



Fire and climatic extremes shape mammal distributions in a fire-prone landscape

Susannah Hale^{1†}, Dale G. Nimmo^{2*†}, Raylene Cooke¹, Greg Holland^{1,3}, Simon James⁴, Michael Stevens^{1,5}, Natasha De Bondi¹, Rachel Woods¹, Michael Castle¹, Kristin Campbell¹, Katharine Senior¹, Simon Cassidy¹, Ryan Duffy⁵, Ben Holmes⁵ and John G. White¹

¹School of Life and Environmental Sciences, Centre for Integrative Ecology, Deakin University, Geelong, VIC 3220, Australia,

²Institute for Land, Water and Society, School of Environmental Science, Charles Sturt University, Albury, NSW 2640, Australia,

³Department of Ecology, Environment and Evolution, La Trobe University, Bundoora, VIC 3086, Australia,

⁴School of Information Technology, Deakin University, Geelong, VIC 3220, Australia,

⁵Parks Victoria, Halls Gap, VIC 3381, Australia

ABSTRACT

Aim Extreme climatic events and large wildfires are predicted to increase as the world's climate warms. Understanding how they shape species' distributions will be critical for conserving biodiversity. We used a 7-year dataset of mammals collected during and after south-east Australia's Millennium Drought to assess the roles of fire history, climatic extremes and their interactions in shaping mammal distributions.

Location Grampians National Park, south-eastern Australia.

Methods We surveyed mammals at 36 sites along a ~50-year post-fire chronosequence in each of the 7 years. We modelled ten mammal species in relation to fire history, productivity and recent rainfall. Next, we examined the consistency of species' fire response curves across each of three climatic phases relating to the Millennium Drought. Finally, we identified the optimal distribution of fire ages for small and medium-sized mammal conservation in each of the three climatic phases.

Results The majority of species were influenced by fire history, and all native species were negatively associated with recently burned vegetation. Seven of ten species responded positively to the end of the Millennium Drought, but six of these declined quickly thereafter. Species' responses to fire history differed depending on the climatic conditions. However, the optimal distribution of fire-age classes consistently emphasized the importance of older age classes, regardless of climatic phase. This distribution is in stark contrast to the current distribution of fire ages across the study region.

Main conclusions Mammals in the study region face an uncertain future. The negative impact of drought, the short-lived nature of post-drought recovery and, now, the possibility of a new drought beginning forewarn of further declines. The stark contrast between the optimal and current fire-age distributions means that reducing the incidence of further fires is critical to enhance the capacity of native mammal communities to weather an increasingly turbulent climate.

Keywords

climatic extremes, disturbance, fire, interactions, optimization, small mammals, succession.

*Correspondence and current address: Dale Nimmo, Institute for Land, Water and Society, School of Environmental Science, Charles Sturt University, Albury 2640, NSW, Australia.

E-mail: dnimmo@csu.edu.au

†Co-lead authors

INTRODUCTION

Fire is a critical component of ecosystems world-wide (Bowman *et al.*, 2009). Fire shapes species' distributions over long time-scales, from decades to centuries (Watson *et al.*, 2012; Smith *et al.*, 2013). Consequently, there is a growing emphasis on understanding how to best manage fire for biodiversity conservation (Driscoll *et al.*, 2010). Concurrently, climate change models for many fire-prone regions predict an increase in climatic extremes in coming decades, resulting in more protracted droughts, punctuated by severe floods (Allen *et al.*, 2010; Intergovernmental Panel on Climate Change, 2013). Such changes pose a direct threat to biodiversity (Jentsch & Beierkuhnlein, 2008), but will also have indirect effects as they alter fire regimes (Flannigan *et al.*, 2000), leading to larger, more frequent and severe fires (Clarke *et al.*, 2011). Given the predicted changes to both fire regimes and climatic extremes, it is crucial to understand to what extent these factors shape ecological communities, and what potential there is for interactions among these two important processes (Driscoll *et al.*, 2010; Kelly *et al.*, 2012).

In virtually all terrestrial ecosystems, precipitation is a critical bottom-up driver (Liu *et al.*, 2013). Changes to precipitation strongly modify vegetation structure and composition (Flannigan *et al.*, 2000), thereby altering resource availability for fauna. Temporal variation in precipitation has been shown to alter the rate of vegetation recovery following fire (Monamy & Fox, 2000; Letnic & Dickman, 2010). Therefore, there exists a strong likelihood of interactions between fire and climatic extremes shaping animal communities in fire-prone regions (Greenville *et al.*, 2012). If species' distributions depend on the interplay between fire history and climatic extremes, then fire management for biodiversity conservation must acknowledge such interactions, for instance, when developing planned burning strategies (Di Stefano *et al.*, 2013). However, our current understanding of such interactions is severely limited as there are few datasets which track the response of ecological communities over prolonged time-scales through climatic extremes (Bennett *et al.*, 2014).

Terrestrial mammal species are often reliant on ground vegetation, and their recovery following fire is commonly associated with changes in its structure and complexity (Fox, 1982). For this reason, mammals have frequently been used as a model group for understanding the effects of fire on fauna (Monamy & Fox, 2000; Kelly *et al.*, 2011). Small mammals have been pivotal in developing theories regarding how biodiversity responds to climatic extremes (Letnic & Dickman, 2010). The concept of 'boom' and 'bust' ecosystems – where mammal populations increase in size rapidly following large rainfall events and then diminish when there is a lack of rainfall – has been a central part of this (Holmgren *et al.*, 2006). Such community dynamics are well documented for arid and semi-arid ecosystems (Lima & Jaksic, 1998; Dickman *et al.*, 2010); however, whether these dynamics are also relevant to more temperate mesic ecosystems is understood to a lesser extent (Kelly *et al.*, 2012). Furthermore, how such

dynamics interact with fire regimes remains critically understudied (Letnic & Dickman, 2010).

Here, we use a large dataset on native mammal communities spanning seven consecutive years (2008–2014). Our study region, the Grampians National Park of south-eastern Australia, has recently experienced strong interactions between fire and climatic extremes, including three large fires (ranging from 35,000 to 85,000 ha) since 2005, and severe drought followed by record-breaking rains. The consecutive multiyear nature of our dataset allows us to investigate the effects of fire and rainfall simultaneously. The region has a diverse range of small-and-medium-sized mammals, including two monotremes, 14 marsupial species and six rodent species (two of which are introduced). Using this dataset, we address four questions of fundamental importance to both ecological theory and applied ecology in fire-prone regions:

1. Does fire history drive mammal abundance and occurrence within this region, and if so, over what time frames?
2. Do climatic extremes affect mammal occurrence, and is there evidence for boom and bust phases within this temperate mesic ecosystem?
3. Do fire history and climatic extremes interact to shape species distributions?
4. What is the optimal distribution of fire-age classes for mammal conservation and does this differ under different climatic phases?

