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Title:
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Date:
2021-03-01

Citation:
Davies, H. F., Visintin, C., Gillespie, G. R. & Murphy, B. P. (2021). Investigating the effects of fire management on savanna biodiversity with grid-based spatially explicit population simulations. Journal of Applied Ecology, 58 (3), pp.677-686. https://doi.org/10.1111/1365-2664.13801.

Persistent Link:
https://hdl.handle.net/11343/273910

Received: 3 July 2020 | Accepted: 12 November 2020

DOI: 10.1111/1365-2664.13801

RESEARCH ARTICLE

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

Investigating the effects of fire management on savanna biodiversity with grid-based spatially explicit population simulations

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Funding information
National Environmental Science Program

Handling Editor: Claire Wainwright

Abstract

1. The development of effective fire management for biodiversity conservation is a global challenge. The highly dynamic nature of fire, 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.
2. We aimed to develop a flexible modelling approach with which to investigate how the spatiotemporal application of fire (i.e. management scenarios) influences savanna biodiversity. We used existing data from a landscape-scale fire experiment to develop population simulations for the common brushtail possum *Trichosurus vulpecula*, grassland melomys *Melomys burtoni* and northern brown bandicoot *Isoodon macrourus* across the Kapalga area of Kakadu National Park in northern Australia. We simulated how populations were expected to change between 1995 and 2015 in response to the fire patterns observed at Kapalga over this period, and under a hypothetical management scenario of extensive prescribed burning.
3. Our models predicted a substantial decline in all three species in response to the observed fire regime at Kapalga, suggesting that the fire patterns observed at Kapalga, with the associated mechanisms and interactions with other ecological processes, were not conducive with the persistence of native mammal populations.
4. Our prescribed burning scenario had little effect on the predicted population trajectory of the common brushtail possum and grassland melomys, but markedly improved the population trajectory of the northern brown bandicoot. These inconsistencies highlight the need for a nuanced approach to fire management across northern Australian savannas, that is tailored to local conditions and management objectives.
5. *Synthesis and applications*. The modelling approach outlined here provides a basis for identifying fire patterns that are beneficial for conserving biodiversity, thereby increasing our capacity to establish clear targets for prescribed fire management. Importantly, this approach is flexible and can be easily adapted to other taxa and fire-prone ecosystems.

KEYWORDS
Australia, decline, fire, mammals, management, population modelling, pyrodiversity, savanna

1 | INTRODUCTION

Fire drives the distribution and ecological function of many of Earth's biomes (Moritz et al., 2014; Parr & Andersen, 2006). As such, the development of effective fire management for biodiversity conservation is a globally important issue. However, the effects of fire on biodiversity are controlled by a range of factors that operate and interact across a range of spatiotemporal scales, such as climate, weather, topography, vegetation, herbivory, predation and fire history (Keyser & Westerling, 2017; Smit et al., 2013). Therefore, the effects of fire on biodiversity are often complex, spatially and temporally variable and difficult to disentangle. Not surprisingly, this complexity poses significant challenges when aiming to identify the optimal approach to fire management for biodiversity conservation in fire-prone landscapes.

The broad hypothesis that 'pyrodiversity begets biodiversity', originally proposed by Martin and Sapsis (1992), assumes that a spatially and temporally heterogeneous fire regime will create a greater variety of ecological niches and therefore support a greater number of species. Despite limited supporting evidence, this hypothesis has been widely adopted into fire management policy and practice across multiple continents (Farnsworth et al., 2014; Parr & Andersen, 2006). Unfortunately, this has often resulted in fire management that is underpinned by vague notions of maximising pyrodiversity, without clear on-ground targets, or the capacity for meaningful evaluation (Parr & Andersen, 2006; Taylor et al., 2012). The highly dynamic nature of fire, 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 for biodiversity conservation (Parr & Andersen, 2006).

Several software options are available for spatiotemporally explicit population modelling, each with their associated advantages and disadvantages (Lurgi et al., 2015). Recently, a feature-rich R package, *'steps'*, has been developed to run spatiotemporally explicit population simulations (Visintin et al., 2020). Importantly, as *steps* is fully customisable and grid-based, it can more realistically model critical fire-related processes, likely resulting in more robust predictions of the effects of fire than other patch-based software e.g. *RAMAS Metapop* (Akçakaya, 2005). Here, we use *steps* to investigate a pressing conservation issue: the marked and ongoing decline of native mammal populations across northern Australian savannas.

