent, and other studies in the region have identified similar trends following patchy prescribed burns, along with increased consumption of these species by foxes (Hradsky *et al.* 2017a). This suggests that these species may be particularly vulnerable to fire and invasive predators in this region, and may benefit from preserving large unburnt refuges and from targeted post-fire interventions to reduce predation, such as the provision of artificial refuges (Watchorn *et al.* 2022).

Looking forward, there are several key research questions which should be prioritised to conserve fauna inside protected areas. The majority of evidence demonstrating increases in cat activity post-fire comes from Australia's tropical north (Doherty *et al.* 2023). It remains unclear whether cats or foxes temporarily adjust their core home range or move long distances to hunt in recently burnt areas in the temperate forests, woodlands, and other ecosystems of southern Australia. Whilst camera traps are useful, their appropriateness for answering this question is limited by their inherently patchy spatial coverage across the landscape, as well as the delay associated with deploying them immediately after prescribed fires, especially in temperate forests. To this end, we recommend future studies employ the BACI experimental framework with animal-borne GPS loggers (Le Pla *et al.* 2023). This will improve our understanding of the fine-scale movements and habitat use of cats, foxes, and native prey species immediately before and after prescribed fire (e.g., McGregor *et al.* 2014). Animal-born video cameras could also provide valuable insight into cat and fox hunting success and prey selection (McGregor *et al.*2015). These approaches, whilst challenging to implement, will allow for a more nuanced understanding of fine-scale responses to prescribed fire, thereby informing more effective management strategies within protected areas.

field.

References

Aguilar, G. D., Farnworth, M. J., and Winder, L. 2015 . Mapping the stray domestic cat (Felis catus) population in New Zealand: Species distribution modelling with a climate change scenario and implications for protected areas. *Applied Geography* **63** , 146–154.

Aikawa, E., and Saito, M. U. 2023 . Effects of intensive agricultural landscapes on farmland use by medium and large mammals in Japan. *Écoscience* **30** , 2–16.

Alexandre, M., Hipólito, D., Ferreira, E., Fonseca, C., and Rosalino, L. M. 2020 . Humans do matter: determinants of red fox (Vulpes vulpes) presence in a western Mediterranean landscape. *Mammal Research* **65** , 203–214.

Arnold, G. W., Steven, D. E., Grassia, A., and Weeldenburg, J.1992 . Home-range size and fidelity of western grey kangaroos (Macropus fuliginosus) living in remnants of wandoo woodland and adjacent farmland. *Wildlife Research* **19** , 137–143.

Ashman, K., Watchorn, D., Lindenmayer, D., and Taylor, M.2021 . Is Australia's environmental legislation protecting threatened species? A case study of the national listing of the greater glider. *Pacific Conservation Biology* .

Avalos, V. D. R. 2011 . Biparental care and nesting success of the swallow-tailed cotinga in northwestern Bolivia. *Wilson Journal of Ornithology* **123** , 251–258. doi:10.1676/09-177.1

Baker, P. J., Harris, S., Robertson, C. P. J., Saunders, G., and White, P. C. L. 2001 . Differences in the capture rate of cage-trapped red foxes Vulpes vulpes and an evaluation of rabies control measures in Britain. *Journal of Applied Ecology* **38** , 823–835.

Banks, P. B. 2001 . Predation-sensitive grouping and habitat use by eastern grey kangaroos: a field experiment. *Animal Behaviour* **61** , 1013–1021.

Barton, K. 2022 . MuMIn: Multi-Model Inference. R package version 1.47.1. Available at: ttps://cran.r-project.org/package=MuMIn

Bliege Bird, R., Bird, D. W., Fernandez, L. E., Taylor, N., Taylor, W., and Nimmo, D. G. 2018 . Aboriginal burning promotes fine-scale pyrodiversity and native predators in Australia's Western Desert. *Biological Conservation* **219** , 110–118. doi:10.1016/j.biocon.2018.01.008

BoM, B. of M. 2021 . Climate statistics for Australian locations: Summary statistics for Aireys Inlet. Available at: http://www.bom.gov.au/climate/averages/tables/cw_090180.shtml [accessed 14 December 2021]

Brodie, J. F., Williams, S., and Garner, B. 2021 . The decline of mammal functional and evolutionary diversity worldwide. *Proceedings of the National Academy of Sciences* **118** , e1921849118.

Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., and Bolker, B. M. 2017 . glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R journal* **9** , 378–400.

Burnham, K. P., and Anderson, D. R. 2004 . Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research* **33** , 261–304. doi:10.1177/0049124104268644

Campbell-Jones, M. M., Bassett, M., Bennett, A. F., Chia, E. K., Leonard, S., and Collins, L. 2022 . Fire severity has lasting effects on the distribution of arboreal mammals in a resprouting forest. *Austral Ecology* **47** , 1456–1469.