METHODS

Study area

The Grampians National Park in south-eastern Australia (168,000 ha), a large conservation reserve embedded within extensive agricultural lands (Enright *et al.*, 1994), is a series of sandstone ranges with east-facing escarpments (Cayley & Taylor, 1997). The region has experienced a 50 year average rainfall of 991 mm, with mean annual rainfall ranging from 601 mm to 1123 mm during the study period and has a temperate climate, experiencing mild winters and hot summers. Native vegetation is dominated by eucalyptus forests, heathy woodlands and open heathlands.

Site selection and description

Thirty-six study sites were selected within the Grampians National Park (Fig. 1). Sites were initially selected to examine the consequences of a large wildfire on the mammal community. The large wildfire occurred in 2006 and burned ~85,000 ha (~50% of the park). Sites were chosen to encompass areas that were burned ($n = 19$) and unburned ($n = 17$) following the fire. Sites not burned in 2006 represented a post-fire age gradient of ~50 years. Sites were spread across the park and were predominately in heathy woodland and sand heathland and were constrained by a further four factors: (1) all sites were located at an elevation < 470 m a.s.l. to account for the influence of elevation on rainfall; (2) all

were established within an intensive fox baiting area, maintaining consistent management practices; (3) all sites were accessible via the road network for time efficiency; and (4) all sites were established with a distance of at least 2 km between them, increasing site independence.

Mammal data

Mammal trapping commenced between April and July in 2008, 2 years after the 2006 wildfire. At each site, a trapping grid of approximately 2.25 ha (150 m × 150 m) was established, with each grid containing 49 Elliott traps (small collapsible aluminium traps; 330 mm × 90 mm × 100 mm) and 16 wire cage traps (490 mm × 205 mm × 175 mm). Elliott traps were laid in a seven-by-seven grid with 25m spacing between traps, with cage traps laid in a four-by-four grid with 50m spacing. All traps contained a bait of rolled oats, peanut butter, honey, vanilla extract and raw linseed oil. Nesting material was placed in each Elliott trap to provide warmth, and both Elliott and cage traps were wrapped in plastic to provide protection from the elements. Each grid was surveyed for four consecutive nights each year, resulting in a total of 260 trap nights per site per year. All traps were checked twice daily with individuals released at the point of capture.

Long-term sampling

The sampling protocol outlined above was repeated from 2009 to 2014, with all sites resampled between April and July. During 2009, one of the 36 sites was not surveyed leading to a total of 251 site-specific surveys across all years. This equates to an overall survey effort of 65,260 trap nights over the duration of the study. During this period, the region experienced a prolonged period of below-average rainfall due to one of south-eastern Australia's most severe droughts on record, the 'Millennium Drought' (van Dijk *et al.*, 2013). This long-term drought (2001–2009) led to an accumulated precipitation deficit twice that of other droughts on record (Leblanc *et al.*, 2012) and had far-reaching impacts on economic and ecological systems across Australia (van Dijk *et al.*, 2013). The Millennium Drought was broken by the 'Big Wet' in 2010–2011 with record-breaking, flooding rains (Leblanc *et al.*, 2012) – after which, annual rainfall fell back to below average (Fig. 1). In addition to the large 2006 wildfire, two further large fires occurred in 2013 and 2014. The 2013 wildfire was 35,000 ha and burned six study sites (two of the original > 20 years sites, one 10–20 years and three 0–10 years), while the 2014 fire was 55,000 ha and burned a further four study sites (one > 20 years, two 10–20 years and one 0–10 years). The cumulative area burned by these large wildfires is 145,263 ha or ~90% of the National Park.

Dependent variables

For each site, annual trap success was calculated to provide a relative measure of mammal abundance for each species

(Caughley, 1980). Trap success (TS) was determined using the following formula:

$$TS = \frac{\text{Number of individuals of a particular species captured}}{\text{total trap nights} - (\text{total number of captures of other species})}$$

where total trap nights = trap nights × total number of traps per site.

This TS calculation was adjusted depending on whether the target species could be caught in only Elliott traps (e.g. house mouse *Mus musculus*), only cage traps (e.g. common brushtail possum *Trichosurus vulpecula*) or both (e.g. heath mouse *Pseudomys shortridgei*).

To account for a trap becoming unavailable once it had been triggered, a frequency–density transformation (Caughley, 1980) was then applied to the TS for each species. The formula used to adjust for trap success was as follows:

$$\text{Adjusted trap success} = \ln(1 - \text{trap success}) \times (-100)$$

where *ln* returns the natural logarithm of a number.

Independent variables

We used four independent variables throughout the study: (1) time since fire for each survey site; (2) average rainfall for 18 months prior to April; (3) productivity; and (4) climatic phase.

Each site was assigned a time since fire based on historical and remotely sensed data from Landsat imagery, provided and prepared by Parks Victoria using geographic information systems.

We quantified rainfall using monthly rainfall averages (mm) from the pooled data of three rainfall stations located between 0 and 4 km from the national park (located at Mirranatwa, Dunkeld and Wartook; Bureau of Meteorology, 2013). Three rainfall lag times were assessed (6, 12 and 18 months prior to trapping), rainfall for the 18 months prior to the commencement of trapping in April each year came out as the best predictor for each species (based on Akaike information criterion, AIC). This is unsurprising as studies have demonstrated that the influence of rainfall takes time to manifest within a system (Recher *et al.*, 2009).

We utilized Normalized Difference Vegetation Index (NDVI) to account for variation between sites in productivity to capture differences in vegetation across the study region (Coops *et al.*, 2013). This variable represents a gradient in vegetation productivity, from infertile rocky outcrops and heathlands (−1) to more productive and moist woodlands (+1) (Lanorte *et al.*, 2014). To measure NDVI, we used the United States Geological Surveys GloVis Landsat data for the 6 years preceding the 2006 wildfire. NDVI was measured annually in a 50m buffer of each study site in the Australian summer months (between January and early March) and then averaged to provide a single NDVI value for each site. Any NDVI cell within the 50m trapping grid buffer that