Australia has the highest rate of mammal extinction on Earth, having lost approximately 10% of its native terrestrial mammal species since European colonisation in 1788 (Woinarski et al., 2015). Alarmingly, as native mammal populations across the savanna landscapes of northern Australia are suffering widespread and ongoing decline (Woinarski et al., 2011), more extinctions are likely. The causes of the northern Australian mammal declines are complex, however there is compelling evidence that changed fire regimes have played a central role. The breakdown of traditional Aboriginal burning practices across northern Australia's savannas throughout the 20th Century is understood to have increased the frequency of large-scale, high-intensity fires (Russell-Smith et al., 2003; Yibarbuk et al., 2001). This shift in the fire regime, coupled with predation by feral predators and grazing by large introduced herbivores, has played a key role in the widespread decline of biodiversity (Woinarski et al., 2015; Ziembicki et al., 2015; Stobo-Wilson et al., 2020). The application of low intensity, prescribed burning in the early dry season (EDS) under relatively mild fire weather conditions, is the most widely applied management action across the savannas of northern Australia, and plays a major role in the savanna burning programmes that now cover more 380,000 km^2 (>20%) of northern Australia's savanna landscapes (Corey et al., 2019). However, while savanna fire management programs are delivering important economic and social benefits (Russell-Smith et al., 2013), co-benefits to biodiversity from such EDS prescribed burning have largely been hypothesised, rather than clearly demonstrated (Corey et al., 2019). Due to the potential for perverse ecological outcomes across a landscape currently experiencing a significant loss of biodiversity, it is critical that we develop ways to better understand the ecological consequences of fire management.

As a step towards a better understanding of the ecological consequences of fire management, we aimed to develop a flexible modelling approach with which to investigate how the spatiotemporal application of fire (i.e. management scenarios) impacts savanna biodiversity. We used existing data from the landscape-scale Kapalga fire experiment (Andersen et al., 1998) to develop spatiotemporally explicit population simulations for three mammal species across the Kapalga area of Kakadu National Park in northern Australia. We simulated how populations were expected to change between 1995 and 2015 in response to the fire patterns observed at Kapalga over this period, and under a hypothetical management scenario of extensive prescribed burning.

2 | MATERIALS AND METHODS

2.1 | Study site and the Kapalga fire experiment

Our study makes use of data collected at Kapalga, an area of ~325 km^2 within Kakadu National Park in northern Australia (Figure 1). The Kapalga area has a flat topography, bounded to the north, east and west by a seasonally inundated floodplain, and to the south by the Arnhem Highway. The vegetation comprises lowland open savanna forest dominated by *Eucalyptus miniata* and *E. tetrodonta* with a predominantly grassy understorey. The area has a tropical monsoonal climate with a humid wet season (November–April) in which over 90% of mean annual rainfall (1,381 mm) occurs. Fire frequency is extremely high across the lowland mesic savannas of northern Australia, with more than 50% burning annually (Russell-Smith et al., 2017). Between 1995 and 2015, an average of 55% ±19% (*SE*) of the Kapalga area burnt each year (Figure 1).

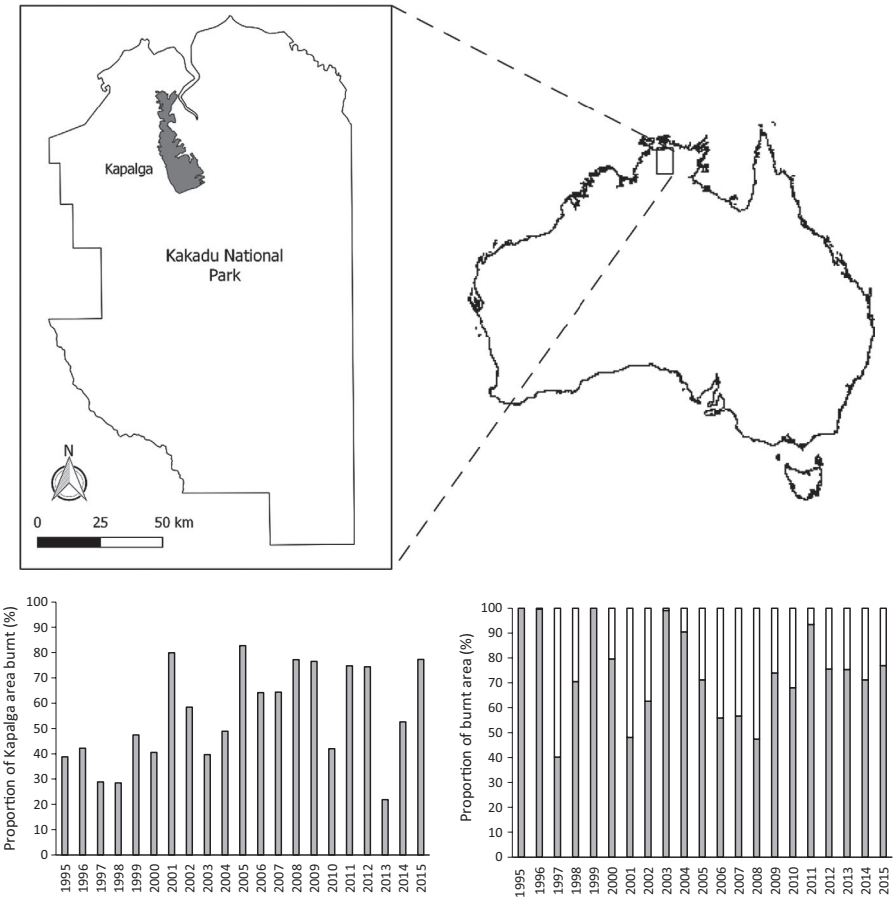

FIGURE 1 The location of the Kapalga area (grey) within Kakadu National Park. The proportion of the Kapalga area that was burnt each year between 1995 and 2015 is shown in the bottom left panel. The bottom right panel shows the proportion burnt in the early dry season (grey) and late dry season (white)