Canadell, J. G., Meyer, C. P. (Mick., Cook, G. D., Dowdy, A., Briggs, P. R., Knauer, J., Pepler, A., and Haverd, V. 2021 . Multi-decadal increase of forest burned area in Australia is linked to climate change. *Nature Communications 2021 12:1* **12** , 1–11. doi:10.1038/s41467-021-27225-4

Carter, A., and Luck, G. W. 2013 . Fox baiting in agricultural landscapes: preliminary findings on the importance of bait-site selection. *Wildlife Research* **40** , 184–195.

Casey, S. 2022 . Mapping and assessing Phytophthora cinnamomi dieback in the eastern Otways.

Catling, P. C., Coops, N., and Burt, R. J. 2001 . The distribution and abundance of ground-dwelling mammals in relation to time since wildfire and vegetation structure in south-eastern Australia. *Wildlife Research* **28** , 555–565.

Chadwick, A., Weston, M. A., Burns, T., Randall, G., Radvan, M., and Rendall, A. R. 2022 . Natural and anthropogenic processes influence the occurrence of vertebrate fauna in coastal dunes. *Estuarine, Coastal and Shelf Science* **276** , 108025.

Chard, M., Foster, C. N., Lindenmayer, D. B., Cary, G. J., MacGregor, C. I., and Blanchard, W. 2022 . Time since fire influences macropod occurrence in a fire-prone coastal ecosystem. *Austral Ecology* **47** , 507–518. doi:10.1111/aec.13127

Cherry, M. J., Warren, R. J., and Conner, L. M. 2017 . Fire-mediated foraging tradeoffs in white-tailed deer. *Ecosphere* **8** , e01784. doi:10.1002/ECS2.1784

Colon, D. K. G. 2020 . Characterizing the Ecological Network of Puerto Rico: The Role of Landscape Connectivity and Land Use on the Distribution and Genetic Structure of the Small Indian Mongoose [Herpestes Auropunctatus]. The University of Wisconsin-Madison.

Culhane, K., Sollmann, R., White, A. M., Tarbill, G. L., Cooper, S. D., and Young, H. S. 2022 . Small mammal responses to fire severity mediated by vegetation characteristics and species traits. *Ecology and Evolution* **12** , e8918.

DEECA 2020 . Fire History Records of Fires primarily on Public Land. *DEECA, Department of Energy, Environment and Climate Action* . Available at: https://datashare.maps.vic.gov.au/ [accessed 13 April 2021]

DEECA 2021a . Fire History showing the number of times areas have been burnt, based on mapped fire history (scars). *DEECA, Department of Energy, Environment and Climate Action* . Available at: https://datashare.maps.vic.gov.au/

DEECA 2021b . Township Boundaries (polygon) - Vicmap Admin. *DEECA, Department of Energy, Environment and Climate Action* . Available at: https://datashare.maps.vic.gov.au/ [accessed 13 April 2021]

DEECA 2021c . Victorian Land Use Information System 2016-2017. *DEECA, Department of Energy, Environment and Climate Action* . Available at: https://datashare.maps.vic.gov.au/ [accessed 13 April 2021]

Dees, C. S., Clark, J. D., and Van Manen, F. T. 2001 . Florida panther habitat use in response to prescribed fire. *The Journal of Wildlife Management* , 141–147.

Dexter, N., Hudson, M., Carter, T., and Macgregor, C. 2011 . Habitat-dependent population regulation in an irrupting population of long-nosed bandicoots (Perameles nasuta). *Austral Ecology* **36** , 745–754.

Doherty, T. S., Bengsen, A. J., and Davis, R. A. 2015 . A critical review of habitat use by feral cats and key directions for future research and management. *Wildlife Research* **41** , 435–446.

Doherty, T. S., Geary, W. L., Jolly, C. J., Macdonald, K. J., Miritis, V., Watchorn, D. J., Cherry, M. J., Conner, L. M., Gonzalez, T. M., Legge, S. M., Ritchie, E. G., Stawski, C., and Dickman, C. R.2022 . Fire as a driver and mediator of predator–prey interactions. *Biological Reviews* **97** , 1539–1558. doi:10.1111/brv.12853

Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., and Dickman, C. R. 2016 . Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences of the United States of America* **113** , 11261–11265. doi:10.1073/pnas.1602480113

Doherty, T. S., Watchorn, D. J., Miritis, V., Pestell, A. J. L., and Geary, W. L. 2023 . Cats, foxes and fire: quantitative review reveals that invasive predator activity is most likely to increase shortly after fire. *Fire Ecology* **19** . doi:10.1186/s42408-023-00183-6

Dormann, C. F., Gruber, B., Winter, M., and Herrmann, D.2010 . Evolution of climate niches in European mammals?*Biology Letters* **6** , 229–232.