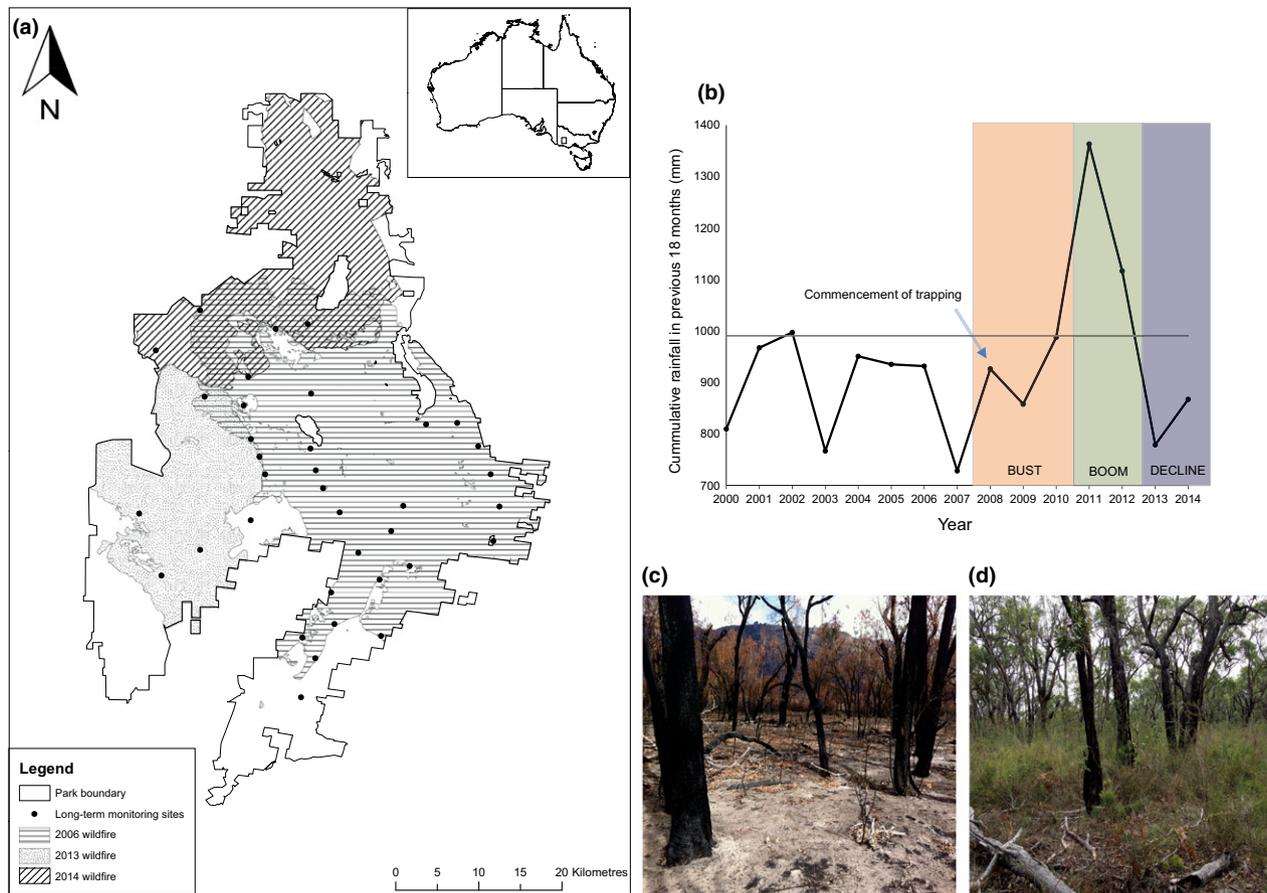


Figure 1 The location of 36 study sites (indicated by black dots) in the Grampians National Park and the wildfires experienced since 2005. Projection UTM UPS, datum GDA 94 (a). Cumulative rainfall (mm) for the 18 month leading up to April, calculated from three rainfall stations (Mirranatwa, Dunkeld and Wartook) in the vicinity of the Grampians National Park. The horizontal line represents the 50 year average. Boom, bust, decline represent three distinct climatic phases used during modelling (b). A recently burnt study site (c) and a longer unburnt study site (d).

included roads was excluded since such areas do not represent habitat for small mammals.

A fourth independent variable indicated which of three climatic phases the region was within, based on Greenville *et al.* (2014): 'bust', 'boom' or 'decline'. The bust phase, from 2008 to 2010, is characterized by below-average rainfall towards the end of south-eastern Australia's decade-long 'Millennium Drought' (van Dijk *et al.*, 2013); the boom phase, from 2011 to 2012, is characterized by far above-average rainfall associated with the flooding rains that signalled the end of the Millennium Drought (Mac Nally *et al.*, 2014); and the decline phase, from 2013 to 2014, is characterized by a return to below-average rainfall following the boom phase (Fig. 1). The distinction between 'bust', 'boom' and 'decline' is therefore based on climatic conditions and the likely availability of resources for small mammals (Greenville *et al.*, 2014).

Statistical analysis

All analyses were conducted in the R statistical package 2.15.3 (R Core Development Team, 2013). For relatively

common species with sufficient data, adjusted trap success (an index of local abundance) was rounded to the nearest integer and modelled using a Poisson distribution and a log link. For mammal species that had little variation in trap success or occurred too infrequently to model trap success, presence/absence models specifying a binomial error structure and a logit link were built.

To model the relationships between mammals and independent variables, we used generalized additive mixed models (GAMMs; Wood, 2006). Mixed models were required due to the repeated sampling of sites over time that can lead to non-independence (Zuur *et al.*, 2009). A unique identifier for each 'site' was included as a random effect in all analyses to account for this repeat sampling.

Two sets of GAMMs were fit. First, to understand the long-term effects of fire and the relative effects of rainfall and productivity, GAMMs were generated for each species that included time since fire, 18-month rainfall and productivity as fixed effects using the Mixed GAM Computation Vehicle (mgcv) package for R (Wood, 2011). Time since fire was entered as a smoothed term to allow for complex

response shapes typical of faunal responses to fire (Nimmo *et al.*, 2012). The amount of smoothing was determined internally during model fitting using maximum likelihood (Wood, 2008). Eighteen-month rainfall and productivity were entered as linear predictors and both were scaled (mean = 0, standard deviation = 1) to allow a direct comparison of their coefficients. A temporal correlation structure (autoregressive correlation, AR1) was also included in these models. This accounts for residual temporal correlation due to surveys closer in time being more correlated than those further apart (Zuur *et al.*, 2009).

Second, to examine whether climatic extremes interact with fire to shape species' distributions, GAMMs were fit with time since fire as a smoothed term and productivity as a linear fixed effect, in addition to a three level categorical predictor that indicated the climatic phase the system was in either bust, boom or decline. An interaction term between time since fire and climatic phase was included using the 'by' command, which allows a separate response curve to time since fire to be produced for each of the three climatic phases. Models of several species failed to converge using *mgcv*, and so we ran models of individual species using the *gamm4* package which experiences fewer convergence issues (Wood & Scheipl, 2015).

We used cross-validation to examine the predictive ability of all models. This involved randomly selecting 50 sites from the dataset, building the model on the remaining sites ($n = 201$) and projecting the model on to the omitted 50 sites. This process was repeated five times, from which the mean of the model validation statistic (outlined below) was calculated. For species modelled using adjusted trap success, we used the Spearman rank correlation coefficient between observed and predicted values as a measure of model predictive capacity (Potts & Elith, 2006). We regard coefficients between 0.00 and 0.19 as indicating weak predictive capacity, 0.20–0.39 as indicating some predictive capacity, 0.40–0.59 as indicating moderate predictive capacity and models with coefficients > 0.60 as having strong predictive capacity. For species modelled using presence/absence data, we calculated the area under the receiver operator curve (AUC). We followed Pearce & Ferrier (2000) in evaluating the predictive ability of models: $AUC \leq 0.5$ having no predictive capacity (random or worse), 0.5–0.7 having some predictive capacity (better than random), 0.7–0.9 having reasonable predictive capacity and > 0.9 having very good predictive capacity.