The Kapalga fire experiment (Andersen et al., 1998) involved the application of four different fire treatments to 22 compartments (15–20 km^2) 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 fire management in the region; 'late' compartments were burnt late in the dry season (September), representative of the unmanaged high-intensity wildfires that occur at this time of year; 'progressive' compartments were burnt progressively throughout the dry season, thought to represent 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 5-year Kapalga fire experiment (1990–1994, inclusive); see Braithwaite and Griffiths (1996) for details.

2.2 | Study species

We developed models to simulate the population trajectory of three native mammal species: the common brushtail possum *Trichosurus vulpecula*, grassland melomys *Melomys burtoni* and northern brown bandicoot *Isoodon macrourus*. These species vary significantly in body size, fecundity, parental care, arboreality and diet.

The north-western Australian subspecies of the common brushtail possum (*T. v. arnhemensis*) that occurs at Kapalga, is a medium-sized (1,300 g), predominantly arboreal marsupial, that dens in tree hollows and feeds mostly on the leaves of trees, shrubs and herbaceous plants, as well as flowers and fruits (Menkhorst & Knight, 2004). It breeds year-round, giving birth to a single offspring 2–3 weeks after mating. Parental care is high, with young remaining in the pouch for 4–5 months, and then carried on the mother's back until independent. On average, adult females produce 1.7 young per year (Kerle, 1998). The common brushtail possum has declined or disappeared across much of its historic range (Stobo-Wilson et al., 2019). Between the mid-1980s and mid-2010s, nightly trap success for the common brushtail possum decreased by 96% at Kapalga (Stokeld et al., 2018).

The grassland melomys is a small (62 g) semi-arboreal rodent that is primarily herbivorous, feeding on leaves, seeds, fruits and flowers. It can breed year-round (Smith, 1985), producing 1–5 young per litter (*mean* = 3). Between 1999 and 2015, nightly trap success for the grassland melomys decreased by 91% at Kapalga (Danielle Stokeld, unpubl. data).

The northern brown bandicoot (1,100 g) is a ground-dwelling, omnivorous marsupial that digs for arthropods, tubers, fruits and seeds on which to feed (Menkhorst & Knight, 2004). They produce 1–7 young per litter (mean = 4), and can have up to five litters per year (Menkhorst & Knight, 2004). Despite their high fecundity, the northern brown bandicoot has suffered

substantial decline across the savannas of northern Australia (Davies, McCarthy, Firth, et al., 2018; Woinarski et al., 2001, 2010). Between the mid-1980s and mid-2010s, nightly trap success for the northern brown bandicoot decreased by 95% at Kapalga (Stokeld et al., 2018).

2.3 | Model inputs

2.3.1 | Demographic parameters

To parameterise our population models, we used published estimates of demographic parameters (Griffiths et al., 2015; Table 1). These parameters were derived from a large (96,160 trap-nights) capture–mark–recapture dataset collected at 2-monthly intervals throughout the 5-year Kapalga fire experiment (1990–1994). Our models included two life stages (juvenile and adult), i.e. a 2 × 2 Lefkovitch transition matrix.

2.3.2 | Fire effects on demographic parameters

Griffiths et al. (2015) quantified fire impact parameters by modelling the change in native mammal demographic rates resulting from both 'early' and 'late' fires. We used these fire impact parameters as stage-specific multipliers of native mammal demographic parameters in our population models (Table 2). However, as our analyses was grid-based, as opposed to the patch-based software RAMAS *Metapop*, used by Griffiths et al. (2015), we were able to model the demographic effects of the fine-scale fire patterns that occurred at Kapalga between 1995 and 2015. To do this, we collated the fire history of the Kapalga area that had previously been mapped by Kakadu National Park using Landsat satellite imagery, at a spatial resolution of 100 m (Russell-Smith et al., 1997). Fires that occurred each year were categorised as either 'early' (fires before August 1st) or 'late' (fires on or after August 1st). These fire patterns were incorporated in raster format with cell values indicating whether a cell was burnt (1) or unburnt (0). During the Kapalga fire experiment 'early' fires were lit during May and June, while 'late' fires were lit in September each year (Andersen et al., 1998). As such, when simulating the demographic effects of the observed Kapalga fire patterns, 'early' fires occurred in the 3rd timestep of each year (corresponding to May–June), while 'late' fires occurred in the 5th timestep of each year (corresponding to September–October; Figure 2a).

We wrote a custom function (R code available as per 'Data Availability Statement') so that each of the four demographic parameters (Table 1) were adjusted for cells where fires occurred, according to the fire impact parameters (Table 2). Our function allowed the demographic effects of fire to last for more than a single 2-monthly timestep, linearly abating to zero at the end of each year.

