



# Pyrodiversity trade-offs: A simulation study of the effects of fire size and dispersal ability on native mammal populations in northern Australian savannas

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## ABSTRACT

Maximising the spatiotemporal variability of prescribed fire (i.e. pyrodiversity) is often thought to benefit biodiversity. However, given mixed empirical support, the generality of the pyrodiversity hypothesis remains questionable. Here, we use a simulation experiment to explore the effects of spatiotemporal fire patterns on the population trajectories of four mammal species in a northern Australian savanna: northern brown bandicoot (*Isodon macrourus*), northern brushtail possum (*Trichosurus vulpecula arnhemensis*), grassland melomys (*Melomys burtoni*), and northern quoll (*Dasyurus hallucatus*). Underpinned by data from a landscape-scale fire experiment, we simulated mammal population trajectories under three scenarios of fire size (ambient, small/dispersed fires, large/clumped fires) and three levels of dispersal ability (low, moderate, high) over a 21-year period across the Kapalga area of Kakadu National Park. The simulated population size of all four species declined markedly, regardless of fire spatial pattern and dispersal ability. However, the predicted final population size (i.e. number of individuals in the final timestep of the simulation) for the northern brown bandicoot, northern brushtail possum and grassland melomys were significantly influenced by fire size, with declines most severe under the small/dispersed fire scenario. Our results suggest that maximising the dispersion of small fires at the expense of disturbance refugia (such as less-frequently burnt areas) may exacerbate the severity of mammal decline. This highlights the importance of considering trade-offs between spatial (i.e. fire dispersion) and temporal (i.e. fire frequency) aspects of pyrodiversity, and the potential risks when applying fire management for biodiversity conservation without a firm understanding of the requirements of the target species.

## 1. Introduction

Anthropogenic disruption of fire regimes is contributing to the global collapse of biodiversity and loss of ecosystem function (Kelly et al., 2020). Consequently, developing and effectively implementing fire management for biodiversity conservation remains a pressing challenge. A critical step towards meeting this challenge is to identify the spatio-temporal patterns of fire that are compatible with the persistence of target species. This can be more difficult than is commonly appreciated because fire is a highly variable form of disturbance with complex effects on biodiversity that are often influenced by many factors that operate

and interact across a range of spatiotemporal scales (e.g. climate, weather, vegetation, land-use, productivity, fire history). Such complexity poses significant difficulties in designing and interpreting field surveys (Andersen, 2021), natural experiments (Ondei et al., 2020) and formal experimental studies (Russell-Smith et al., 2003) that investigate the effects of fire on biodiversity.

The difficulties associated with elucidating fire–biodiversity relationships may explain the scarcity of examples where fire management is specifically designed to meet the requirements of target species. An alternative approach is to base fire management on the assumption that a spatiotemporally diverse fire regime will conserve biodiversity by

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creating a greater variety of ecological niches: that pyrodiversity promotes biodiversity (henceforth referred to as the ‘pyrodiversity hypothesis’) (Martin and Sapsis, 1992). There is evidence that pyrodiversity promotes biodiversity in some systems (Tingley et al., 2016; Ponsio et al., 2016), but not others (Taylor et al., 2012; Farnsworth et al., 2014). In a detailed review of the pyrodiversity hypothesis and its usefulness to fire management, Parr and Andersen (2006) questioned the applicability of the pyrodiversity hypothesis in some fire-prone systems, such as the savanna landscapes of Australia and South Africa. They asserted that fire patterns are often ecologically unimportant and suggested that a priority should be the identification of the aspects, including spatiotemporal patterns, of the fire regime that are particularly important for conserving species, and how best to implement them. More recently, Kelly and Brotons (2017) posited the potential benefits to biodiversity of developing more spatially-tailored fire management if it is both guided by ecological theory and underpinned by the demonstrated requirements of target species.

Ensuring fire management is compatible with biodiversity conservation is particularly important across the vast tropical savannas of northern Australia, where the loss of Aboriginal fire management is widely considered to be a key factor contributing to widespread biodiversity decline (Bowman et al., 2004). The increased frequency of large, high-intensity fires in these landscapes has been strongly implicated in the decline of numerous species and ecological communities, including stands of northern cypress pine (*Callitris intratropica*) (Bowman and Panton, 1993), sandstone heathlands (Russell-Smith et al., 2002), rainforests (Ondei et al., 2017), granivorous birds (Franklin, 1999), and small mammals (Woinarski et al., 2010; Woinarski et al., 2011). To mitigate these declines, contemporary fire management aims to apply smaller, low-intensity fires, under relatively mild fire weather conditions. While there is evidence that this approach can effectively reduce the extent of high-intensity wildfires (Evans and Russell-Smith, 2019), the flow-on effects on biodiversity often remain unclear, and potentially deleterious (Bowman et al., 2022). Corey et al. (2019) recently cautioned that the extensive use of prescribed burning to reduce the extent of high-intensity wildfires in northern Australian savannas has the potential to deliver perverse outcomes for biodiversity, because benefits to biodiversity are often assumed rather than demonstrated.

Given the potential for perverse outcomes of fire management in a system experiencing biodiversity decline (Corey et al., 2019), it is critical we develop a more robust understanding of the ecological implications of prescribed burning across northern Australian savannas. Unfortunately, fire–biodiversity relationships are often complex, spatially and temporally variable, and difficult to disentangle. Furthermore, the difficulty in replicating ‘real-world’ fire experiments and the need to understand population changes at large spatiotemporal scales make computer simulations particularly useful for identifying optimal fire management regimes for biodiversity conservation. While simulations lack realism and do not represent the ‘full picture’ of any given ecosystem, they enable us to isolate individual (or multiple) processes and test the effect of those on biodiversity components such as long-term population viability. For example, previous simulation studies have demonstrated that the interaction of spatial patterns of fire and a species’ capacity for dispersal can influence demography and genetic diversity, but that the outcomes are likely to be species- and context-specific (Davies et al., 2016; Banks et al., 2017), thereby highlighting that simulation models parameterised to replicate specific ecosystems are required to inform conservation.

Here, we use a simulation experiment to investigate how the spatiotemporal patterns of fire, and animal dispersal ability, influence the population trajectory of native mammal species in northern Australian savannas. While the influence of fire size on northern Australian mammal populations has been investigated previously at extremely coarse scales (~16 km<sup>2</sup> fire patches) (Griffiths et al., 2015), the development of new modelling approaches now permits this to be addressed at a fine spatial resolution (1 ha). Specifically, we compare

population trajectories of four mammal species, with contrasting life histories (semelparous vs. iteroparous) and ecologies (arboreal, semi-arboreal and terrestrial), under three fire size scenarios (ambient, small/dispersed fires, large/clumped fires) and three levels of dispersal ability (low, moderate, high) across the Kapalga area of Kakadu National Park. Given the demonstrated negative impacts of large savanna fires on populations of small native mammals (Legge et al., 2008), we hypothesised that (compared to contemporary ‘ambient’ fire patterns) the small/dispersed fire scenario would improve mammal population trajectories, while large/clumped fires would be detrimental to mammal population trajectories. We also hypothesised that population trajectories would improve with the increased dispersal ability of a mammal species.