Dorph, A., Swan, M., Di Stefano, J., and Penman, T. D.2021 . Relating mammal species richness to landscape patterns across multiple spatial scales. *Landscape Ecology* **8** , 1–20. doi:10.1007/s10980-021-01208-8

Driscoll, D. A., Lindenmayer, D. B., Bennett, A. F., Bode, M., Bradstock, R. A., Cary, G. J., Clarke, M. F., Dexter, N., Fensham, R., Friend, G., Gill, M., James, S., Kay, G., Keith, D. A., MacGregor, C., Russell-Smith, J., Salt, D., Watson James, J. E. M., Williams Richard J., R. J., and York, A. 2010 . Fire management for biodiversity conservation: Key research questions and our capacity to answer them.*Biological Conservation* **143** , 1928–1939. doi:10.1016/j.biocon.2010.05.026

Eby, S. L., Anderson, T. M., Mayemba, E. P., and Ritchie, M. E.2014 . The effect of fire on habitat selection of mammalian herbivores: the role of body size and vegetation characteristics.*Journal of Animal Ecology* **83** , 1196–1205.

Elmhagen, B., Berteaux, D., Burgess, R. M., Ehrich, D., Gallant, D., Henttonen, H., Ims, R. A., Killengreen, S. T., Niemimaa, J., and Noren, K. 2017 . Homage to Hersteinsson and Macdonald: climate warming and resource subsidies cause red fox range expansion and Arctic fox decline. *Polar Research* **36** , 3.

Engeman, R. M., and Linnell, M. A. 1998 . Trapping strategies for deterring the spread of brown tree snakes from Guam.*Pacific Conservation Biology* **4** , 348–353.

ESRI, A. D. 2014 . Release 10.2. 2. *Redlands, CA, USA: Environmental Systems Research Institute* .

Fordyce, A., Hradsky, B. A., Ritchie, E. G., and Di Stefano, J.2016 . Fire affects microhabitat selection, movement patterns, and body condition of an Australian rodent (Rattus fuscipes).*Journal of Mammalogy* **97** , 102–111. doi:10.1093/jmammal/gyv159

Frey, S., Fisher, J. T., Burton, A. C., and Volpe, J. P.2017 . Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities.*Remote Sensing in Ecology and Conservation* **3** , 123–132. doi:10.1002/rse2.60

Gazzard, T., Walshe, T., Galvin, P., Salkin, O., Baker, M., Cross, B., and Ashton, P. 2020 . What is the 'appropriate' fuel management regime for the Otway Ranges, Victoria, Australia? Developing a long-term fuel management strategy using the structured decision-making framework. *International Journal of Wildland Fire* **29** , 354–370. doi:10.1071/WF18131

Geary, W. L., Doherty, T. S., Nimmo, D. G., Tulloch, A. I. T., and Ritchie, E. G. 2020 . Predator responses to fire: A global systematic review and meta-analysis. *Journal of Animal Ecology* **89** , 955–971. doi:10.1111/1365-2656.13153

Geary, W. L., Wayne, A. F., Tulloch, A. I. T., Ritchie, E. G., Maxwell, M. A., and Doherty, T. S. 2022 . Fox and cat responses to fox baiting intensity, rainfall and prey abundance in the Upper Warren, Western Australia. *Wildlife Research* **50** , 201–211.

Geldmann, J., Barnes, M., Coad, L., Craigie, I. D., Hockings, M., and Burgess, N. D. 2013 . Effectiveness of terrestrial protected areas in reducing habitat loss and population declines.*Biological Conservation* **161** , 230–238.

Geyle, H. M., Stevens, M., Duffy, R., Greenwood, L., Nimmo, D. G., Sandow, D., Thomas, B., White, J., and Ritchie, E. G.2020 . Evaluation of camera placement for detection of free-ranging carnivores; implications for assessing population changes.*Ecological Solutions and Evidence* **1** , e12018. doi:10.1002/2688-8319.12018

GISD 2023 . 100 of the World's Worst Invasive Alien Species. *Global Invasive Species Database* . Available at: http://www.iucngisd.org/gisd/100_worst.php on 20-09-2023 [accessed 20 September 2023]

Gosselink, T. E., Van Deelen, T. R., Warner, R. E., and Joselyn, M. G. 2003 . Temporal habitat partitioning and spatial use of coyotes and red foxes in east-central Illinois. *The Journal of Wildlife Management* , 90–103.

Greenberg, C. H., Miller, S., and Waldrop, T. A. 2007 . Short-term response of shrews to prescribed fire and mechanical fuel reduction in a Southern Appalachian upland hardwood forest. *Forest Ecology and Management* **243** , 231–236.