2.3.3 | Fire effects on habitat suitability

Fire typically consumes resources that are used by native mammals. For example, even low-intensity fires can consume a large proportion of the understorey vegetation, leaf litter and logs. For native mammals, this reduces the availability of food, shelter (increasing their exposure to predators) and den sites. These impacts are amplified by fires of higher intensity that consume a greater amount of vegetation. We wrote a custom function that reduces habitat suitability following both 'early' and 'late' fires (R code available as per 'Data Availability Statement'). As our study species vary in their ecology (arboreality, diet, fecundity etc.), we estimated a species-specific effect of fire on habitat suitability (Table 3). We acknowledge that these estimates are based on little empirical data. To account for the uncertainty around these estimates of habitat reduction, our function includes a 'noise' parameter. The 'noise' parameter sets the standard deviation of a normal distribution from which values are drawn around a mean equal to the specified reduction values. We specified that the effect of fire would adjust habitat suitability as per

TABLE 2 Fire impact parameters of 'early' and 'late' dry season fires. Used as stage-specific multipliers on native mammal demographic parameters (i.e. 0.83 = 17% reduction; from Griffiths et al., 2015)

	Juvenile survival	Adult survival	Transition	Recruitment
Common brushtail possum				
Early fire	0.83	0.83	0.83	0.46
Late fire	0.70	0.70	0.70	0.02
Grassland melomys				
Early fire	0.58	0.58	0.58	1.90
Late fire	0.65	0.65	0.65	1.26
Northern brown bandicoot				
Early fire	0.86	0.86	0.86	1.00
Late fire	0.60	0.60	0.60	0.21

TABLE 1 Demographic parameter estimates for our three study species (from Griffiths et al., 2015). *SD* is the standard deviation. Probabilities of survival and transition, and recruitment rate, are expressed per 2-month period

	Probability of juvenile survival (±*SD*)	Probability of adult survival (±*SD*)	Probability of transition from juvenile to adult (±*SD*)	Recruitment rate (±*SD*)
Common brushtail possum	0.55 (0.09)	0.79 (0.08)	0.25 (0.11)	0.46 (0.26)
Grassland melomys	0.36 (0.05)	0.77 (0.05)	0.20 (0.04)	0.78 (0.23)
Northern brown bandicoot	0.55 (0.07)	0.75 (0.11)	0.36 (0.10)	0.45 (0.12)

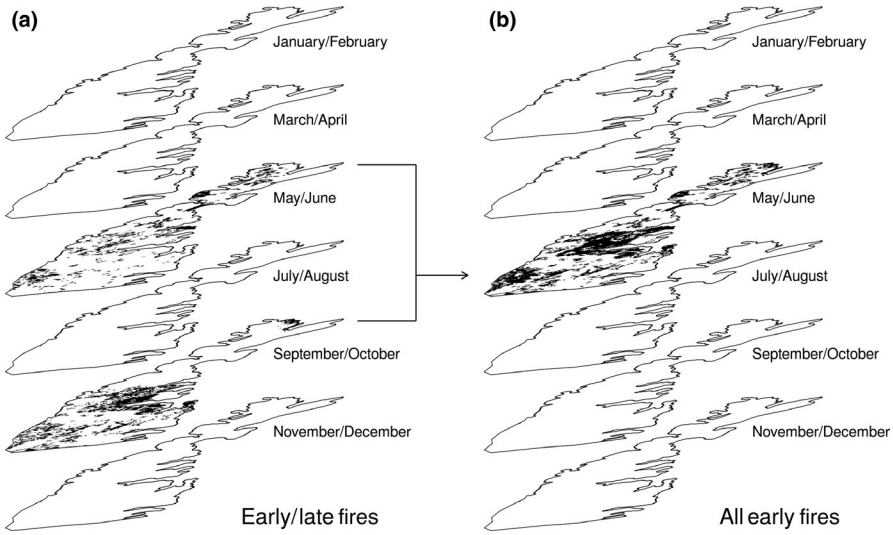

FIGURE 2 A visualisation of how and when grid-based fire patterns (black calls) were incorporated into our models for: (a) the observed fire history: 'early' and 'late' fires occurring in the 3rd and 5th 2-monthly timestep of each year; (b) the EDS prescribed burning scenario: all 'late' fires were reclassified as 'early' fires such that timestep 3 in (b) is equal to sum of timestep 3 and 5 in (a)

TABLE 3 The estimated reduction in habitat suitability following 'early' and 'late' fires for our study species. Values indicate the multiplier used to reduce habitat suitability (i.e. 0.90 = 10% reduction)

	Reduction in habitat suitability following 'early' fires	Reduction in habitat suitability following 'late' fires
Common brushtail possum	0.90	0.75
Grassland melomys	0.70	0.40
Northern brown bandicoot	0.50	0.30

Table 3, and set the 'noise' parameter to 0.1. Again, these effects on habitat suitability also abate linearly through time, returning to zero by the end of each year.