Optimization

To examine the impact of climatic extremes on fire management targets, we calculated the allocation of fire ages across the study landscape that would maximize the geometric mean of abundance (G) of the native mammal species (Di Stefano *et al.*, 2013, Kelly *et al.* 2015). Maximizing G has been advocated as a way to identify the optimal distribution of fire ages within a landscape as a target for fire management (Di Stefano *et al.*, 2013). We followed Di Stefano *et al.*

(2013) by (1) using adjusted trap success to represent all species' abundances to ensure that all species were on a common scale (i.e. whereas GAMMs were generated using adjusted trap success or presence/absence data, depending on commonness), (2) using this abundance data to calculate G of the native mammal community and (3) using optimization (outlined in detail in Di Stefano *et al.* (2013)) to determine the distribution of fire ages within a landscape that would maximize G . In contrast to Di Stefano *et al.* (2013), we chose to use linear optimization as, unlike nonlinear solvers, it is guaranteed to reach a global minimum (although the results were near identical). R code for linear optimization of the geometric mean is provided (see Appendix S1 in supporting information). We repeated this processes for (1) all mammal data over all years combined and (2) for data within each of the three climatic phases separately (i.e. bust, boom and decline phases) to reveal whether the target for fire management differs depending on climatic phase. Only native mammals were considered in this analysis.

RESULTS

There were 5439 captures of 13 different mammal species (11 native and two introduced) over 65,260 trap nights across the seven-year study period (Table S1). Total captures varied markedly across the study period. In the first year of survey (2008) following the 2006 fire, there were 445 captures, of which 85% were of introduced species (*M. musculus* and black rat *Rattus rattus*). Captures peaked at 1501 in 2012 following the breaking of the drought; 91% of these captures were of native species. With the return of below-average rainfall, captures dropped to 342 by 2014, with 83% of these being native species. Due to inadequate data, the eastern pygmy possum *Cercartetus nanus*, sugar glider *Petaurus breviceps* and the smoky mouse *Pseudomys fumeus* were excluded from analysis.

Time since fire

Pooling the seven years of survey data revealed all but one species (the common dunnart *Sminthopsis murina*) displayed a relationship with time since fire (Table 1). Most species were uncommon in recently burnt areas, with the exception of the introduced *M. musculus*, whose numbers peaked around 2 years post-fire and persisted in high numbers until approximately 10 years post-fire (Fig. 2). The adjusted trap success of the agile antechinus *Antechinus agilis* and the swamp rat *R. lutreolus* was high 20 years post-fire with low trap success in recently burnt areas (Fig. 2). *Antechinus agilis* remained in the system longer than *R. lutreolus* with both species having a resurgence at 45 years post-fire. However, confidence intervals are wide at high time since fire values due to small sample sizes (Fig. 2). *Pseudomys shortridgei* had high trap success in areas approximately 10 years post-fire before reducing in number until approximately 30 years post-fire (Fig. 2). The probability of occurrence of the

Table 1 Results of generalized additive mixed models describing the distribution of mammals in the Grampians National Park. Details of smoothed terms for time since fire are shown for each species as well as model validation statistics. Coefficients of linear terms also included in the models (18 month rainfall and NDVI) are presented in Table S2.

Species	Smoothed term for time since fire			NDVI		Rainfall		Model validation	
	edf	<i>F</i>	<i>P</i> -value	Estimate	SE	Estimate	SE	Discrimination	SE
<i>Antechinus agilis</i>	3.600	8.590	<0.001	0.780	0.267	0.321	0.059	0.563 ^P	0.050
<i>Antechinus flavipes</i>	2.800	6.610	<0.001	-0.661	0.376	0.177	0.151	0.734 ^{AUC}	0.022
<i>Antechinus swainsonii</i>	3.660	8.250	<0.001	1.637	0.512	-0.014	0.159	0.869 ^{AUC}	0.013
<i>Isoodon obesulus</i>	5.290	6.700	<0.001	0.489	0.702	1.869	0.194	0.862 ^{AUC}	0.044
<i>Mus musculus</i>	3.690	13.170	<0.001	-0.063	0.157	0.320	0.079	0.391 ^P	0.033
<i>Pseudomys shortridgei</i>	5.980	8.520	<0.001	0.032	0.206	0.306	0.062	0.516 ^P	0.064
<i>Rattus lutreolus</i>	7.970	9.990	<0.001	1.156	0.511	0.540	0.063	0.507 ^P	0.033
<i>Rattus rattus</i>	5.450	14.050	<0.001	1.084	0.527	1.299	0.157	0.483 ^P	0.022
<i>Sminthopsis murina</i>	1.000	0.010	0.923	-0.139	0.412	0.901	0.149	0.716 ^{AUC}	0.024
<i>Trichosurus vulpecula</i>	3.870	4.320	<0.001	0.064	0.461	-0.043	0.152	0.713 ^{AUC}	0.029

edf = Estimated degrees of freedom. Model discrimination was measured using spearman's correlation coefficient (ρ) for species modelled using adjusted trap success or area under the receiver operating characteristic curve (AUC) for species modelled using presence/absence data.

yellow-footed antechinus *Antechinus flavipes* was highest 15 years post-fire before a decrease in their occupancy, while the dusky antechinus' *Antechinus swainsonii* presence was highest 20 years post-fire (Fig. 2).

Rainfall and productivity

Seven of 10 species were positively associated with rainfall (Table 1). Previous eighteen-month rainfall was associated with higher trap success of *A. agilis*, *M. musculus*, *P. shortridgei* and *R. lutreolus* (Table 1) and the presence of the southern brown bandicoot *Isoodon obesulus*, *R. rattus*, *S. murina* (Table 1). No species had a negative association with 18 month rainfall (Table 1). Four of 10 species increased with higher productivity (Table S2). *Antechinus agilis*, *A. swainsonii*, *R. lutreolus* and *R. rattus* were positively associated with productivity (Table 1). The trap success of *A. flavipes* decreased in higher productivity areas likely representing the species preference for open woodland communities (Table 1).

The models for time since fire, rainfall and productivity had some predictive capacity for the adjusted trap success of one species and moderate predictive capacity for all other species ($n = 4$) (Table 1). All models using presence/absence data ($n = 5$) had a reasonable predictive capacity (Table 1).

Interactions between fire and climatic phase

Fitting separate fire response curves in each of the three climatic phases (bust, boom and decline) showed temporal variability in the response of individual species to fire (Fig. 3). Seven of the ten species were associated with time since fire in at least one of the climatic phases (Table 2). Significant responses to fire history were most commonly observed during the bust phase (six species), followed by the boom phase (four species) and the decline phase (two species). Only two species showed associations with fire history

in each of the three climatic phases (Table 2). Fire response curves of individual species differed in their form (i.e. the shape of the response curve) and amplitude (i.e. the size of values of adjusted trap success or probability of occurrence) between climatic phases (Fig. 3). For example, during the bust phase, *M. musculus* displayed a nonlinear relationship with time since fire, being most abundant following fire and rapidly declining thereafter (Fig. 3a). During the boom phase, this species was still related to time since fire, but its preference was less strong, and the relationship with fire history more linear (Fig. 3a). Finally, during the decline phase, *M. musculus* was rare across all fire ages and was not significantly related to time since fire (Fig. 3a; Table 2). Differences in amplitude between climatic phases are attributed to the strong effect of climatic phase, which had a significant impact on all but two species (*A. swainsonii* and *T. vulpecula*; Table S3).