Griffiths, A. D., and Brook, B. W. 2014 . Effect of fire on small mammals: a systematic review. *International Journal of Wildland Fire* **23** , 1034–1043. doi:10.1071/WF14026

Hale, S., Mendoza, L., Yeatman, T., Cooke, R., Doherty, T., Nimmo, D., and White, J. G. 2021 . Evidence that post-fire recovery of small mammals occurs primarily via in situ survival.*Diversity and Distributions* **00** , 1–13. doi:10.1111/ddi.13283

Hale, S., Nimmo, D. G., Cooke, R., Holland, G., James, S., Stevens, M., De Bondi, N., Woods, R., Castle, M., Campbell, K., Senior, K., Cassidy, S., Duffy, R., Holmes, B., and White, J. G. 2016 . Fire and climatic extremes shape mammal distributions in a fire-prone landscape. *Diversity and Distributions* **22** , 1127–1138. doi:10.1111/ddi.12471

Hanser, S. E., Leu, M., Aldridge, C. L., Nielsen, S. E., and Knick, S. T. 2011 . Occurrence of small mammals: deer mice and the challenge of trapping across large spatial extents. *Mammalia***11** , 337–356.

Hartig, F. 2022 . DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.6. Available at: https://cran.r-project.org/package=DHARMa

Haslem, A., Leonard, S. W. J., Bruce, M. J., Christie, F., Holland, G. J., Kelly, L. T., MacHunter, J., Bennett, A. F., Clarke, M. F., and York, A. 2016 . Do multiple fires interact to affect vegetation structure in temperate eucalypt forests? *Ecological Applications* **26** , 2412–2421. doi:10.1002/eap.1399

Hradsky, B. A. 2020 . Conserving Australia's threatened native mammals in predator-invaded, fire-prone landscapes.*Wildlife Research* **47** , 1–15. doi:10.1071/WR19027

Hradsky, B. A., Mildwaters, C., Ritchie, E. G., Christie, F., and Di Stefano, J. 2017a . Responses of invasive predators and native prey to a prescribed forest fire. *Journal of Mammalogy***98** , 835–847. doi:10.1093/jmammal/gyx010

Hradsky, B. A., Penman, T. D., Ababei, D., Hanea, A., Ritchie, E. G., York, A., and Di Stefano, J. 2017b . Bayesian networks elucidate interactions between fire and other drivers of terrestrial fauna distributions. *Ecosphere* **8** , e01926. doi:10.1002/ecs2.1926

Hradsky, B. A., Robley, A., Alexander, R., Ritchie, E. G., York, A., Di Stefano, J., and Stefano, J. Di 2017c . Human-modified habitats facilitate forest-dwelling populations of an invasive predator, Vulpes vulpes. *Scientific Reports 2017 7:1* **7** , 1–12. doi:10.1038/s41598-017-12464-7

Ivan, J. S., and Newkirk, E. S. 2016 . CPW Photo Warehouse: a custom database to facilitate archiving, identifying, summarizing and managing photo data collected from camera traps. *Methods in Ecology and Evolution* **7** , 499–504.

Jolly, W. M., Cochrane, M. A., Freeborn, P. H., Holden, Z. A., Brown, T. J., Williamson, G. J., and Bowman, D. M. J. S. 2015 . Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature Communications* **6** , 1–11. doi:10.1038/ncomms8537

Joly, K., Dale, B. W., Collins, W. B., and Adams, L. G. 2003 . Winter habitat use by female caribou in relation to wildland fires in interior Alaska. *Canadian Journal of Zoology* **81** , 1192–1201.

Kearney, S. G., Cawardine, J., Reside, A. E., Fisher, D. O., Maron, M., Doherty, T. S., Legge, S., Silcock, J., Woinarski, J. C. Z., Garnett, S. T., Wintle, B. A., and Watson, J. E. M. 2019 . Corrigendum to: The threats to Australia's imperilled species and implications for a national conservation response. *Pacific Conservation Biology* **25** , 328. doi:10.1071/PC18024

Klop, E., van Goethem, J., and de Iongh, H. H. 2007 . Resource selection by grazing herbivores on post-fire regrowth in a West African woodland savanna. *Wildlife Research* **34** , 77–83.

Laux, A., Waltert, M., and Gottschalk, E. 2022 . Camera trap data suggest uneven predation risk across vegetation types in a mixed farmland landscape. *Ecology and Evolution* **12** , e9027.

Lawes, M. J., Murphy, B. P., Fisher, A., Woinarski, J. C. Z., Edwards, A. C., and Russell-Smith, J. 2015 . Small mammals decline with increasing fire extent in northern Australia: Evidence from long-Term monitoring in Kakadu National Park. *International Journal of Wildland Fire* **24** , 712–722. doi:10.1071/WF14163

Leahy, L., Legge, S. M., Tuft, K., McGregor, H. W., Barmuta, L. A., Jones, M. E., and Johnson, C. N. 2016 . Amplified predation after fire suppresses rodent populations in Australia's tropical savannas. *Wildlife Research* **42** , 705–716. doi:10.1071/WR15011

Lees, D. M., Watchorn, D. J., Driscoll, D. A., and Doherty, T. S. 2022 . Microhabitat selection by small mammals in response to fire. *Australian Journal of Zoology* . doi:10.1071/zo21022

Legge, S., Rumpff, L., Garnett, S. T., and Woinarski, J. C. Z. 2023 . Loss of terrestrial biodiversity in Australia: Magnitude, causation, and response. *Science* **381** , 622–631.