## 2. Method

### 2.1. Study site

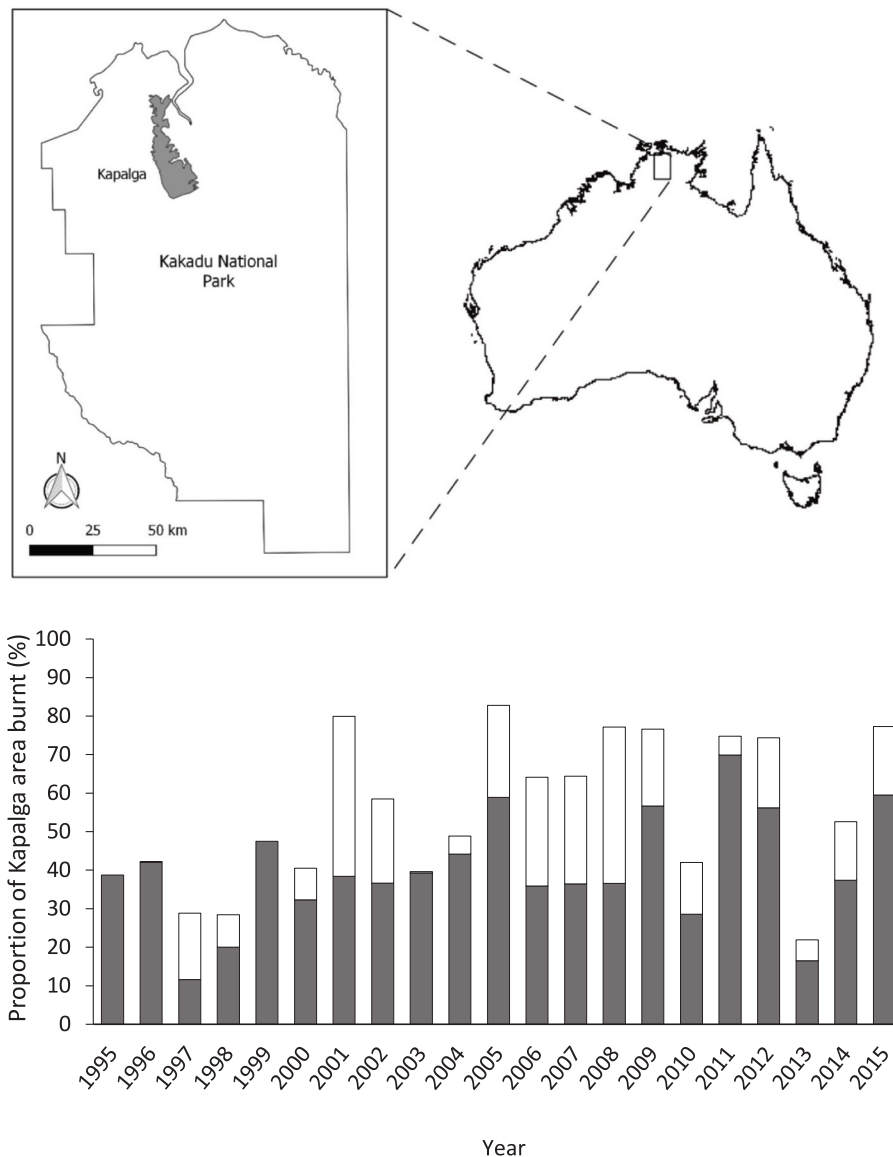
Our study site is the Kapalga area of Kakadu National Park in northern Australia (Fig. 1). This area has a flat topography, mostly surrounded by a seasonally-inundated floodplain, and bounded to the south by the Arnhem Highway. The vegetation is lowland open savanna forest dominated by *Eucalyptus miniata* and *E. tetradonta* with a grassy understorey, with riverine forests along creek-lines, and swamp forests fringing wetland areas. The area has a tropical monsoonal climate with a humid wet season (November–April) in which over 90 % of annual rainfall (mean = 1381 mm) occurs. Fire frequency at Kapalga is extremely high, with an average of 55 % ± 19 % (SE) of the Kapalga area burning each year between 1995 and 2015 (Fig. 1). On average, 74 % and 26 % of the total area burnt each year, occurred in the early (March–July) and late (August–December) dry seasons, respectively. The seasonality of fires across Kapalga aligns with that of areas under prescribed burning (Evans and Russell-Smith, 2019).

### 2.2. Kapalga fire experiment

The Kapalga fire experiment involved the application of four different fire treatments to 22 large compartments (15–20 km<sup>2</sup>) over a 5-year period (1990–1994, inclusive). ‘Early’ compartments were burnt in the early dry season (in May or June), representative of the predominant approach to prescribed burning in the region; ‘late’ compartments were burnt late in the dry season (September), representative of unmanaged high-intensity wildfires; ‘progressive’ compartments were burnt progressively throughout the dry season, in an attempt to represent assumed traditional Aboriginal burning practices; and ‘unburnt’ compartments were not burnt (Andersen et al., 1998). Each experimental treatment was replicated at least three times. Within two of the replicated compartments of each fire treatment, native mammals were surveyed using two live-trapping grids conducted for two consecutive nights at 2-monthly intervals throughout the Kapalga fire experiment; see Braithwaite and Griffiths (1996) for details of the trapping regime.

### 2.3. Study species

We simulated the population trajectory of four native mammal species: the northern brushtail possum (*Trichosurus vulpecula arnhemensis*), northern brown bandicoot (*Isodon macrourus*), grassland melomys (*Melomys burtoni*) and northern quoll (*Dasyurus hallucatus*). Both the northern quoll and northern brushtail possum are listed as threatened (Endangered and Vulnerable, respectively) under Australian national legislation, given rapid ongoing declines in their range and abundance (Woinarski et al., 2001; Stobo-Wilson et al., 2019; von Takach et al., 2020). The northern brown bandicoot is not listed as threatened, but has undergone a significant decline in abundance in parts of monsoonal northern Australia in recent decades (Davies et al., 2018). The grassland melomys is not known to have undergone widespread decline, however,



**Fig. 1.** The location of the Kapalga area (grey) within Kakadu National Park. The proportion of the Kapalga area (32,513 ha) that was burnt each year between 1995 and 2015 is also shown, with the proportion burnt in the early dry season (indicated in grey) and late dry season (indicated in white). Burnt areas are mapped from Landsat satellite imagery, and are from an updated version of the dataset described by Russell-Smith et al. (1997).

has declined significantly at Kapalga in the last two decades (Stokeld et al., 2016). The four study species vary significantly in life history, body size, fecundity, parental care, arboreality and diet.

#### 2.4. Modelling approach

Davies et al. (2021) outlined an approach to simulate the effects of fire on savanna mammals using the R package *steps* (Visintin et al., 2020). We used the same approach to investigate how manipulating the spatial pattern of fires might influence the population trajectory of our four study species. Model steps and inputs outlined sequentially below.

##### 2.4.1. Model parameterisation

The initial population size for each species was determined by multiplying the density ( $\text{ha}^{-1}$ ) of each species with the size of the Kapalga landscape (32,513 ha). The density of common brushtail possum ( $0.78 \text{ ha}^{-1}$ ), northern brown bandicoot ( $0.79 \text{ ha}^{-1}$ ), grassland melomys ( $0.43 \text{ ha}^{-1}$ ) and female northern quoll ( $0.43 \text{ ha}^{-1}$ ) resulted in initial population sizes of 25,360, 25,685, 13,980 and 13,980

individuals, respectively (Griffiths et al., 2015). Our population models were parameterised with two life-stages (juvenile and adult). The proportion of adults and juveniles in the initial population of each species was based on the stable-age distribution outlined in Griffiths et al. (2015): common brushtail possum 52 % adult; northern brown bandicoot 53 % adult; northern quoll 53 % adult; grassland melomys 0.45 % adult. The initial population of each species was randomly distributed across the Kapalga landscape.

We parameterised our population models with published estimates of demographic rates (Table 1a). These estimates were derived from a large capture-mark-recapture dataset collected at 2-monthly intervals throughout the Kapalga fire experiment and therefore represent survival and transition probabilities, and per capita recruitment rate, per 2-monthly timestep in the absence of fire (Griffiths et al., 2015). Given their synchronous breeding strategy, northern quoll models were female-only, with transition and recruitment constrained to occur only within the third (May/June) and sixth (November/December) timestep of each year, respectively (Oakwood, 2000).

We specified that the population in each cell would change according

**Table 1**

A summary of: a) baseline model parameters ( $\pm$ standard deviation) for each study species derived by Griffiths et al. (2015). Adjusted demographic rates ( $\pm$ standard deviation) in cells following the occurrence of: b) early dry season fires; and c) late dry season fires.

	Northern brown bandicoot	Northern brushtail possum	Grassland melomys	Northern quoll*
<b>a) Baseline parameters</b>				
Juvenile survival ( $\pm$ SD)	0.55 (0.07)	0.55 (0.09)	0.36 (0.05)	0.37 (0.11)
Adult survival ( $\pm$ SD)	0.75 (0.11)	0.79 (0.08)	0.77 (0.05)	0.88 (0.08)
Transition ( $\pm$ SD)	0.36 (0.10)	0.25 (0.11)	0.20 (0.04)	1.00 (0.00) <sup>†</sup>
Recruitment ( $\pm$ SD)	0.45 (0.12)	0.46 (0.26)	0.78 (0.23)	0.57 (0.27) <sup>†</sup>
<b>b) Following early dry season fire</b>				
Juvenile survival ( $\pm$ SD)	0.47 (0.07)	0.46 (0.09)	0.21 (0.05)	0.37 (0.11)
Adult survival ( $\pm$ SD)	0.65 (0.11)	0.66 (0.08)	0.45 (0.05)	0.88 (0.08)
Transition ( $\pm$ SD)	0.31 (0.10)	0.21 (0.11)	0.12 (0.04)	1.00 (0.00) <sup>†</sup>
Recruitment ( $\pm$ SD)	0.45 (0.12)	0.21 (0.26)	1.48 (0.23)	0.61 (0.27) <sup>†</sup>
<b>c) Following late dry season fire</b>				
Juvenile survival ( $\pm$ SD)	0.33 (0.07)	0.39 (0.09)	0.23 (0.05)	0.30 (0.11)
Adult survival ( $\pm$ SD)	0.45 (0.11)	0.55 (0.08)	0.50 (0.05)	0.70 (0.08)
Transition ( $\pm$ SD)	0.22 (0.10)	0.18 (0.11)	0.13 (0.04)	1.00 (0.00) <sup>†</sup>
Recruitment ( $\pm$ SD)	0.10 (0.12)	0.01 (0.26)	0.98 (0.23)	0.15 (0.27) <sup>†</sup>

\* Female only model.