2.3.4 | Initial populations

We calculated the total size of our initial populations by multiplying the density estimates (ha^{-1}) of Griffiths et al. (2015) by the total number of 1-ha cells in our landscape (32,513). As our initial populations were comprised of two life stages (juvenile and adult), we calculated the number of juveniles and adults in the initial population using estimates of stable-age distribution (Griffiths et al., 2015). We then created two raster layers, the first with the number of juveniles randomly distributed across the Kapalga area, and the second with the number of adults randomly distributed across the Kapalga area. We reasoned that complete uniformity of density across the Kapalga area was an unrealistic assumption, and that working with whole individuals was more realistic than fractions of individuals per cell.

2.4 | Model description

For each of our three native mammal species we simulated population trajectories over a 21-year period, starting in January 1995 and finishing in December 2015. As each year has six 2-monthly timesteps, our simulations had 126 timesteps in total. We modelled the entire Kapalga landscape (325 km^2) at a spatial resolution of 100 × 100 m, totalling 32,513 grid cells.

We created a landscape object that was composed of our initial population rasters, a habitat suitability raster layer, a carrying capacity object (a function that related carrying capacity to habitat suitability) and our fire rasters. Given the uniformity of the Kapalga area (flat, open savanna), we set the initial habitat suitability to be constant (i.e. "1") across our landscape. Following Griffiths et al. (2015), we set a ceiling density carrying capacity for the common brushtail possum, grassland melomys and northern brown bandicoot equal to 2.46, 1.08 and 2.00 ha^{-1} respectively. We specified a user-defined logistic function so that the maximum number of individuals per cell (i.e. carrying capacity) at each timestep was related to the habitat suitability of that cell.

We then defined population dynamics to be executed on the landscape object at each timestep. We specified that the population would grow according to a baseline transition matrix (i.e. values in Table 1), with stochasticity dictated by each parameter's standard deviation. For each cell in which a fire occurred, the local cell transition matrix was adjusted according to the fire impact parameters (Table 2). We used cellular-automata (i.e. individual based) dispersal, and based the maximum number of the cells across which individuals could move in each timestep on recent estimates of home range size, and the expected site-fidelity following fire. For example, given that northern brown bandicoots are restricted to the ground-layer they may need to travel large distances post-fire to find a place to shelter, while common brushtail possums show much stronger site-fidelity due to their use of more persistent resources such as

tree hollows. As such, we set the maximum number of cells that an individual possum could disperse to three, an individual grassland melomys to ten and a northern brown bandicoot to 50. As juveniles are more likely to disperse (Griffiths et al., 2015), we set the maximum proportions dispersing for juvenile and adult to be 1.0 and 0.1 respectively. We also controlled the proportion of individuals dispersing based on how close the population in a cell was to its carrying capacity. The Kapalga area is predominantly surrounded by floodplain, which is considered inhospitable for our study species (Griffiths et al., 2015). While the dispersal of animals to cells outside the study area is prevented, animals can disperse to any suitable cells (based on available carrying capacity, habitat suitability and dispersal distance) within the Kapalga area. Each simulation was replicated 1,000 times.

2.5 | Model scenarios

2.5.1 | Fire pattern scenarios

To investigate how different fire patterns might have influenced native mammal population trajectories at Kapalga, we simulated native mammal population trajectories under two fire scenarios:

1. The observed fire history at Kapalga from 1995 to 2015; and
2. A fire management regime of extensive EDS prescribed burning.

While savanna fire management programs often have a limited ability to reduce the overall frequency and extent of fire, they can successfully shift the timing of fires from the late dry season (LDS) to the EDS (Andersen et al., 2005; Gill et al., 2000; Russell-Smith et al., 2013). We constructed an artificial fire history that reflects the application of extensive EDS prescribed burning by reclassifying the observed fire history of the Kapalga area so that all LDS fires instead occurred in the EDS (Figure 2b). Therefore, our EDS prescribed burning scenario had the exact same area burnt, spatial arrangement and frequency of fire, but with a shift in season of burning. The extent to which our EDS prescribed burning scenario differed from the observed fire history at Kapalga varied between years due to the inter-annual variation in the proportion of area that was burnt in the early and late dry season in each year (Figure 1). We note that the complete elimination of LDS fires is unrealistic in practice; however, as it represents an aspirational objective of savanna fire managers in northern Australia, we believe it remains a useful hypothetical scenario.