Lothian, A. J., Denny, M. J., and Tong, N. W. 2022 . Mammalian responses to fire on Newnes Plateau: A yardstick for future recovery. *Australian Zoologist* **42** , 278–303. doi:10.7882/az.2022.025

Louppe, V., Leroy, B., Herrel, A., and Veron, G. 2020 . The globally invasive small Indian mongoose Urva auropunctata is likely to spread with climate change. *Scientific Reports* **10** , 7461.

Lozano, J., Virgos, E., Malo, A. F., Huertas, D. L., and Casanovas, J. G. 2003 . Importance of scrub–pastureland mosaics for wild-living cats occurrence in a Mediterranean area: implications for the conservation of the wildcat (Felis silvestris). *Biodiversity & Conservation* **12** , 921–935.

Maguire, G., Ramp, D., and Coulson, G. 2006 . Foraging behaviour and dispersal of eastern grey kangaroos (Macropus giganteus) in an ideal free framework. *Journal of Zoology* **268** , 261–269.

Di Marco, M., Boitani, L., Mallon, D., Hoffmann, M., Iacucci, A., Meijaard, E., Visconti, P., Schipper, J., and Rondinini, C. 2014 . A retrospective evaluation of the global decline of carnivores and ungulates. *Conservation Biology* **28** , 1109–1118.

Mariani, M., Connor, S. E., Theuerkauf, M., Herbert, A., Kuneš, P., Bowman, D., Fletcher, M.-S., Head, L., Kershaw, A. P., Haberle, S. G., Stevenson, J., Adeleye, M., Cadd, H., Hopf, F., and Briles, C.2022 . Disruption of cultural burning promotes shrub encroachment and unprecedented wildfires. *Frontiers in Ecology and the Environment* . doi:10.1002/FEE.2395

Maxwell, S. L., Cazalis, V., Dudley, N., Hoffmann, M., Rodrigues, A. S. L., Stolton, S., Visconti, P., Woodley, S., Kingston, N., and Lewis, E. 2020 . Area-based conservation in the twenty-first century. *Nature* **586** , 217–227.

May, S. A., and Norton, T. W. 1996 . Influence of fragmentation and disturbance on the potential impact of feral predators on native fauna in Australian forest ecosystems. *Wildlife Research* **23** , 387–400.

McCain, C. M. 2019 . Assessing the risks to United States and Canadian mammals caused by climate change using a trait-mediated model. *Journal of Mammalogy* **100** , 1808–1817.

McCain, C. M., King, S. R. B., Szewczyk, T., and Beck, J.2018 . Small mammal species richness is directly linked to regional productivity, but decoupled from food resources, abundance, or habitat complexity. *Journal of Biogeography* **45** , 2533–2545. doi:10.1111/jbi.13432

McGregor, H., Legge, S., Jones, M. E., and Johnson, C. N.2015 . Feral Cats Are Better Killers in Open Habitats, Revealed by Animal-Borne Video. *PLOS ONE* **10** , e0133915. doi:10.1371/JOURNAL.PONE.0133915

McGregor, H., Moseby, K., Johnson, C. N., and Legge, S.2020 . The short-term response of feral cats to rabbit population decline: are alternative native prey more at risk?*Biological Invasions* **22** , 799–811.

McGregor, H. W., Cliff, H. B., and Kanowski, J. 2016a . Habitat preference for fire scars by feral cats in Cape York Peninsula, Australia. *Wildlife Research* **43** , 623–633. doi:10.1071/WR16058

McGregor, H. W., Legge, S., Jones, M. E., and Johnson, C. N.2016b . Extraterritorial hunting expeditions to intense fire scars by feral cats. *Scientific Reports* **6** , 1–7. doi:10.1038/srep22559

McGregor, H. W., Legge, S., Jones, M. E., and Johnson, C. N.2014 . Landscape management of fire and grazing regimes alters the fine-scale habitat utilisation by feral cats. *PLoS ONE***9** . doi:10.1371/journal.pone.0109097

McHugh, D., Goldingay, R. L., Link, J., and Letnic, M.2019 . Habitat and introduced predators influence the occupancy of small threatened macropods in subtropical Australia. *Ecology and Evolution* **9** , 6300–6317. doi:10.1002/ece3.5203

Mills, D., Fattebert, J., Hunter, L., and Slotow, R.2019 . Maximising camera trap data: Using attractants to improve detection of elusive species in multi-species surveys. *PloS one***14** , e0216447.

Miritis, V., Dickman, C. R., Nimmo, D. G., and Doherty, T. S.2023 . After the 'Black Summer' fires : faunal responses to megafire depend on fire severity, proportion burnt, and vegetation type.*Journal of Applied Ecology (in press)* .