<sup>†</sup> Values constrained to occur in a specific timestep within each year to reflect synchronous breeding.

to the baseline demographic rates (unless a fire occurred in that cell — see below), with stochasticity determined by each parameter's standard deviation. We used a ceiling density carrying capacity as per Griffiths et al. (2015): common brushtail possum ( $2.46 \text{ ha}^{-1}$ ); northern brown bandicoot ( $2.00 \text{ ha}^{-1}$ ); grassland melomys ( $1.08 \text{ ha}^{-1}$ ); and northern quoll ( $1.06 \text{ ha}^{-1}$ ).

#### 2.4.2. Incorporating the effects of fire

Fire can influence native mammal demographic rates through changes in resource availability (i.e. food and den sites) and exposure to predators. The impacts of fire on our study species were quantified by Griffiths et al. (2015). Given differences in fire intensity and timing, and the life-history traits of each species, these impacts varied between early and late season fires, and were species specific. In our models, early dry season fires occurred in the third timestep (May/June) in each year, with late dry season fires occurred in the fifth timestep (September/October) in each year (Davies et al., 2021). Fire patterns were incorporated as a stack of raster layers (one layer for each timestep) with cell values indicating where fires occurred (cell value of '1') or did not occur (cell values of '0'). Cells burnt in the early dry season could not be burnt again in the late dry season. As our simulations were based on the five-year Kapalga experiment, we were unable to incorporate the effect of longer-term changes in habitat quality on native mammal demographic rates, including the potential implications of long-term fire exclusion (Woinarski et al., 2004) and longer-term changes in resource availability such as tree hollows (Penton et al., 2021). Therefore, in cells where fires

occurred, the baseline demographic rates were adjusted as per the fire impact parameters derived by Griffiths et al. (2015) (Table 1). These adjusted demographic rates linearly abated to zero by the end of each year.

#### 2.4.3. Dispersal

We used the cellular-automata dispersal function in the *steps* package. This function allowed individual animals to move randomly through the landscape up to a specified number of cells (see Section 2.6) until they came across a cell with available carrying capacity. We set the proportion of juveniles and adults dispersing to be 1.0 and 0.1 respectively.

#### 2.4.4. Spatial scale, resolution, and replication

We simulated the population trajectory of native mammals across the entire Kapalga area at a spatial resolution of 1 ha (32,513 cells in total) over a 21-year period, from January 1995 to December 2015 (i.e. 126 2-month timesteps). We simulated the population trajectory of the four native mammal species under nine different sets of simulations (i.e. three fire scenarios, each with three levels of dispersal ability — see below). Each set of simulations was replicated 100 times. R code and spatial fire rasters are freely available (see Davies et al., 2023).

#### 2.5. Fire scenarios

We investigated three fire scenarios of contrasting spatial patterns:

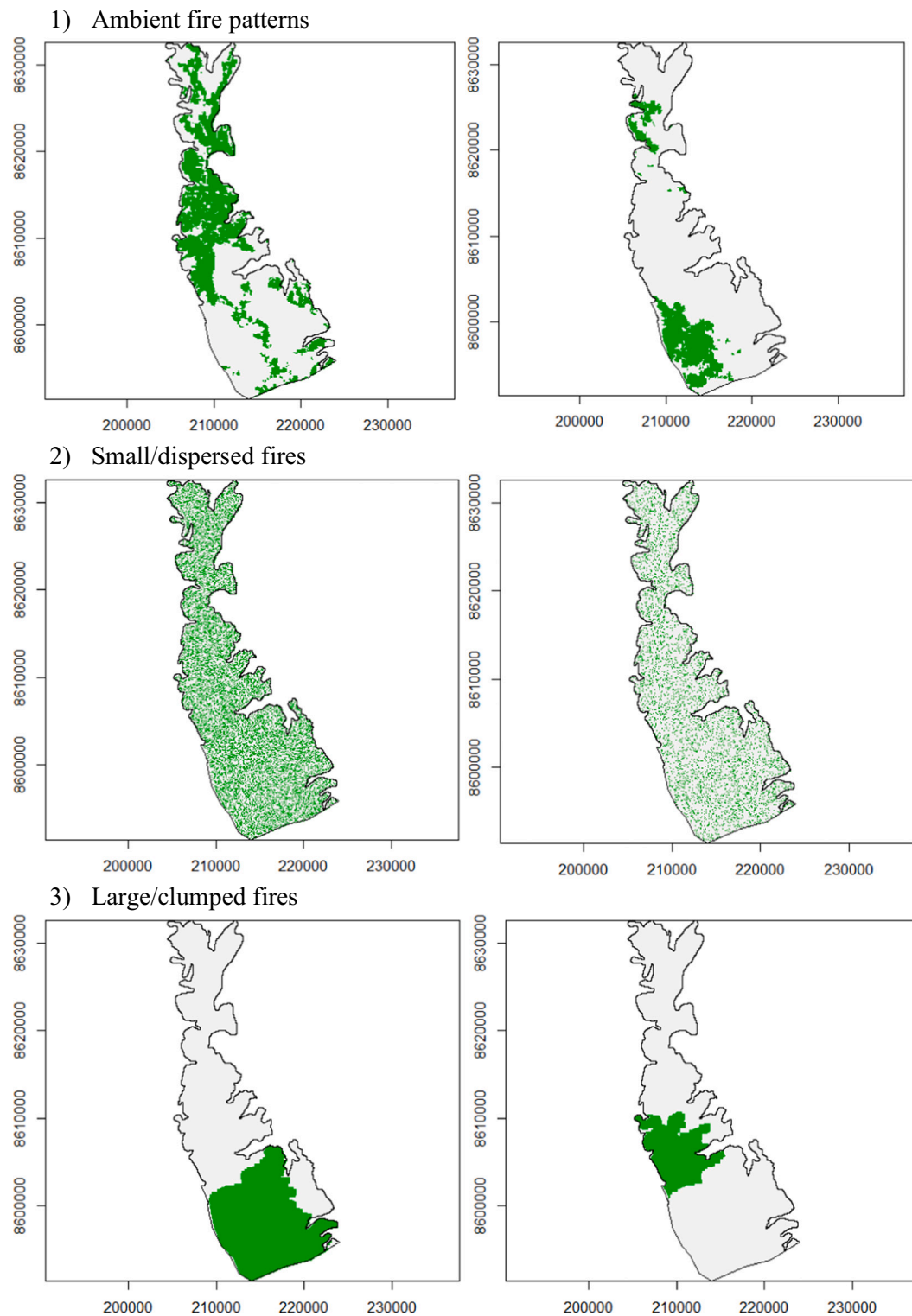
- 1) Ambient fire patterns: the true fire patterns that occurred across the Kapalga area (1995–2015).
- 2) Small, dispersed fires: small (1 ha) fires dispersed randomly across the Kapalga area.
- 3) Large, clumped fires: large, contiguous fires occurring randomly across the Kapalga area.

The ambient fire patterns (scenario 1) were mapped from Landsat satellite imagery and are an updated version of the dataset described by Russell-Smith et al. (1997). Scenarios 2 and 3 were created so that the extremes of fire spatial pattern could be isolated and contrasted. While representing a markedly different spatial pattern of fires, scenarios 2 and 3 were equal to the ambient fire patterns (scenario 1) in fire seasonality (i.e. the proportion burnt each year in the early and late dry season), total annual fire extent (i.e. number of cells burnt each year), and mean landscape fire frequency (i.e. number of times each cell was burnt, averaged across all cells) (Fig. 2). Our small/dispersed fire scenario was created by randomly selecting cells across the Kapalga landscape equal to the total annual fire extent of the ambient fire patterns. Our large/clumped fire scenario was created by randomly selecting a single ignition cell, with the fire then propagating across the landscape through a random selection of neighbouring cells, until the desired annual fire extent was obtained. Once these artificial 21-year fire scenarios were created they were consistent through each of the 100 replicates of each scenario. Varying the dispersion of fires across the landscape inevitably resulted in subtle changes to temporal aspects of the fire regime, including the variability (i.e. standard deviation) of landscape fire frequency, and mean landscape time since fire (recorded at the end of the simulation) (Table 2). The effect of this variation on mammal population size was investigated (see model comparison section).