2.5.2 | Adjusting for fire intensity

The mean Byram fire-line intensities of the experimental 'early' and 'late' fires applied during the Kapalga fire experiment were 2,100 and 7,700 kW/m, respectively (Williams et al., 1998), significantly higher than the intensity of the majority of 'real-world' fires recorded at these times of the year (Russell-Smith & Edwards, 2006; Russell-Smith, Murphy, Lawes, et al., 2015). These high-intensity experimental fires reflect the 'perimeter burning' approach used during the Kapalga fire experiment (Russell-Smith & Edwards, 2006). It is therefore likely that the fire impact parameters estimated during the Kapalga fire experiment may exaggerate the negative effects of fire on small mammal populations. To account for this, we ran our two

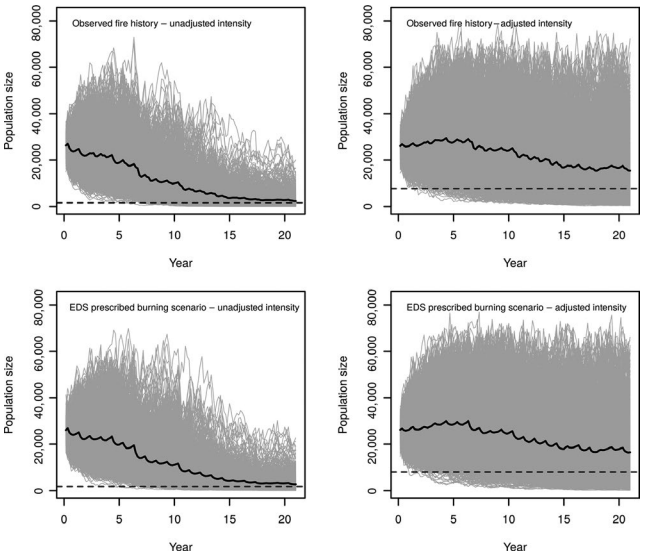

FIGURE 3 The predicted population trajectory of the common brushtail possum under our two fire scenarios (with both unadjusted and adjusted fire intensity) at Kapalga from 1995 to 2015. Grey lines represent each simulation replicate, solid black line represents mean population trajectory, dashed line is the mean expected minimum abundance

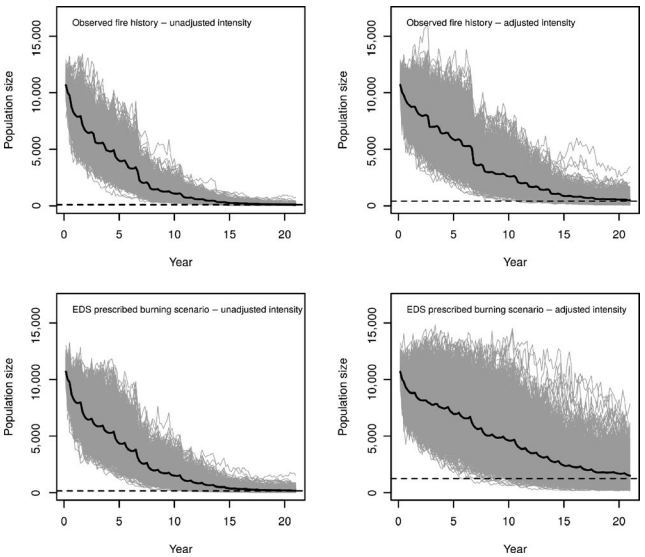

FIGURE 4 The predicted population trajectory of the grassland melomys under our two fire scenarios (with both unadjusted and adjusted fire intensity) at Kapalga from 1995 to 2015. Grey lines represent each simulation replicate, solid black line represents mean population trajectory, dashed line is the mean expected minimum abundance

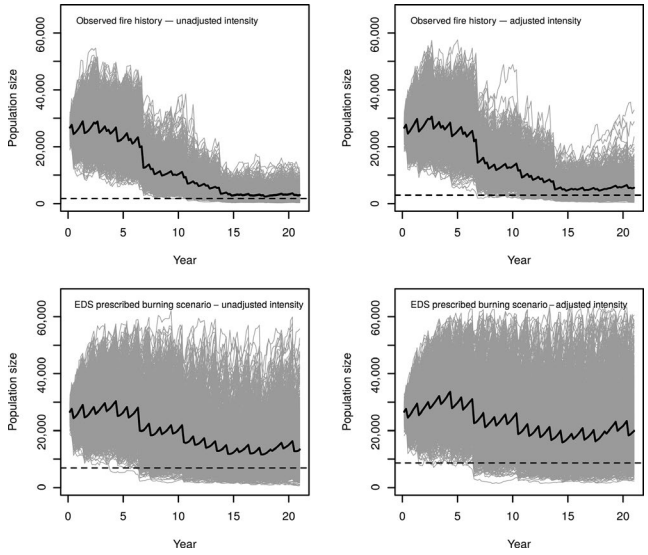

FIGURE 5 The predicted population trajectory of the northern brown bandicoot under our two fire scenarios (with both unadjusted and adjusted fire intensity) at Kapalga from 1995 to 2015. Grey lines represent each simulation replicate, solid black line represents mean population trajectory, dashed line is the mean expected minimum abundance

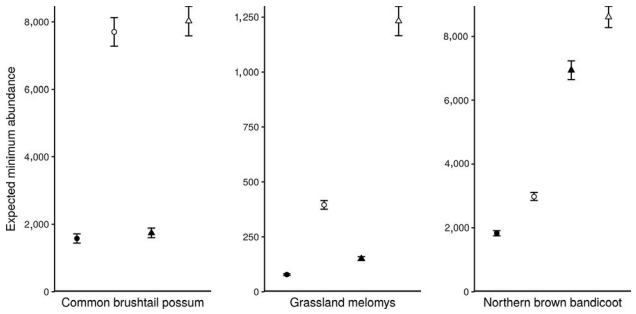

FIGURE 6 The mean expected minimum abundance for the three native mammal species under our two fire scenarios: the observed fire history at Kapalga from 1995 to 2015 (circular symbols) and our early dry season (EDS) prescribed burning scenario (triangular symbols) with unadjusted (filled symbols) and adjusted fire intensity (open symbols). Large symbols indicate the mean of 1,000 replicate simulations, error bars indicate 95% confidence intervals

fire scenarios (outlined above) with both the unadjusted fire impact parameters outlined in Table 2, as well as with these parameters reduced by 50%.