Miritis, V., Rendall, A. R., Doherty, T. S., Coetsee, A. L., and Ritchie, E. G. 2020 . Living with the enemy: A threatened prey species coexisting with feral cats on a fox-free island. *Wildlife Research* **47** , 633–642. doi:10.1071/WR19202

Moore, D., Kearney, M. R., Paltridge, R., McAlpin, S., and Stow, A. 2018 . Feeling the pressure at home: Predator activity at the burrow entrance of an endangered arid-zone skink. *Austral Ecology* **43** , 102–109. doi:10.1111/aec.12547

Moore, H. A., Dunlop, J. A., Valentine, L. E., Woinarski, J. C. Z., Ritchie, E. G., Watson, D. M., and Nimmo, D. G. 2019 . Topographic ruggedness and rainfall mediate geographic range contraction of a threatened marsupial predator. *Diversity and Distributions***25** , 1818–1831. doi:10.1111/ddi.12982

Morandini, M., Mazzamuto, M. V., and Koprowski, J. L.2023 . Foraging Behavior Response of Small Mammals to Different Burn Severities Marina. *Fire* **6** . doi:10.3390/fire6090367

Morris, G., Hostetler, J. A., Oli, M. K., and Conner, L. M.2011 . Effects of predation, fire, and supplemental feeding on populations of two species of Peromyscus mice. *Journal of Mammalogy* **92** , 934–944. doi:10.1644/10-MAMM-A-419.1

Myneni, R. B., Maggion, S., Iaquinta, J., Privette, J. L., Gobron, N., Pinty, B., Kimes, D. S., Verstraete, M. M., and Williams, D. L. 1995 . Optical remote sensing of vegetation: modeling, caveats, and algorithms. *Remote sensing of environment***51** , 169–188.

Nalliah, R., Sitters, H., Smith, A., and Di Stefano, J.2022 . Untangling the influences of fire, habitat and introduced predators on the endangered heath mouse. *Animal Conservation***25** , 208–220. doi:10.1111/acv.12731

Nichols, M., Ross, J., Glen, A. S., and Paterson, A. M.2019 . An evaluation of systematic versus strategically-placed camera traps for monitoring feral cats in New Zealand. *Animals***9** , 687.

Niedballa, J., Sollmann, R., Courtiol, A., and Wilting, A.2016 . camtrapR: an R package for efficient camera trap data management. *Methods in Ecology and Evolution* **7** , 1457–1462.

ODBPC, O. D. B. P. C. 2021 . Otway District Strategic Fire Management Plan 2021-24. Shires of Corangamite, Colac Otway and Surf Coast.

van Oldenborgh, G. J., Krikken, F., Lewis, S., Leach, N., Lehner, F., Saunders, K., van Weele, M., Haustein, K., Li, S., Wallom, D., Sparrow, S., Arrighi, J., Singh, R., van Aalst, M., Philip, S., Vautard, R., and Otto, F. 2020 . Attribution of the Australian bushfire risk to anthropogenic climate change. *Natural Hazards and Earth System Sciences* , 1–46. doi:10.5194/nhess-2020-69

Pacifici, M., Di Marco, M., and Watson, J. E. M. 2020 . Protected areas are now the last strongholds for many imperiled mammal species. *Conservation Letters* **13** , e12748.

Le Pla, M., Hradsky, B. A., Di Stefano, J., Farley-Lehmer, T. C., Birnbaum, E. K., and Pascoe, J. H. 2023 . Movement and ranging behaviour of long-nosed potoroos (Potorous tridactylus) in south-west Victoria, Australia. *Wildlife Research* .

Pyke, G. H., Pulliam, H. R., and Charnov, E. L. 1977 . Optimal foraging: a selective review of theory and tests. *The quarterly review of biology* **52** , 137–154.

R Core Team 2022 . R: A language and environment for statistical computing. R Foundation for Statistical Computing. Available at: https://www.r-project.org/

Ralph, A. 2021 . Where have the diggers gone? The occupancy and distribution of the long-nosed potoroo and the southern brown bandicoot in the Gariwerd landscape.

Raynor, E. J., Joern, A., and Briggs, J. M. 2015 . Bison foraging responds to fire frequency in nutritionally heterogeneous grassland. *Ecology* **96** , 1586–1597. doi:10.1890/14-2027.1

Reid, A. M., Murphy, B. P., Vigilante, T., Corporation, W. G. A., and Bowman, D. M. J. S. 2023 . Pyric Herbivory and the Nexus Between Forage, Fire and Native and Introduced Large Grazing Herbivores in Australian Tropical Savannas. *Ecosystems***26** , 610–626.

Rija, A. A., Critchlow, R., Thomas, C. D., and Beale, C. M.2020 . Global extent and drivers of mammal population declines in protected areas under illegal hunting pressure. *PLoS One***15** , e0227163.

Rivarola, M. D. 2022 . Broadscale Outcome and Monitoring Assessment to Evaluate Protected Area Effectiveness in Northern Patagonia.