#### 2.6. Varying dispersal ability

We investigated how the dispersal ability of native mammals influenced their response to fire. To do this we constrained the maximum dispersal ability of each species to three levels: low, moderate and high (Table 3). The moderate dispersal ability simulations represent our 'best guess' of dispersal ability for each species. We first estimated the 'straight-line' dispersal ability for each species based on published





**Fig. 2.** A visualisation of the spatial pattern of fires (green) occurring in a particular year (2014 shown) under the three fire scenarios. Early dry season fires are shown in the left panels, late dry season fires shown in the right panels. Total annual fire extent and seasonality held constant. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

literature, using closely related species where necessary. Then, given our models used a cellular automata dispersal function, with individual animals able to move through the landscape (i.e. not in a straight-line), we then estimated the appropriate maximum number of cells each animal could move using the *steps* R package. Our northern brown bandicoot estimate (2 km) was based on the estimated dispersal ability

of the southern brown bandicoot (Li et al., 2015). Our estimate of northern brushtail possum dispersal (1.5 km) was based on the relative short dispersal distance for this species and estimates of northern brushtail possum movement (Kerle, 1998; Johnson et al., 2001). Our estimate of dispersal for the grassland melomys (1 km) was based on movement data for the related fawn footed melomys (*M. cervinipes*)

**Table 2**

Variation in temporal aspects ( $\pm$ SD) of the fire regime under our three scenarios arising due to changes to fire dispersion with annual fire extent held constant.

Fire scenario	Landscape fire frequency	Time since fire
Ambient fire patterns	11.6 $\pm$ 3.1	1.0 $\pm$ 1.5
Small/dispersed fires	11.6 $\pm$ 2.1	0.9 $\pm$ 1.0
Large/clumped fires	11.6 $\pm$ 2.4	1.1 $\pm$ 1.3

**Table 3**

The maximum number of cells an individual animal from each species could move (per 2-month timestep) under the three levels of dispersal ability.

Species	Low dispersal ability	Moderate dispersal ability	High dispersal ability
Northern brown bandicoot	2	512	1024
Northern brushtail possum	2	288	576
Grassland melomys	2	128	256
Northern quoll	2	1152	2304

(Bentley, 2008). Our estimate of dispersal for the northern quoll (3 km) was based on dispersal estimates for the eastern quoll (*D. viverrinus*) (Hamer et al., 2022). From these ‘straight-line’ estimates, we determined that in each timestep northern brown bandicoot, common brushtail possum, grassland melomys and northern quoll could disperse up to a maximum of 512, 288, 128 and 1151 cells, respectively (Table 3).

In the low dispersal ability simulations, movement of animals was constrained to a maximum of two cells. In the high dispersal ability simulations, animals could move twice as far as under the moderate dispersal ability.

## 2.7. Model comparison

To test whether the spatial pattern of fire and dispersal distance influenced the predicted final population size, we extracted the predicted final population size (i.e. in timestep 126) from each of the 100 replicates from the nine scenarios for each species. Using these 900 observations of population size for each species, we conducted a two-factor analysis of variance (ANOVA) using the R package *AICmodavg*. For each species we tested whether variation in the predicted final population size was significantly influenced by fire scenario, dispersal ability, or an interaction between fire scenario and dispersal ability. To do this we fit five models: 1) a null model; 2) the single main effects of fire scenario; 3) the single main effects of dispersal ability; 4) the additive effect of fire scenario and dispersal ability; and 5) the interactive

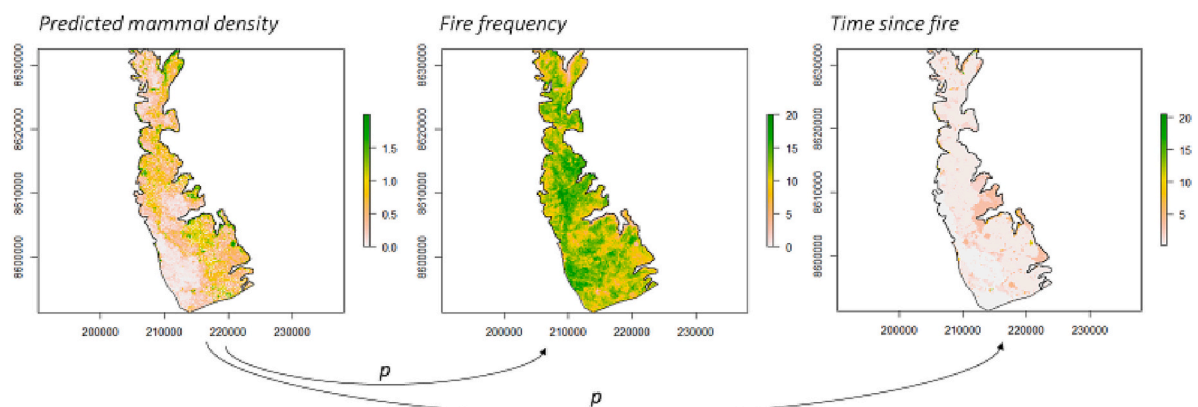
effect of fire scenario and dispersal ability. We then identified the most parsimonious model using Akaike’s information criterion adjusted for small sample size (AICc). Model assumptions were assessed and rectified where needed. Where the most parsimonious model indicated a significant parameter effect, we used a Tukey’s Honestly-Significant-Difference test to identify the levels of that parameter that were significantly different. Effect size was based on Eta-squared ( $\eta^2$ ), derived using the *effectsize* package in R, and interpreted as suggested by Cohen (1988). To aid the interpretation of our results, we investigated the spatial correlation between the final predicted mammal population (the predicted distribution and abundance in the final timestep of the simulation) and both landscape fire frequency and time since fire for each fire scenario (Fig. 3). This was done by deriving Spearman’s pairwise correlation coefficient from a sample of 25 % of the pixels of each raster.

## 2.8. Sensitivity analysis

The demographic parameters, and the effect of fire, recorded during the Kapalga fire experiment were derived from 15 to 20 km<sup>2</sup> compartments. An important assumption in our simulations is that post-fire mammal survival is consistent across our varying fire scenarios despite the stark variation in fire size. Given evidence that post-fire mammal survival may vary with fire size (Santos et al., 2022), we tested the influence of this assumption on our model predictions with a sensitivity analysis. To do this we varied the estimated effect of fire on small mammal survival ( $\pm$ 25 %) for our two artificial fire scenarios (i.e. small/dispersed and large/clumped fire). Dispersal ability was held constant across these simulations at each animal’s ‘moderate dispersal ability’ estimate. This resulted in an additional four simulations for each of the four species, and were each replicated 100 times. Relative sensitivity was calculated as the proportional change in the predicted final population size (i.e. the abundance in the final timestep of the simulation) compared to the baseline model with unaltered post-fire survival.

## 3. Results

The modelled population trajectories of each mammal species remained generally consistent regardless of fire size and dispersal ability (Figs. 4–7). While the population size of the northern brown bandicoot decreased by around 50 % over the 20-year simulation, the population sizes of the other three species decreased severely (>90 %). The northern quoll population declined precipitously, being completely extirpated by around the eighth year of the simulation. As a result, we could not investigate the correlates of the predicted final population size for this species. Fire scenario was the strongest predictor of the final population size for the northern brown bandicoot, northern brushtail



**Fig. 3.** We derived Spearman’s pairwise correlation coefficient ( $\rho$ ) between the rasters of predicted mammal density at the end of the simulation (left panel) with both fire frequency (middle panel) and time since fire (right panel).