The models for the interaction between fire and climatic phase had some predictive capacity for the adjusted trap success of two species and moderate capacity for all other species ($n = 3$) (Table 2). For species modelled using presence/absence data, one model had some predictive capacity and four had reasonable predictive capacity (Table 2).

Geometric mean of abundance

Optimization of the geometric mean of mammal abundance revealed that these shifts in distributions had a relatively minor impact on the optimal distribution of fire-age classes for mammal conservation (Fig. 3). A consistent feature of the optimal fire-age distributions within each of the three climatic phases was the importance of mid-successional (10–25) and long unburned (> 25 years post-fire) vegetation. In each case, the distributions included a mix of mid-successional and long unburned vegetation, with long unburned vegetation making up the majority (Table S4). During the

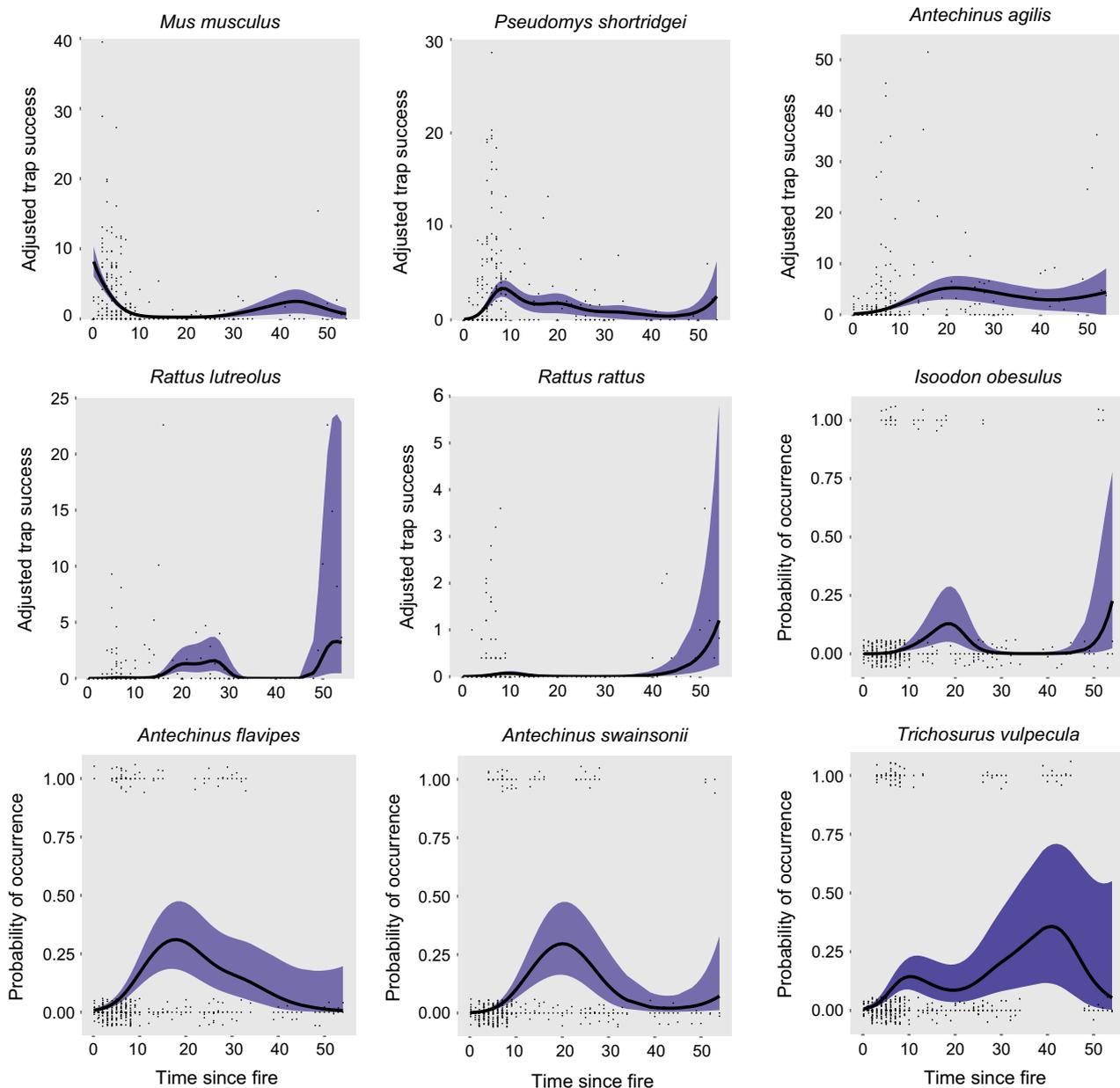


Figure 2 Responses of the adjusted trap success and probability of occurrence of nine terrestrial mammals in relation to time since fire in the Grampians National Park. Black lines represent predicted values from generalized additive mixed models. Shaded areas represent 95% confidence intervals for predictions.

bust and particularly during the decline phases, the optimal allocation included a larger proportion of long unburned vegetation (Fig. 3). The optimal G differed substantially between the three time periods: G increased by 198% (from 0.55 to 1.64) during the boom phase relative to the bust phase, but then declined by 72% during the decline phase (from 1.64 to 0.46), at which time G was 16% lower than during the bust phase (0.46 compared to 0.55). Currently, the landscape configuration of fire-age classes is far from optimal, with 85% of the landscape recently burnt (< 9 years since fire), 7% in mid-successional and 8% being long unburnt.

DISCUSSION

Our work adds to a growing body of research documenting the long-term (i.e. multidecadal) impacts of fire on fauna (Watson *et al.*, 2012; Smith *et al.*, 2013). When data across all 7 years were pooled, all but one species responded to fire history and fluctuations in the occurrence of mammal species continued throughout the ~50 years chronosequence. All native species displayed a negative association with recently burned areas (i.e. areas < 5 years since fire) and species such as *I. obesulus* were most common in areas unburned for > 50 years. These responses are consistent with