Robley, A., Fanson, B., and PV, P. V. W. C. D. T.2019 . The Otway Ark: response of predators and native species 2016–2018. Available at: www.ari.vic.gov.au [accessed 23 February 2022]

Robley, A., Thomson, J., Johnson, G., Wemyss, E., Woodford, L., and Melgaard, G. 2023 . Barry Mountains Ark—managing the Great Dividing Range Long-footed Potoroo population 2007–2022.

Šálek, M., Červinka, J., Banea, O. C., Krofel, M., Ćirović, D., Selanec, I., Penezić, A., Grill, S., and Riegert, J. 2014 . Population densities and habitat use of the golden jackal (Canis aureus) in farmlands across the Balkan Peninsula. *European Journal of Wildlife Research* **60** , 193–200.

Schwemmer, P., Weiel, S., and Garthe, S. 2021 . Spatio-temporal movement patterns and habitat choice of red foxes (Vulpes vulpes) and racoon dogs (Nyctereutes procyonoides) along the Wadden Sea coast. *European Journal of Wildlife Research***67** , 49.

Scroggie, M. P., Forsyth, D. M., McPhee, S. R., Matthews, J., Stuart, I. G., Stamation, K. A., Lindeman, M., and Ramsey, D. S. L.2018 . Invasive prey controlling invasive predators? European rabbit abundance does not determine red fox population dynamics.*Journal of Applied Ecology* **55** , 2621–2631.

Senior, K. L., Giljohann, K. M., McCarthy, M. A., and Kelly, L. T. 2022 . A field test of mechanisms underpinning animal diversity in recently burned landscapes. *Journal of Applied Ecology* , 1–12. doi:10.1111/1365-2664.14315

Shaw, R. E., James, A. I., Tuft, K., Legge, S., Cary, G. J., Peakall, R., and Banks, S. C. 2021 . Unburnt habitat patches are critical for survival and in situ population recovery in a small mammal after fire. *Journal of Applied Ecology* **58** , 1325–1335.

Sitters, H., Di Stefano, J., Christie, F. J., Sunnucks, P., and York, A. 2015 . Bird diversity increases after patchy prescribed fire: implications from a before–after control–impact study. *International Journal of Wildland Fire* **24** , 690–701.

Sokos, C., Birtsas, P., Papaspyropoulos, K. G., Tsachalidis, E., Giannakopoulos, A., Milis, C., Spyrou, V., Manolakou, K., Valiakos, G., and Iakovakis, C. 2016 . Mammals and habitat disturbance: the case of brown hare and wildfire. *Current Zoology* **62** , 421–430.

Stobo-Wilson, A. M., Murphy, B. P., Legge, S. M., Caceres-Escobar, H., Chapple, D. G., Crawford, H. M., Dawson, S. J., Dickman, C. R., Doherty, T. S., Fleming, P. A., Garnett, S. T., Gentle, M., Newsome, T. M., Palmer, R., Rees, M. W., Ritchie, E. G., Speed, J., Stuart, J. M., Suarez-Castro, A. F., Thompson, E., Tulloch, A., Turpin, J. M., and Woinarski, J. C. Z. 2022 . Counting the bodies: Estimating the numbers and spatial variation of Australian reptiles, birds and mammals killed by two invasive mesopredators Ed J. Brito.*Diversity and Distributions* **28** , 976–991. doi:10.1111/ddi.13497

Stobo-Wilson, A. M., Stokeld, D., Einoder, L. D., Davies, H. F., Fisher, A., Hill, B. M., Mahney, T., Murphy, B. P., Stevens, A., Woinarski, J. C. Z., Rangers, B., Warddeken, R., and Gillespie, G. R.2020 . Habitat structural complexity explains patterns of feral cat and dingo occurrence in monsoonal Australia. *Diversity and Distributions* **26** , 832–842. doi:10.1111/ddi.13065

Styger, J. K., Kirkpatrick, J. B., Marsden-Smedley, J. O. N., and Leonard, S. W. J. 2011 . Fire incidence, but not fire size, affects macropod densities. *Austral Ecology* **36** , 679–686.

Sukma, H. T., Di Stefano, J., Swan, M., and Sitters, H.2019 . Mammal functional diversity increases with vegetation structural complexity in two forest types. *Forest Ecology and Management* **433** , 85–92.