3 | RESULTS

Given the observed fire history at Kapalga between 1995 and 2015, our models that were unadjusted for intensity, predicted a very large decline in populations of the common brushtail possum, grassland melomys and northern brown bandicoot (Figures 3, 4, and 5). Relative to the observed fire history, our EDS prescribed burning scenario increased the mean expected minimum abundance of common brushtail possum and grassland melomys populations by only 164 and 73 individuals, respectively (Figures 3, 4 and 6), but increased the mean expected minimum abundance of northern brown bandicoot populations by 5,102 individuals (Figures 5 and 6). Accounting for the potentially exaggerated effects of the experimental fire intensity reduced the rate of population decline and increased the mean expected minimum abundance for the common brushtail possum (Figures 3 and 6). Accounting for the potentially exaggerated effects of the experimental fire intensity improved the mean expected minimum abundance for the grassland melomys and northern brown bandicoot. This improvement was especially evident for the grassland melomys under our EDS prescribed burning scenario (Figures 4, 5 and 6).

4 | DISCUSSION

The development of effective fire management for biodiversity conservation is a global challenge. The highly dynamic nature of fire, 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. We have outlined a grid-based modelling approach that will improve our ability to identify the specific fire patterns that are beneficial for conserving biodiversity, and increase our capacity to establish clear targets for prescribed fire management in northern Australian savannas. Importantly, this approach is flexible and can be easily adapted to other fire-prone systems.

Our models predicted that the observed fire history between 1995 and 2015 would lead to decreases in the population sizes of the common brushtail possum and northern brown bandicoot of 96% and 94% respectively. These predictions are comparable to the observed decrease in nightly trap success of these species at Kapalga between the mid-1980s and mid-2010s reported by Stokeld et al. (2018; i.e. 96% and 95% decrease respectively). For the grassland melomys, our model predicted a 99% decrease in population size, compared to the observed 91% decrease in nightly trap success at Kapalga between 1999 and 2015 (D. Stokeld, unpubl. data). The similarity between our predicted population trajectories, and the observed change in trap success at Kapalga, may suggest that our models are adequately capturing the main drivers of population decline for these three species, thereby indicating that the fire patterns at Kapalga observed between 1995 and 2015 were not conducive to the persistence of these native mammal populations.

Our EDS prescribed burning scenario had little effect on common brushtail possum and grassland melomys, but greatly enhanced the population of the northern brown bandicoot. These species-specific responses highlight how one particular approach to fire management may benefit some species but disadvantage others. This aligns with research from other fire-prone environments (Kelly et al., 2015; Taylor et al., 2012), and illustrates that there is not a 'one-size fits-all' approach to

fire management for native species conservation in northern Australian savannas (Davies, McCarthy, Rioli, et al., 2018). Instead, there is a need for a more spatially nuanced approach to fire management that is tailored to local conditions and management objectives (Kelly & Brotons, 2017).

Our EDS prescribed burning scenario, which simulated the complete exclusion of LDS fires, represents an extreme example of savanna fire management. For comparison, the West Arnhem Land Fire Abatement Project (WALFA), a successful savanna burning program, has reduced the proportion of the project area burnt in the late dry season from 32% to 11% per annum (Russell-Smith et al., 2013). Therefore, the predicted improvement in the population trajectory of the northern brown bandicoot may be an exaggeration of what can be achieved under savanna fire management scenarios. While it is promising that this hypothetical scenario was predicted to be beneficial for northern brown bandicoot, it is disconcerting that such an aspirational scenario had little beneficial effects on the population trajectory of common brushtail possum and grassland melomys. To better investigate the potential impacts of EDS prescribed fire management on savanna mammal populations, we suggest that future work use more realistic fire pattern scenarios, based on the demonstrated outcomes of existing savanna fire management programs.

The grid-based modelling approach demonstrated here represents an important proof of concept and sets a foundation from which to explore the population-level implications of varying fire management scenarios in fire-prone landscapes. However, we acknowledge that our models included assumptions based on limited data, including a random distribution of the initial populations, the reduction in habitat suitability following fires, noise parameter, dispersal distances and the linear abatement of fire effects. As a thorough interrogation of our model assumptions using sensitivity analysis was beyond the scope of this paper, we currently do not have a clear understanding of how strongly our results were influenced by these assumptions. Until these the validity of these assumptions are tested, with either newly collected data or sensitivity analysis, our results need to be interpreted with caution.