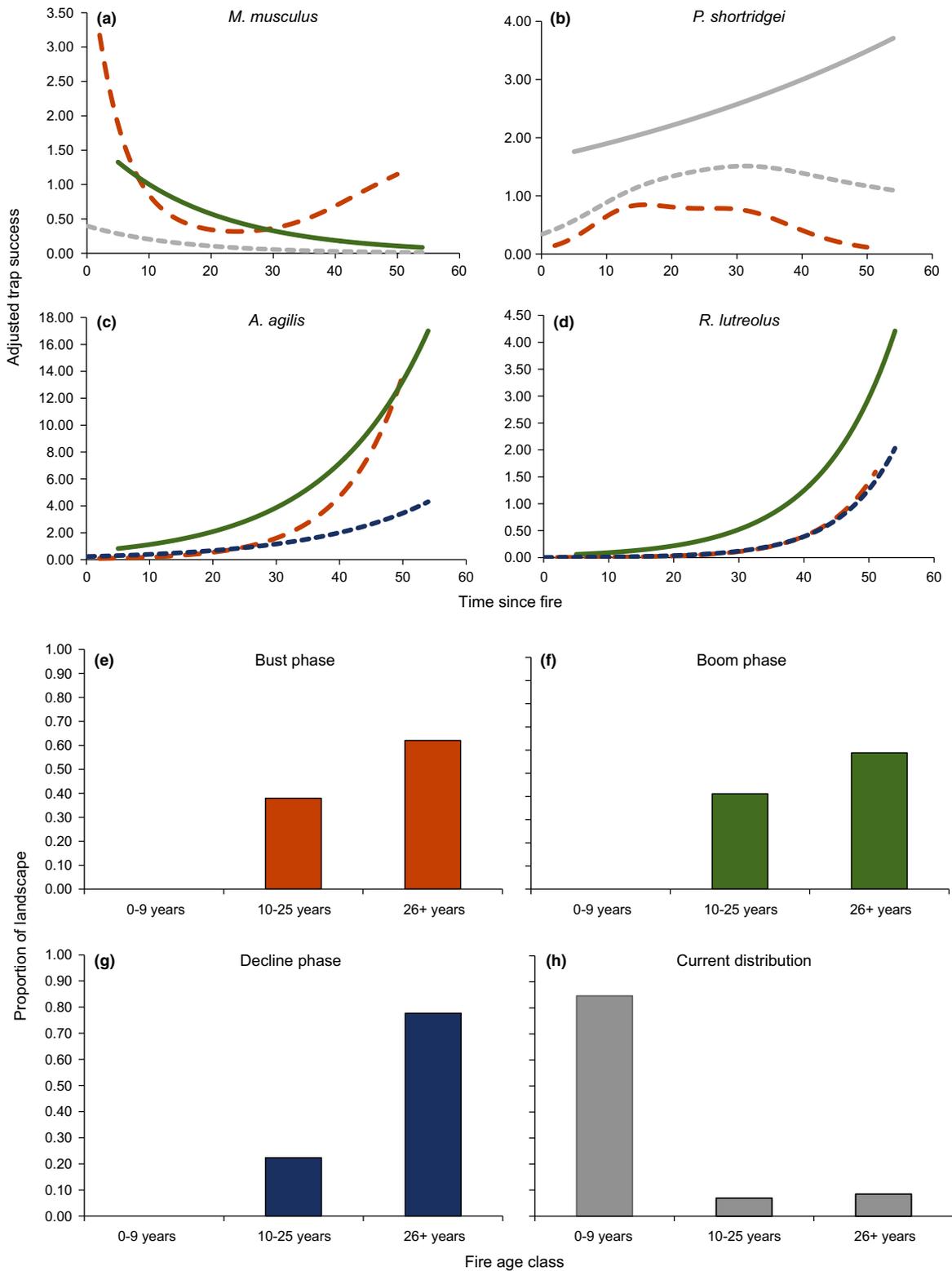


Figure 3 The effects of fire and climatic extremes on mammals. (a, b, c, d) Predictions from generalized additive mixed models investigating time since fire in each of three climatic phases for individual species of mammal. Coarse broken line = 'bust' phase (2008–2010), solid line = 'boom' phase (2011–2012) and fine dotted line = 'decline' phase (2013–2014). Coloured lines = significant smoothed term for fire since fire (i.e. $P < 0.05$), grey lines = insignificant smoothed term. Only species that respond to fire in more than one climatic phases are shown. (e, f, g, h) The distribution of fire-age classes that would optimize the geometric mean of abundance of small and medium-sized mammal communities in the Grampians National Park during the 'bust' (2008–2010), 'boom' (2011–2012) and during 'decline' phase (2013–2014) in relation to south-eastern Australia's Millennium Drought, compared to the current fire-age distribution in the Grampian National Park.

Table 2 Results of generalized additive mixed models describing the distribution of mammals in the Grampians National Park. Details of smoothed terms for time since fire in each of three climatic phases are shown for each species as well as model validation statistics. Parameter estimates for linear terms also included in the models (climatic phase and NDVI) are provided in Tables S2 and S3.

Species	Bust			Boom			Decline			Model validation	
	edf	χ^2	P-value	edf	χ^2	P-value	edf	χ^2	P-value	Discrimination	SE
<i>Antechinus agilis</i>	1.000	24.573	<0.001	1.000	8.299	0.004	1.000	6.962	0.008	0.557 ^P	0.050
<i>Antechinus flavipes</i>	1.000	3.651	0.056	1.000	0.022	0.882	1.000	0.850	0.357	0.753 ^{AUC}	0.033
<i>Antechinus swainsonii</i>	1.000	0.854	0.355	1.000	6.370	0.012	1.000	2.497	0.114	0.829 ^{AUC}	0.031
<i>Isoodon obesulus</i>	1.000	0.465	0.495	1.000	1.366	0.242	1.000	0.215	0.643	0.715 ^{AUC}	0.083
<i>Mus musculus</i>	2.119	16.878	<0.001	1.000	7.074	0.008	1.000	3.190	0.074	0.516 ^P	0.065
<i>Pseudomys shortridgei</i>	2.738	13.312	0.003	1.000	0.399	0.528	1.962	4.424	0.106	0.276 ^P	0.060
<i>Rattus lutreolus</i>	1.000	10.255	0.001	1.000	5.683	0.017	1.000	10.200	0.001	0.305 ^P	0.077
<i>Rattus rattus</i>	1.000	0.164	0.685	1.000	0.275	0.600	1.000	0.498	0.480	0.401 ^P	0.048
<i>Sminthopsis murina</i>	1.000	0.003	0.960	1.000	1.981	0.159	1.000	0.683	0.409	0.704 ^{AUC}	0.040
<i>Trichosurus vulpecula</i>	1.000	4.329	0.038	1.000	1.346	0.246	1.000	0.518	0.472	0.694 ^{AUC}	0.016

edf = Estimated degrees of freedom. Model discrimination was measured using spearman’s correlation coefficient (ρ) for species modelled using adjusted trap success or area under the receiver operating characteristic curve (AUC) for species modelled using presence/absence data.

the preferences of many small and medium-sized native mammals for structurally complex vegetation (Paull, 1995). By contrast, the early post-fire environment was dominated by the invasive *M. musculus* – a species that is commonly associated with recently burnt areas (Kelly *et al.*, 2011), perhaps due to enhanced food resources post-fire, such as green shoots and seeds (Kelly *et al.*, 2011). The importance of later successional stages is emerging as a consistent theme among fire ecology studies in Australia and internationally. For example, research in semi-arid environments north of the study region found long unburned vegetation was important for reptiles (Nimmo *et al.*, 2012) and small mammals (Kelly *et al.*, 2012). The importance of later successional stages has also been observed for mammal populations in New South Wales, Australia (Fox, 1982), and increases in mammal diversity have been observed in long unburned areas in

northern America (Vamstad & Rotenberry, 2010). The large proportion of species related to fire history, an aversion to recently burned vegetation among native species, and the long-term nature of post-fire responses highlight the need for careful, long-term planning of fire regimes focussed on limiting the occurrence of large wildfires.