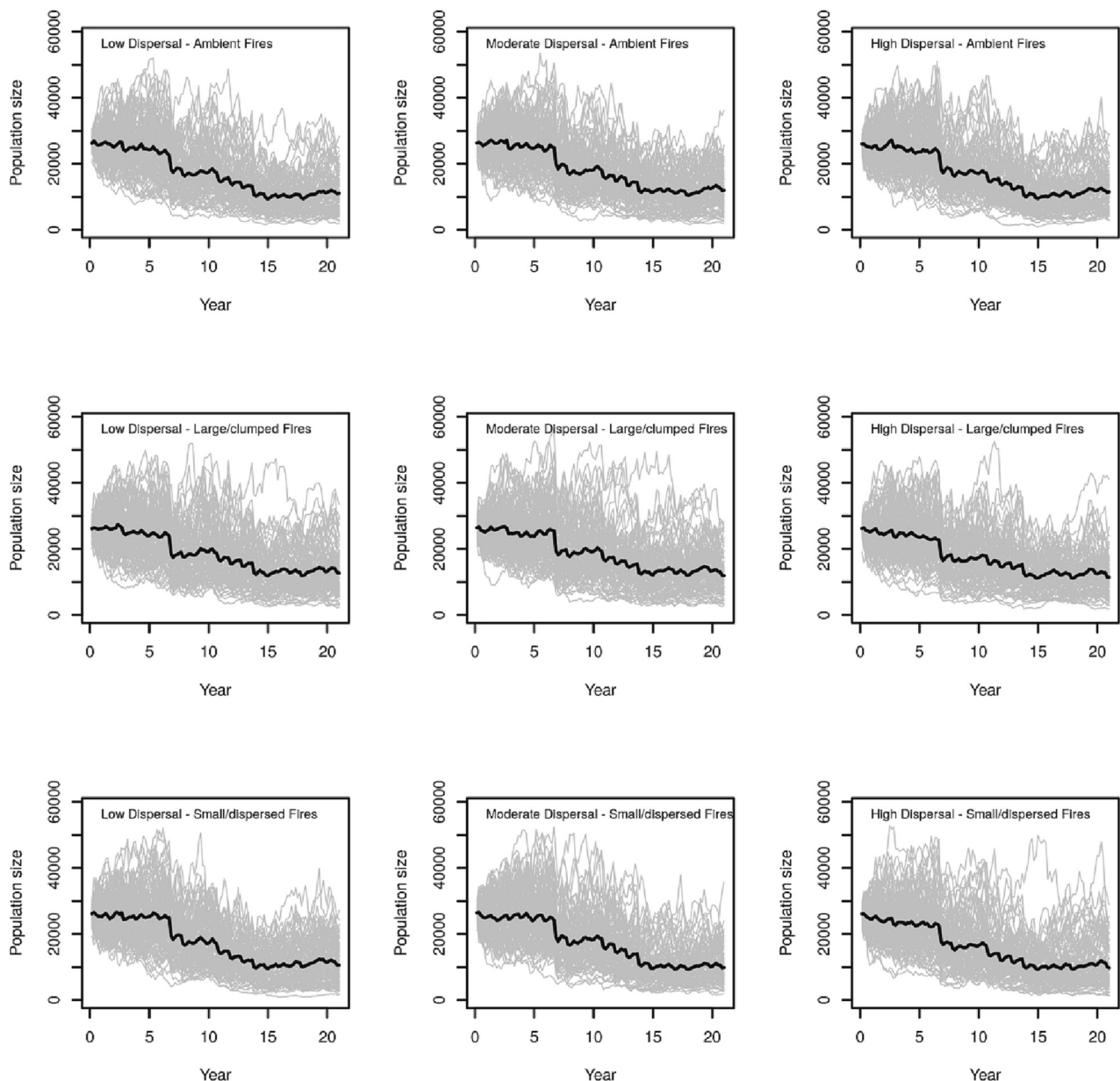


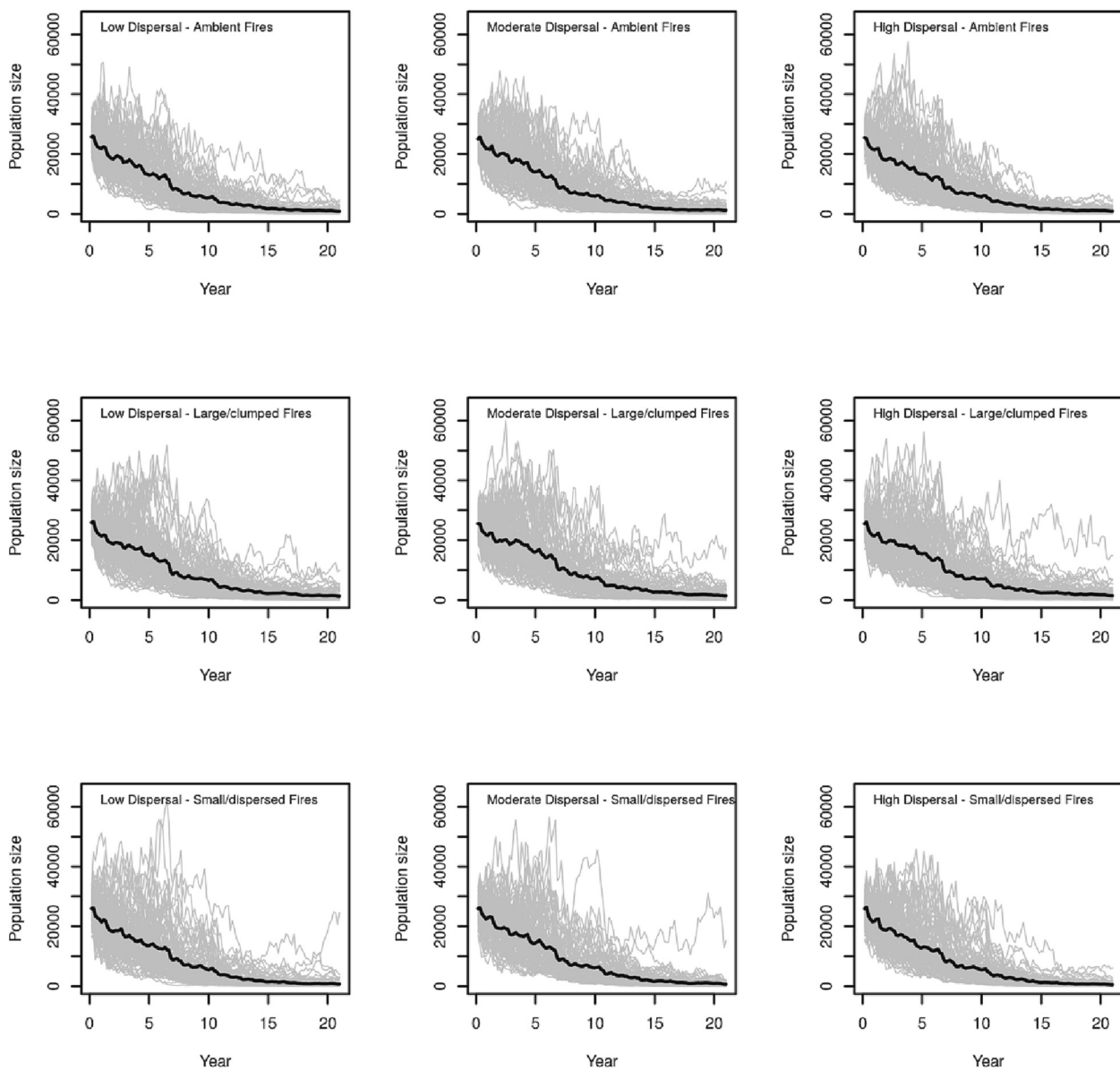
Fig. 4. Predicted population trajectories of the northern brown bandicoot at Kapalga from 1995 to 2015 under our three fire (rows) and dispersal (columns) scenarios. Grey lines represent each of the 100 replicate simulations, the solid black lines represent the mean population trajectory.

possum and grassland melomys (Table 4). However, the size of this effect varied, being small for the northern brown bandicoot ( $\eta^2 = 0.02$ ), but larger for northern brushtail possum and grassland melomys ( $\eta^2 = 0.15$  and  $\eta^2 = 0.24$ , respectively). We did not find that small/dispersed fires increased mammal populations, or slowed their rates of decline; in fact, we found the opposite. In contrast to our original hypothesis, the predicted final population sizes of the northern brown bandicoot, northern brushtail possum and grassland melomys were lowest under the small/dispersed fire scenario (Fig. 8). For the northern brown bandicoot and northern brushtail possum, there was no significant difference in the final population size under the ambient and large/clumped fire scenarios. For the grassland melomys, final population size was larger under the ambient fire scenario compared to the large/clumped fire scenario. The strength of the correlation between the predicted final distribution and density of northern brown bandicoot was similar for fire frequency and time since fire (Table 5). Densities of the northern brushtail possum and grassland melomys were more strongly correlated with landscape patterns of fire frequency than time since fire (Table 5).

Our sensitivity analysis demonstrated that varying the effect of fire on native mammal survival did not markedly change the overall population trajectory of each species (Supplementary Table A1), but did influence the predicted final population for common brushtail possum, grassland melomys and northern brown bandicoot. As the northern quoll was completely extirpated in all scenarios, we could not calculate the proportional change in final population size. Our grassland melomys models were most sensitive to variation in post-fire survival rates, with a 25 % increase in post-fire survival resulting in a three-fold increase in the final population size (Supplementary Table A1).

#### 4. Discussion

The complexity of fire–biodiversity relationships presents a substantial challenge to the development of effective fire policy and management for biodiversity conservation. In the absence of knowledge of the particular fire requirements of target species, fire managers often fall back on the heuristic that maximising pyrodiversity will benefit



**Fig. 5.** Predicted population trajectories of the northern brushtail possum at Kapalga from 1995 to 2015 under our three fire (rows) and dispersal (columns) scenarios. Grey lines represent each of the 100 replicate simulations, the solid black lines represent the mean population trajectory.