We recommend this modelling approach be used to address the knowledge gaps surrounding the development of effective fire management policy outlined by Parr and Andersen (2006): establishing the relationship between pyrodiversity and biodiversity (i.e. determining how much pyrodiversity is required and at what scale); the identification of whether management intervention is required; and the formulation of clear, attainable targets with operational guidelines of how such targets are to be achieved. For example, Andersen et al. (2005) advocated for an increase in the amount of long-unburnt vegetation in northern Australian savannas, but highlighted that the ideal amount remained unclear, or how such a figure should be derived. Grid-based population simulation models can address these uncertainties, and determine both the optimal amount, and spatial arrangement of long-unburnt vegetation. Furthermore, as management is inevitably constrained by budgets, future work using *steps* could be improved by ensuring fire management scenarios are also economically viable. Such analyses could take into account the direct financial cost of implementing fire management scenarios, as well as the income generated through the abatement of greenhouse gases and sale of carbon credits (Russell-Smith, Murphy, Edwards, et al., 2015).

As with any model, the utility of our approach is contingent on the input data. Given the data collected in the Kapalga fire experiment, we were unable to separately model the effects of fire, grazing by large herbivores and predation on native mammal populations. Instead, the effects of these other contributing factors are encompassed within our estimates of mammal demographic rates and fire effects. While this does not preclude useful simulations of fire management scenarios, our simulations have the inherent assumption that the effects of these other contributing factors have remained constant. This reduces the flexibility of our models as we are unable to gauge the potential implications of other management actions, such as reducing large herbivore or invasive predator populations. This limits our ability to investigate the potential implications of applying multiple management actions simultaneously, an approach shown to be particularly important (Legge et al., 2019). The inherent assumption that the effects of these other contributing factors have remained constant, also has potential ramifications when investigating the fire patterns required to recover these populations. While we may predict population recovery under certain fire scenarios, such recovery would be unlikely to occur if the Kapalga area has experienced a significant change in the threat environment (e.g. a higher density of large herbivores or predators). For example, the density of buffalo likely increased at Kapalga following the cessation of intensive culling associated with the Brucellosis and Tuberculosis Eradication Campaign in 1992, potentially exacerbating the impacts of fire on native mammal populations and reducing the likelihood of mammal population recovery (Legge et al., 2011, 2019; Petty et al., 2007). Future simulations would be improved if the demographic impact of each threatening process, and their interactions, could be explicitly modelled.

Our fire scenarios were based on a simple EDS versus LDS dichotomy, with early dry season fires assumed to have a constant, and consistently lower impact on native mammal demographics than fires occurring in the late dry season. This may be an oversimplification because low-intensity fires can occur after the July 31st cut-off, just as high-intensity fires can occur before this date (Murphy & Russell-Smith, 2010; Russell-Smith & Edwards, 2006). When investigating the effects of fire on biodiversity, a continuous measure of fire severity could better capture the impact of each individual fire (Davies, Maier, et al. 2020; Maier, 2010).

The effects of fire on biodiversity are often complex, spatially- and temporally-variable, and difficult to disentangle. As a result, it can be extremely difficult to identify the optimal fire patterns for biodiversity conservation (Parr & Andersen, 2006). Regardless of these difficulties, the widespread application of prescribed fire management, based on vague notions of maximising pyrodiversity, without a clear understanding of its ecological consequences, may inadvertently threaten biodiversity values (Corey et al., 2019). By advancing our understanding of how the spatiotemporal application of fire influences biodiversity, our grid-based modelling approach will increase our ability to establish specific targets based on the demonstrated requirements of target species, resulting in prescribed fire management that is tailored to local conditions and management objectives.

Importantly, this approach is flexible and can be easily adapted to all fire-prone ecosystems on Earth.

ACKNOWLEDGEMENTS

This study was supported by funding from the Australian Government's National Environmental Science Program via the Threatened Species Recovery Hub. We wish to thank the traditional owners of the Kapalga area of Kakadu National Park, as well as Michael McCarthy, Nick Golding and Alyson Stobo-Wilson for their helpful advice regarding model development, Jay Evans for assistance in collating the fire history of the Kapalga area and Alaric Fisher for helpful feedback on earlier drafts.

AUTHORS' CONTRIBUTIONS

H.F.D., G.R.G., C.V. and B.P.M. conceived the ideas and designed methodology; H.F.D., B.P.M. and C.V. collated the data; H.F.D., B.P.M. and C.V. analysed the data; H.F.D., G.R.G., C.V. and B.P.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data/R code available via the Dryad Digital Repository https://doi.org/10.5061/dryad.sbcc2fr54 (Davies, Visintin, et al., 2020).

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How to cite this article: Davies HF, Visintin C, Gillespie GR, Murphy BP. Investigating the effects of fire management on savanna biodiversity with grid-based spatially explicit population simulations. *J Appl Ecol.* 2021;58:677–686. https://doi.org/10.1111/1365-2664.13801