The role of climatic extremes in driving the distribution of fauna is well documented in arid environments (Letnic *et al.*, 2005; Letnic & Dickman, 2006), but less so in temperate ecosystems (Kelly *et al.*, 2012). Here, we demonstrate that small mammal communities appear to display classic rainfall-driven ‘boom and bust’ phases (Letnic & Dickman, 2006) typical of small mammal communities in arid regions (Letnic *et al.*, 2005; Dickman *et al.*, 2010). The mechanisms driving the boom and bust patterns in small mammals likely include increased vegetation growth and

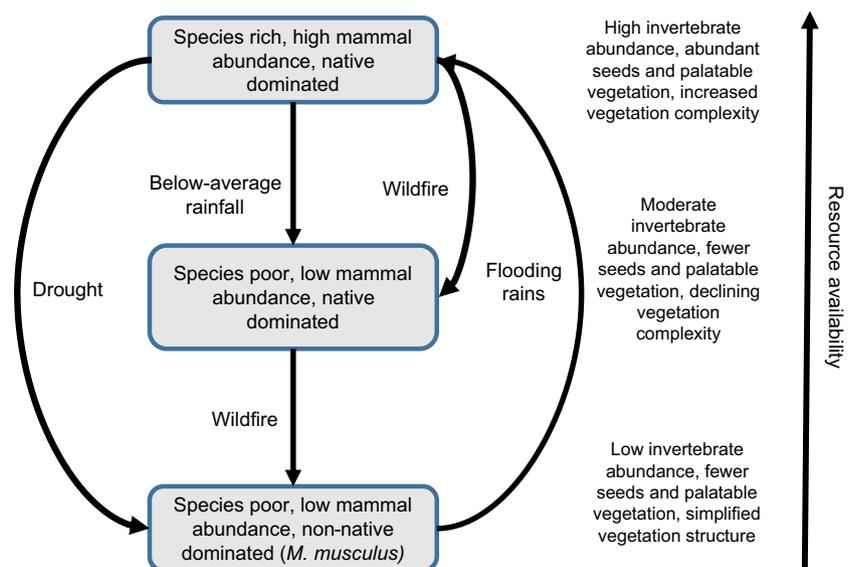


Figure 4 Conceptual model of how the Grampians mammal community is shaped by fire and climatic extremes and the proximate drivers underpinning mammal distributions, adapted from Letnic & Dickman (2010).

food availability (e.g. seeds, invertebrates) in wet periods (Letnic & Dickman, 2010), leading to increased reproductive success (Lima & Jaksic, 1998, Fig 4). The strong effect of precipitation in this system meant that, during dry periods (i.e. during the Millennium Drought), some species were rarely or not recorded (e.g. *I. obesulus*, *A. swainsonii* and *R. lutreolus*).

We observed a change in species' responses to fire history across the three climatic phases (bust, boom and decline), indicating that fire history and climate can interact to shape species' occurrence. What mechanisms would underpin such an interaction? One possibility is that climate alters the relationship between vegetation structure and fire history (Fried *et al.*, 2004), affecting the relationship between fire and animal distributions in turn. Such an effect would be consistent with the 'dynamic vegetation' hypothesis, which proposes that vegetation dynamics post-fire interact with climate to produce geographically or temporally variable responses to fire history (Nimmo *et al.*, 2014). This was supported when explaining geographically variable responses of reptiles to fire (Nimmo *et al.*, 2014). Similarly, Monamy & Fox (2000) found that small mammals were affected by vegetation cover more strongly than time since fire itself. It is also possible that particular fire ages experience a flush of food resources during wet periods (Free *et al.*, 2013) that may be unavailable during drier periods, allowing species to extend distributions into otherwise marginal habitats.

Variability within species in the significance of time since fire between the climatic phases highlights that the ability to detect the impact of fire on a species may be contingent on the prevailing climatic conditions. This reinforces the view that it is important to survey at a high intensity when effect sizes are small to reduce the risk of type II error (Smith *et al.*, 2013) and that species with no response to fire history should be treated cautiously (Nimmo *et al.*, 2014). The fact that the largest numbers of significant associations with fire were observed during the 'bust' phase suggests that species' responses to fire may be more obvious when the system is under stress, and species are more restricted to their preferred habitats under such conditions.

Despite the interplay between fire history and climate, targets for optimal fire management of mammals were relatively consistent over time. By identifying the fire-age distributions that would maximize the geometric mean of abundances of mammals (Di Stefano *et al.*, 2013), we demonstrated that although the optimal distribution differs somewhat depending on climatic conditions, there was a consistent need for retaining a large proportion of the landscape in older fire-age classes (i.e. 10–25 and 26+ years since fire). The relative consistency of the optimal distributions is reassuring as there is obviously limited capacity for land managers to substantially shift the fire-age composition of a landscape in response to droughts and floods, particularly in regions with multidecadal fire regimes. It is of great concern, however, that the optimal distributions are in stark contrast to the current distribution of fire ages in the region which, due to

several large fires in the past decade, is dominated by areas < 10 years post-fire.

Implications and conclusions

The strong association between mammals and rainfall means that a future with increasingly intense and longer-term droughts could imperil many species. In addition, large-scale wildfires have established the majority of the ecosystem in an early successional period. This trend of larger, more frequent and intense fires is predicted to continue under scenarios of climate change (Intergovernmental Panel on Climate Change, 2013). Fires occurring during protracted droughts will be particularly damaging and have the potential to drive species towards local extinction. Fire management must aim to burn strategically to minimize the size of these fires and retain as larger areas as possible in older successional states, particularly during drought.

ACKNOWLEDGEMENTS

Funding and field support was provided by Parks Victoria, Deakin University and Holsworth Wildlife Research Endowment. We thank the Grampians research team and volunteers who assisted with research. This study was carried in accordance with the regulations of the Animal Ethics Committee at Deakin University (permit number A8 2008, A4 2011 and B06 2014) and research permits from the Department of Environment and Primary Industries (permit numbers 10005800 and 10007121).

REFERENCES

- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.
- Bennett, J.M., Nimmo, D.G., Clarke, R.H., Thomson, J.R., Cheers, G., Horrocks, G.F.B., Hall, M., Radford, J.Q., Bennett, A.F., Mac Nally, R. & Duncan, R. (2014) Resistance and resilience: can the abrupt end of extreme drought reverse avifaunal collapse? *Diversity and Distributions*, **20**, 1321–1332.
- Bowman, D.M.J.S., Balch, J.K., Artaxo, P. *et al.* (2009) Fire in the Earth System. *Science*, **324**, 481–484.
- Bureau of Meteorology. (2013) *Weather station directory*. Available at: (accessed 02/10/2013 2013).
- Caughley, G. (1980) *Analysis of vertebrate populations*. John Wiley and Sons Ltd., New York.
- Cayley, R.A. & Taylor, D.H. (1997) Grampians special map area geological report. In: Geological Survey of Victoria. State Government Victoria.