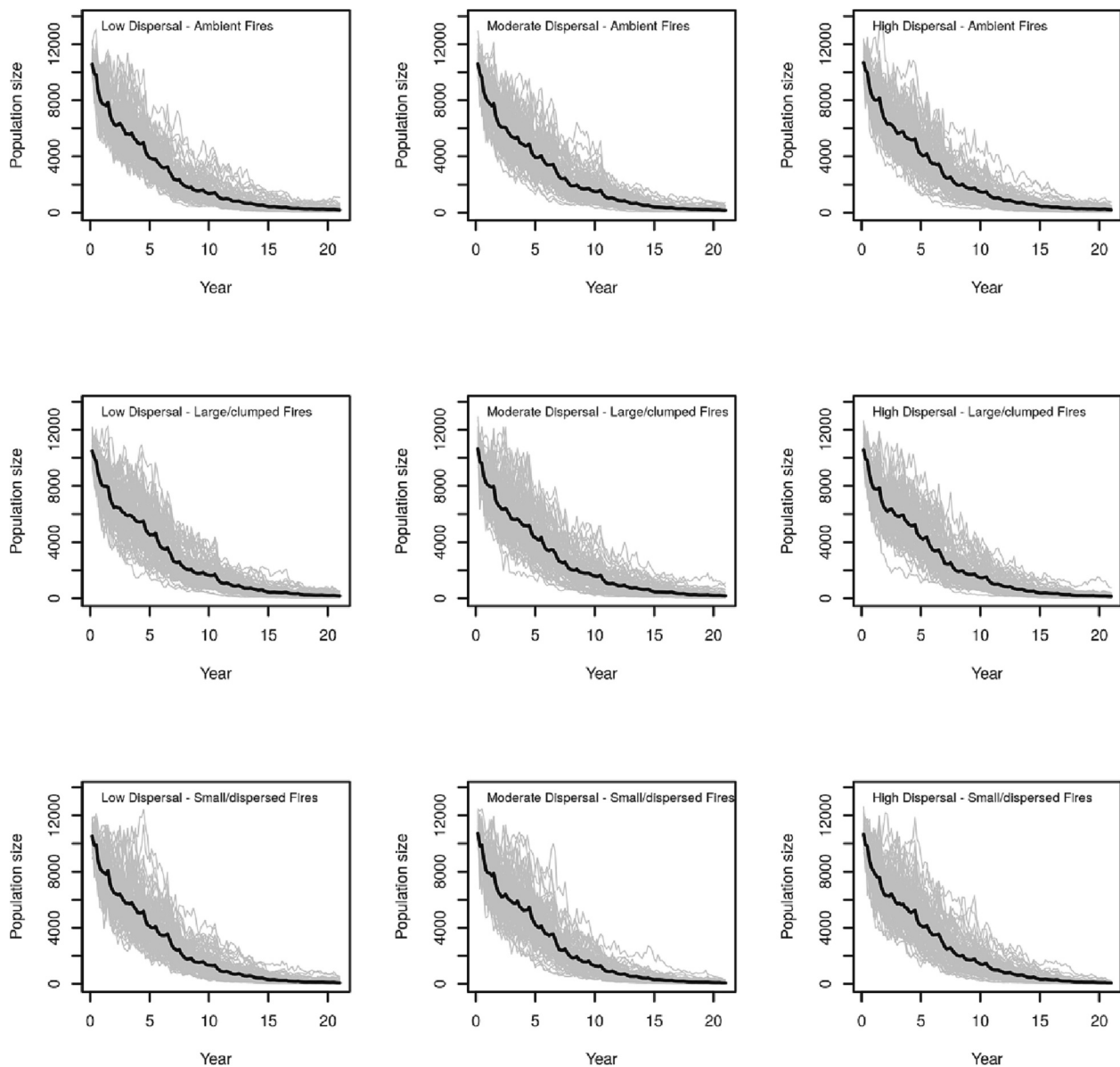
biodiversity. Our simulation study highlights how manipulating the size and spatial dispersion of fires can potentially influence temporal aspects of the fire regime, with important flow-on effects for biodiversity. This highlights the importance of considering the trade-offs that can exist between spatial (i.e. fire dispersion) and temporal (i.e. fire frequency) aspects of pyrodiversity, and the potential risks when applying fire management for biodiversity conservation without a firm understanding of the requirements of the target species.

#### 4.1. Model concordance with field studies

The population trajectories for each of the four mammal species predicted by our simulation models are analogous to the massive decrease in native mammal trap-success observed at Kapalga since the 1980s (Fig. 9). Despite modelling the effects of fire at a much finer spatial resolution, our results align with previous research showing that the spatial patterning of fires, and dispersal ability, can have minimal influence on the overall trajectory of native mammal populations across northern Australian savannas (Griffiths et al., 2015). Griffiths et al.

(2015) suggested that temporal aspects of the fire regime, such as fire frequency, have a stronger influence on the persistence of declining native mammal populations (but see Russell-Smith et al. (2015) for a critique of their conclusions). The hypothesis that fire frequency and/or total area burnt each year, not the spatial pattern of burning, are predominant drivers of native mammal population trajectory is problematic for fire managers, because these factors remain largely unchanged under the prevailing fire management paradigm of early dry season burning and associated current prescribed burning programs (Russell-Smith et al., 2013; Murphy et al., 2015; Evans and Russell-Smith, 2019). However, this quandary highlights and reaffirms the need to ensure that the aspects of the fire regime that are effectively manipulated by fire management programs (e.g. fire size and dispersion) are well-understood, in order to minimise any potential perverse outcomes for biodiversity (Corey et al., 2019). Unfortunately, there remain numerous knowledge gaps regarding how different fire regime variables influence native mammal populations across northern Australia, particularly the importance of comparatively long-unburned habitat for wildlife, and the optimal size and spatial arrangement of these refugia. These knowledge





**Fig. 6.** Predicted population trajectories of the grassland melomys at Kapalga from 1995 to 2015 under our three fire (rows) and dispersal (columns) scenarios. Grey lines represent each of the 100 replicate simulations, the solid black lines represent the mean population trajectory.

gaps must be addressed in order to achieve ecologically sustainable fire management (Radford et al., 2021).

Contrary to what we hypothesised, in our modelling the northern brown bandicoot, northern brushtail possum and grassland melomys declined most severely when very small fires, that burned that same area as the ambient regime, were dispersed widely across the landscape. While this effect was small for the northern brown bandicoot, it was large for the northern brushtail possum and grassland melomys, with species contracting to areas of low fire frequency. Such areas have been shown empirically to support a higher abundance and diversity of native mammals in northern Australian savannas, likely reflecting increased resources (e.g. tree hollows and logs, mature fruiting and seed-producing trees) and reduced exposure to predation (Leahy et al., 2016; Davies et al., 2017; Ondei et al., 2020; Stobo-Wilson et al., 2020). While all three of our fire scenarios had the same annual burnt area, our ‘small/dispersed’ fire scenario involved exposing a greater portion of the landscape to fire (rather than fire repeatedly occurring in the same areas, year after year), this reduced the variability (i.e. standard deviation) of landscape fire frequency. This is a key finding of this study, as it

suggests that current modes of fire management, which focus on maximising the dispersion of fires across the landscape could reduce the availability of fire refugia (such as less-frequently burnt areas) with the potential to negatively impact biodiversity. However, we note that this suggestion may be contingent on the random placement of fires in our simulations (McCarthy and Burgman, 1995). It is unknown, for example, how more dispersed fires, and hence more fire edges, may affect predator-prey interactions (Geary et al., 2020). Our results align with research showing that 1) spatially-focused disturbance (i.e. sacrificial areas) can lead to enhanced environmental outcomes compared to a random disturbance regime (Andersen et al., 2005; Zentelis et al., 2017); and 2) alteration to the variability in landscape fire frequency can have a marked effect on extinction risk, particularly when taxa are sensitive to temporal aspects of the fire regime (Bradstock et al., 1996).

Our fire scenarios were purposely designed to represent extreme hypothetical examples of fire size and dispersion, beyond what could be realistically achieved. Although the ability to examine such scenarios represents one of the main advantages of simulation modelling, consideration of how our fire scenarios differ from reality is an