Swan, M., Christie, F., Sitters, H., York, A., and Di Stefano, J. 2015 . Predicting faunal fire responses in heterogeneous landscapes: The role of habitat structure. *Ecological Applications* **25** , 2293–2305. doi:10.1890/14-1533.1

Swan, M., Christie, F., Steel, E., Sitters, H., York, A., and Di Stefano, J. 2020 . Ground-dwelling mammal diversity responds positively to productivity and habitat heterogeneity in a fire-prone region. *Ecosphere* **11** . doi:10.1002/ecs2.3248

Swan, M., Galindez-Silva, C., Christie, F., York, A., and Di Stefano, J. 2016 . Contrasting responses of small mammals to fire and topographic refugia. *Austral Ecology* **41** , 443–451. doi:10.1111/aec.12331

Swan, M., Le, M., Julian, P., Stefano, D., Pascoe, J., and Penman, T. D. 2021 . Species distribution models for conservation planning in fire-prone landscapes. *Biodiversity and Conservation* . doi:10.1007/s10531-021-02136-4

Tedeschi, L., Biancolini, D., Capinha, C., Rondinini, C., and Essl, F. 2022 . Introduction, spread, and impacts of invasive alien mammal species in Europe. *Mammal Review* **52** , 252–266.

Thompson, C. M., Augustine, D. J., and Mayers, D. M.2008 . Swift fox response to prescribed fire in shortgrass steppe. *Western North American Naturalist* , 251–256.

Tucker, C. J., Fung, I. Y., Keeling, C. D., and Gammon, R. H.1986 . Relationship between atmospheric CO2 variations and a satellite-derived vegetation index. *Nature* **319** , 195–199.

Watchorn, D. J., Cowan, M. A., Driscoll, D. A., Nimmo, D. G., Ashman, K. R., Garkaklis, M. J., Wilson, B. A., and Doherty, T. S.2022 . Artificial habitat structures for animal conservation: design and implementation, risks and opportunities. *Frontiers in Ecology and the Environment* .

Wayne, A. F., Wilson, B. A., and Woinarski, J. C. Z.2017 . Falling apart? Insights and lessons from three recent studies documenting rapid and severe decline in terrestrial mammal assemblages of northern, south-eastern and south-western Australia.*Wildlife Research* **44** , 114. doi:10.1071/wr16178

White, J. G., Sparrius, J., Robinson, T., Hale, S., Lupone, L., Healey, T., Cooke, R., and Rendall, A. R. 2022 . Can NDVI identify drought refugia for mammals and birds in mesic landscapes?*Science of the Total Environment* **851** , 158318. doi:10.1016/j.scitotenv.2022.158318

Wilson, B. A., Aberton, J. G., and Reichl, T. 2001 . Effects of fragmented habitat and fire on the distribution and ecology of the swamp antechinus (Antechinus minimus maritimus) in the eastern Otways, Victoria B. *Wildlife Research* **28** , 527–536.

Wilson, B. A., and Garkaklis, M. J. 2020 . Patterns of decline of small mammal assemblages in vegetation communities of coastal south-east Australia: Identification of habitat refuges.*Australian Mammalogy* . doi:10.1071/AM20032

Wilson, B. A., Lock, M., and Garkaklis, M. J. 2018 . Long-term fluctuations in distribution and populations of a threatened rodent (Pseudomys novaehollandiae) in coastal woodlands of the Otway Ranges, Victoria: A regional decline or extinction? *Australian Mammalogy* **40** , 281–293. doi:10.1071/AM17036

Wilson, B. A., Zhuang-Griffin, L., and Garkaklis, M. J.2017 . Decline of the dasyurid marsupial Antechinus minimus maritimus in south-east Australia: implications for recovery and management under a drying climate. *Australian Journal of Zoology***65** , 203. doi:10.1071/zo17041

Woinarski, J. C. Z., Braby, M. F., Burbidge, A. A., Coates, D., Garnett, S. T., Fensham, R. J., Legge, S. M., McKenzie, N. L., Silcock, J. L., and Murphy, B. P. 2019a . Reading the black book: The number, timing, distribution and causes of listed extinctions in Australia. *Biological Conservation* **239** . doi:10.1016/j.biocon.2019.108261

Woinarski, J. C. Z., Burbidge, A. A., and Harrison, P. L.2015 . Ongoing unraveling of a continental fauna: Decline and extinction of Australian mammals since European settlement.*Proceedings of the National Academy of Sciences of the United States of America* **112** , 4531–4540. doi:10.1073/pnas.1417301112

Woinarski, J. C. Z., Legge, S. M., and Dickman, C. R.2019b . 'Cats in Australia: companion and killer'. (CSIRO Publishing: Clayton South.)

Youngentob, K. N., Yoon, H. J., Stein, J., Lindenmayer, D. B., and Held, A. A. 2015a . Where the wild things are: using remotely sensed forest productivity to assess arboreal marsupial species richness

and abundance. *Diversity and Distributions* **21** , 977–990. doi:10.1111/DDI.12332

Youngentob, K. N., Yoon, H. J., Stein, J., Lindenmayer, D. B., and Held, A. A. 2015b . Where the wild things are: Using remotely sensed forest productivity to assess arboreal marsupial species richness and abundance. *Diversity and Distributions* **21** , 977–990. doi:10.1111/DDI.12332

Zwolak, R., and Foresman, K. R. 2007 . Effects of a stand-replacing fire on small-mammal communities in montane forest. *Canadian Journal of Zoology* **85** , 815–822.