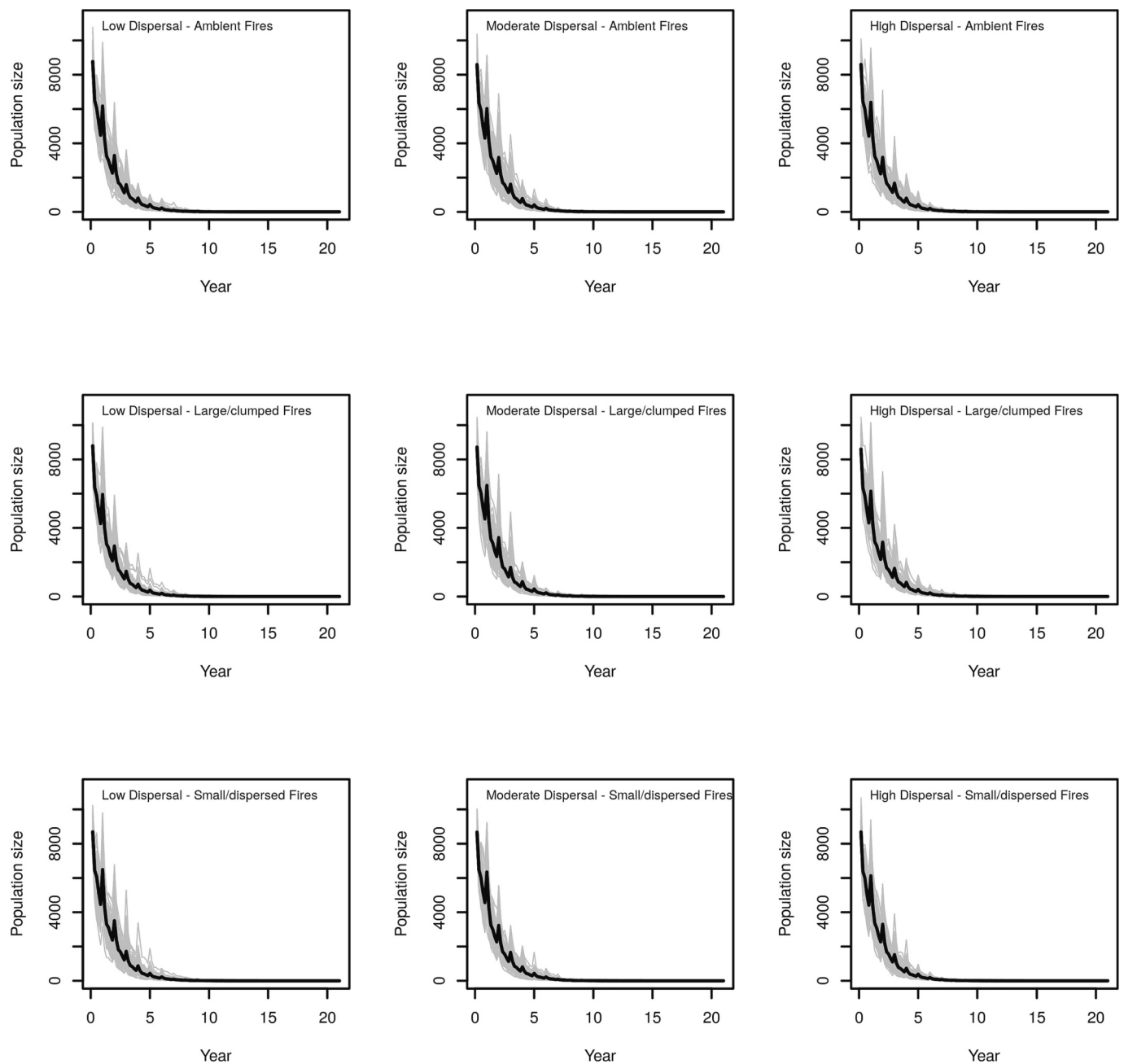


Fig. 7. Predicted population trajectories of the northern quoll at Kapalga from 1995 to 2015 under our three fire (rows) and dispersal (columns) scenarios. Grey lines represent each of the 100 replicate simulations, the solid black lines represent the mean population trajectory.

important step in guiding a useful discussion that bridges the divide between our simulation results and ‘real-world’ application of prescribed burning. Dispersing fires across the northern Australian savanna landscapes has the effect of breaking up continuous grassy fuel loads that can otherwise propagate very large, high-intensity wildfires late in the dry season. Therefore, dispersed fire can benefit a range of species, including some mammals, that are negatively impacted by high fire frequencies and/or intensities (Radford et al., 2020). However, our results suggest that maximising the dispersion of fires at the expense of the availability of fire refugia can also be detrimental to native mammal populations (Krawchuk et al., 2020). While moderate levels of fire dispersion can benefit biodiversity, there may be a point at which the negative impacts of dispersing fires too widely across the landscape outweigh these benefits. For example, the northern brown bandicoot, grassland melomys and northern brushtail possum are thought to be

disadvantaged by the heightened exposure to predators and reduced food availability following fire (Kerle and Burgman, 1984). The greater vulnerability to highly dispersed small fires exhibited by the grassland melomys and northern brushtail possum (compared to the northern brown bandicoot) could reflect their lower intrinsic population growth rate (Griffiths et al., 2015), and hence slower recovery time. There remains a critical need to better understand the mechanisms driving native mammal demographic rates in northern Australian savannas, and how they interact with fire mosaics and associated spatial variation in habitat quality.

While our fire scenarios involved a random placement of fires across the entire landscape, prescribed fires could be more strategically placed to avoid unburnt areas (Andersen et al., 2005). This approach could benefit native mammal populations by reducing the risk of extensive wildfires while maintaining areas of relatively long unburnt vegetation,

**Table 4**

Summary of models of the final population size of the northern brown bandicoot, northern brushtail possum and grassland melomys at Kapalga.  $k$  = number of parameters,  $\Delta\text{AICc}$  is the difference between each model's AICc and that of the best model,  $w_i$  = Akaike weight.

Species	Model	$k$	$\Delta\text{AICc}$	$w_i$
Northern brown bandicoot	Fire	4	0.0	0.76
	Fire + Dispersal	6	2.5	0.22
	Fire $\times$ Dispersal	10	7.8	0.02
	Null	2	18.4	0.00
	Dispersal	4	20.9	0.00
Northern brushtail possum	Fire	4	0.0	0.79
	Fire + Dispersal	6	2.8	0.19
	Fire $\times$ Dispersal	10	7.6	0.02
	Null	2	141	0.00
	Dispersal	4	143.5	0.00
Grassland melomys	Fire	4	0.0	0.58
	Fire $\times$ Dispersal	10	1.4	0.30
	Fire + Dispersal	6	3.4	0.12
	Null	2	241.8	0.00
	Dispersal	4	245.1	0.00

thereby increasing the variability in fire frequency across the landscape. Reducing the variability in landscape fire frequency has been predicted to benefit fire-sensitive plant species such as obligate seeders (Bradstock et al., 1996), and could offer similar benefits to native fauna. However, we suggest that managers should continue to strive to reduce landscape fire extent and frequency where possible, and that fire management aiming to maintain patches of long-unburnt vegetation should carefully consider the mechanisms and spatial scale of post-fire mammal recovery (Shaw et al., 2021), including the distance to other refuges (i.e. creek lines) (Kerle and Burgman, 1984). It is also important to note that fire management aiming to increase unburned habitat alone may not guarantee the long-term persistence of native mammals in northern Australian savannas (Firth et al., 2010), and that any positive response of native mammal populations to prescribed burning in northern Australian savannas can be contingent on the concurrent management of other factors, such as predation by feral cats (*Felis catus*) or habitat modification by feral herbivores (e.g. cattle, *Bos taurus*, and buffalo,

*Bubalus bubalis*), both of which are likely to interact with fire (Legge et al., 2019). Unfortunately, our simulations were not sophisticated enough to explicitly account for such processes, which may therefore explain the overall muted response of native mammal populations to fire.

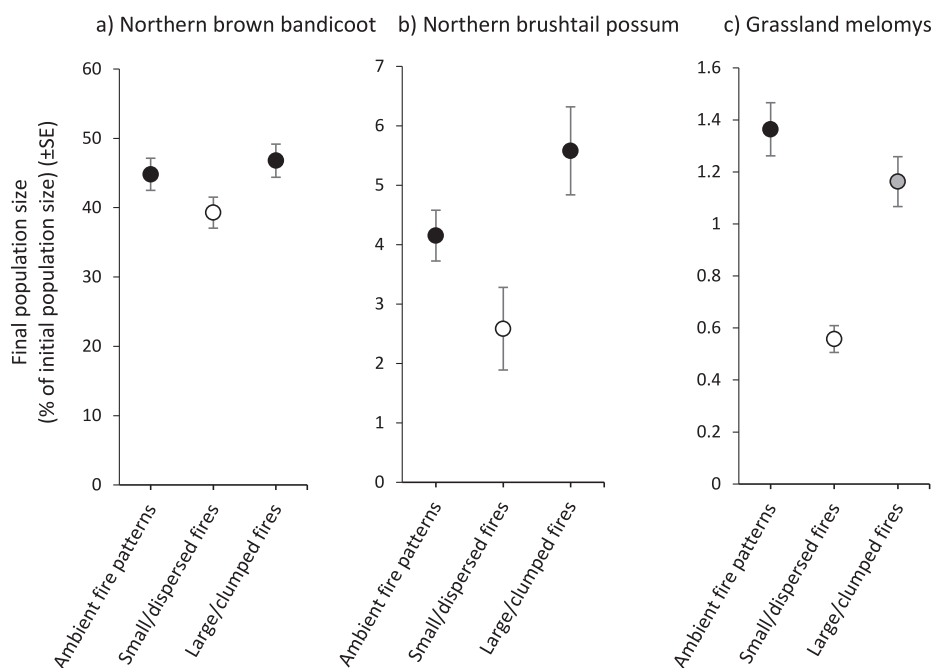
#### 4.2. Model caveats

As with all models, the usefulness and applicability of our simulations are contingent on the input data and model parameterisation. It is therefore imperative that we critically assess our ability to effectively investigate fire–biodiversity relationships given the data available. Despite coupling demographic parameters derived from the largest dataset describing the effects of fire on northern Australian mammal population dynamics (Griffiths et al., 2015) with newly developed modelling software (Visintin et al., 2020), there remains some important limitations to our study. First, the estimates of demographic parameters, and the effect of fire, recorded during the Kapalga fire experiment (on which our simulations are based) were derived via the application of different fire treatments to 15–20 km<sup>2</sup> compartments. Our simulations have the inherent assumption that these demographic effects are unaffected by fire size, such as the ‘continuous response’ between

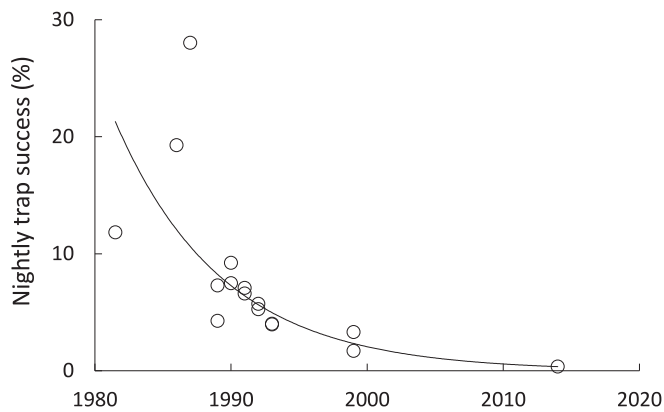
**Table 5**

Spearman's pairwise correlation coefficient ( $\rho$ ) between the final predicted population distribution and abundance of each mammal species and landscape fire frequency and time since fire under each fire scenario.

	Fire scenario	Fire frequency	Time since fire
Northern brown bandicoot	Ambient	−0.36	0.38
	Small/dispersed	−0.30	0.27
	Large/clumped	−0.56	0.59
Northern brushtail possum	Ambient	−0.54	0.17
	Small/dispersed	−0.41	0.08
	Large/clumped	−0.44	0.20
Grassland melomys	Ambient	−0.16	0.04
	Small/dispersed	−0.17	0.03
	Large/clumped	−0.17	0.06



**Fig. 8.** The variation in the predicted final population size (i.e. the average population size from all simulation replicates in the final timestep), expressed as a percentage of the initial population size, under each of the three fire scenarios for: a) the northern brown bandicoot; b) northern brushtail possum; and c) grassland melomys. Error bars indicate standard error. Statistically significant differences in final population size for each species indicated by different shading.



**Fig. 9.** Native mammal trap-success recorded across the Kapalga area of Kakadu National Park (Friend and Taylor, 1985; Braithwaite and Muller, 1997; Woinarski et al., 2010; Stokeld et al., 2016). The line shows the predictions of an ordinary least-squares regression, defined as:  $\ln \text{trap-success} = -0.1264 \text{ year} + 253.6$ , with  $R^2$  of 0.85.

disturbance size and disturbance impact described by Romme et al. (1998). However, it is also plausible that a threshold response to fire size exists (Romme et al., 1998). Similarly, the benefits afforded to native mammals by unburnt patches may also be influenced by spatial thresholds (Radford et al., 2020). Our models (particularly those of the grassland melomys) were sensitive to variation in post-fire survival which can be influenced by fire size (Santos et al., 2022). A better understanding of how native mammal survival is influenced by fire size in northern Australian savannas could reduce model uncertainty and should be the focus of future research. As highlighted by Davies et al. (2021), the effect of fire as measured during the Kapalga fire experiment encapsulates multiple, interacting factors such as predation (including by feral cats) and habitat modification by feral herbivores. As a result, we could not explicitly model the effect of these other factors, and instead assumed that they remained constant throughout the 21-year simulation. We also note that our dispersal function assumed the same dispersal ability for both males and female animals. While males often disperse further than females (Lawson Handley and Perrin, 2007), given the little influence of dispersal ability in general, the overall influence of this simplification on our study is thought to be minimal. Following Griffiths et al. (2015), we modelled the Kapalga area as a closed system. We acknowledge that animal movement (immigration/emigration) across the southern boundary (corresponding to a major highway) may have occurred but contend that this would have had limited impact on overall population trajectories. Finally, as our simulations were based on the 5-year Kapalga fire experiment, we were unable to incorporate longer-term changes in habitat quality on native mammal demographic rates, including the potential implications of long-term fire exclusion (Woinarski et al., 2004) and longer-term changes in resource availability such as tree hollows (Penton et al., 2021). While the caveats, and the inherent artificial nature of our simulations, severely limit the direct application of our simulation results to wildlife management, they offer useful insights into how to design optimal fire management strategies for biodiversity conservation in fire-prone landscapes.

#### 4.3. Future directions

Since the Kapalga fire experiment in the 1990s, significant advances have been made in our functional understanding of the decline of mammal species across northern Australia (Stobo-Wilson et al., 2020), as well as technological advances in ecological monitoring and modelling (i.e. fine-scale satellite imagery, camera-traps, DNA analyses, LiDAR, drones, animal tracking/telemetry, simulation modelling). Unfortunately, despite our increased capacity to design and implement large-scale experiments with which to develop our mechanistic

understanding of native mammal populations, such experiments have not occurred in northern Australia since the 1990s. This likely reflects the high cost of large-scale experiments, as well as the ever-increasing difficulty of obtaining useful demographic data due to the ongoing decline of mammal populations across virtually all of northern Australia. However, it is important to note that, given sufficient funding, such large-scale experiments (including lower-cost 'natural experiments') are still currently possible and desperately needed to develop our mechanistic understanding of mammal demography (Andersen, 2021). They can help us to: 1) disentangle the factors involved in the decline of native mammals across northern Australia; 2) develop robust simulation models on which to base on-ground management decisions; 3) understand the on-ground ecological implications of remote-sensed fire metrics; and 4) progress our understanding of the pyrodiversity hypothesis. We suggest a multifaceted natural experiment designed to better establish the relationship between native mammal population dynamics and spatial fire patterns, especially those achieved under savanna burning programs. Such a natural experiment would need to be conducted across areas that continue to support relatively healthy populations of native mammals, such as the North Kimberley, Cobourg Peninsula, the Tiwi Islands and Groote Eylandt (Davies et al., 2018; Heiniger et al., 2020; Ondei et al., 2020). Importantly, the inherent variation between these areas would allow us to establish the relationship between native mammal population dynamics and spatial fire patterns across a broad range of environmental settings and tease apart the relative importance of often confounded contributing factors. We envisage the use of a combination of optimised monitoring approaches (Geyle et al., 2018), including live-trapping and animal tracking/telemetry, camera-trapping, LiDAR and landscape genetics. Such experiments must be underpinned by accurate and high-resolution fire scar mapping. Next generation satellites and unoccupied aerial vehicles (UAV or drones) can provide metre-scale fire-scar mapping, and historical reconstruction of pyrodiversity can be achieved through blending older satellite records with contrasts of temporal and spatial scales (e.g. MODIS vs. Landsat) (Williamson et al., 2022).

#### 5. Conclusion

The development of fire management for biodiversity conservation remains a globally important issue and is especially important across fire-prone ecosystems suffering ongoing biodiversity loss, such as northern Australian savannas. As species decline, our ability to understand fire–biodiversity relationships diminishes, such that ecologically sustainable fire management becomes increasingly elusive. Our work again highlights the potential risks of fire management based on vague notions of maximising pyrodiversity without a firm understanding of the requirements of the target species. However, given the potential limitations of the data that often underpin modelling studies investigating fire–biodiversity relationships, we also emphasise caution surrounding the strength of conclusions drawn from modelling studies for species where demographic parameters are highly uncertain. An improved mechanistic understanding of how different fire regime attributes influence biodiversity, achieved by formal and 'natural' experiments, would improve the reliability of studies simulating fire–biodiversity relationships and mark an important and necessary step towards ecologically sustainable fire management across northern Australia.

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## CRedit authorship contribution statement

**Hugh F. Davies:** Conceptualization, Methodology, Formal analysis, Writing – original draft. **Casey Visintin:** Methodology, Writing – review & editing, Formal analysis, Resources, Software. **Brett P. Murphy:** Conceptualization, Methodology, Writing – review & editing, Supervision. **Euan G. Ritchie:** Conceptualization, Methodology, Writing – review & editing, Supervision. **Sam C. Banks:** Methodology, Writing – review & editing, Funding acquisition, Supervision. **Ian D. Davies:** Methodology, Writing – review & editing, Supervision. **David M.J.S. Bowman:** Conceptualization, Methodology, Writing – review & editing, Supervision, Funding acquisition.

## Declaration of competing interest

Authors declare no conflict interests.

## Data availability

Data will be made available on request.

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