- Clarke, H.G., Smith, P.L. & Pitman, A.J. (2011) Regional signatures of future fire weather over eastern Australia from global climate models. *International Journal of Wildland Fire*, **20**, 550–562.
- Coops, N., Schaepman, M. & Múcher, C. (2013) What multiscale environmental drivers can best be discriminated from a habitat index derived from a remotely sensed vegetation time series? *Landscape Ecology*, **28**, 1529–1543.
- Di Stefano, J., McCarthy, M.A., York, A., Duff, T.J., Slingo, J. & Christie, F. (2013) Defining vegetation age class distributions for multispecies conservation in fire-prone landscapes. *Biological Conservation*, **166**, 111–117.
- Dickman, C.R., Greenville, A.C., Beh, C.L., Tamayo, B. & Wardle, G.M. (2010) Social organization and movements of desert rodents during population “booms” and “busts” in central Australia. *Journal of Mammalogy*, **91**, 798–810.
- van Dijk, A.I.J.M., Beck, H.E., Crosbie, R.S., de Jeu, R.A.M., Liu, Y.Y., Podger, G.M., Timbal, B. & Viney, N.R. (2013) The Millennium Drought in southeast Australia (2001–2009): natural and human causes and implications for water resources, ecosystems, economy, and society. *Water Resources Research*, **49**, 1040–1057.
- Driscoll, D.A., Lindenmayer, D.B., Bennett, A.F., Bode, M., Bradstock, R.A., Cary, G.J., Clarke, M.F., Dexter, N., Fensham, R., Friend, G., Gill, M., James, S., Kay, G., Keith, D.A., MacGregor, C., Russell-Smith, J., Salt, D., Watson, J.E.M., Williams, R.J. & York, A. (2010) Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation*, **143**, 1928–1939.
- Enright, N.J., Miller, B.P. & Crawford, A. (1994) Environmental correlates of vegetation patterns and species richness in the northern Grampians, Victoria. *Australian Journal of Ecology*, **19**, 159–168.
- Flannigan, M.D., Stocks, B.J. & Wotton, B.M. (2000) Climate change and forest fires. *Science of the Total Environment*, **262**, 221–229.
- Fox, B.J. (1982) Fire and mammalian secondary succession in an Australian coastal heath. *Ecology*, **63**, 1332–1341.
- Free, C.L., Baxter, G.S., Dickman, C.R. & Leung, L.K. (2013) Resource pulses in desert river habitats: productivity-biodiversity hotspots, or mirages? *PLoS ONE*, **8**, 1–13.
- Fried, J.S., Torn, M.S. & Mills, E. (2004) The impact of climate change on wildfire severity: a regional forecast for northern California. *Climatic Change*, **64**, 169–191.
- Greenville, A.C., Wardle, G.M. & Dickman, C.R. (2012) Extreme climatic events drive mammal irruptions: regression analysis of 100-year trends in desert rainfall and temperature. *Ecology and evolution*, **2**, 2645–2658.
- Greenville, A., Wardle, G., Tamayo, B. & Dickman, C. (2014) Bottom-up and top-down processes interact to modify intraguild interactions in resource-pulse environments. *Oecologia*, **175**, 1349–1358.
- Holmgren, M., Stapp, P., Dickman, C.R., Gracia, C., Graham, S., Gutiérrez, J.R., Hice, C., Jaksic, F., Kelt, D.A., Letnic, M., Lima, M., López, B.C., Meserve, P.L., Milstead, W.B., Polis, G.A., Previtali, M.A., Richter, M., Sabaté, S. & Squeo, F.A. (2006) Extreme climatic events shape arid and semiarid ecosystems. *Frontiers in Ecology and the Environment*, **4**, 87–95.
- Intergovernmental Panel on Climate Change. (2013) Climate Change 2013 - the physical science basis. *Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change* (ed. T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley), p. 1535. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Jentsch, A. & Beierkuhnlein, C. (2008) Research frontiers in climate change: effects of extreme meteorological events on ecosystems. *Comptes Rendus Geoscience*, **340**, 621–628.
- Kelly, L.T., Nimmo, D.G., Spence-Bailey, L.M., Haslem, A., Watson, S.J., Clarke, M.F. & Bennett, A.F. (2011) Influence of fire history on small mammal distributions: insights from a 100-year post-fire chronosequence. *Diversity and Distributions*, **17**, 462–473.
- Kelly, L.T., Nimmo, D.G., Spence-Bailey, L.M., Taylor, R.S., Watson, S.J., Clarke, M.F. & Bennett, A.F. (2012) Managing fire mosaics for small mammal conservation: a landscape perspective. *Journal of Applied Ecology*, **49**, 412–421.
- Kelly, L.T., Bennett, A.F., Clarke, M.F. & McCarthy, M.A. (2015) Optimal fire histories for biodiversity conservation. *Conservation Biology*, **29**, 473–481.
- Lanorte, A., Lasaponara, R., Lovallo, M. & Telesca, L. (2014) Fisher-Shannon information plane analysis of SPOT/VEGETATION Normalized Difference Vegetation Index (NDVI) time series to characterize vegetation recovery after fire disturbance. *International Journal of Applied Earth Observation and Geoinformation*, **26**, 441–446.
- Leblanc, M., Tweed, S., Van Dijk, A. & Timbal, B. (2012) A review of historic and future hydrological changes in the Murray-Darling Basin. *Global and Planetary Change*, **80–81**, 226–246.
- Letnic, M. & Dickman, C.R. (2006) Boom means bust: interactions between the El Niño/Southern Oscillation (ENSO), rainfall and the processes threatening mammal species in arid Australia. *Biodiversity and Conservation*, **15**, 3847–3880.
- Letnic, M. & Dickman, C.R. (2010) Resource pulses and mammalian dynamics: conceptual models for hummock grasslands and other Australian desert habitats. *Biological Reviews Cambridge Philosophical Society*, **85**, 501–521.
- Letnic, M., Tamayo, B. & Dickman, C.R. (2005) The responses of mammals to La Niña (El Niño southern oscillation) – associated rainfall, predation, and wildfire in central Australia. *Journal of Mammalogy*, **86**, 689–703.

- Lima, M. & Jaksic, F.M. (1998) Delayed density-dependent and rainfall effects on reproductive parameters of an irruptive rodent in semiarid Chile. *Acta Theriologica*, **43**, 225–234.
- Liu, Y.Y., van Dijk, A.I.J.M., McCabe, M.F., Evans, J.P. & de Jeu, R.A.M. (2013) Global vegetation biomass change (1988–2008) and attribution to environmental and human drivers. *Global Ecology and Biogeography*, **22**, 692–705.
- Mac Nally, R., Nerenberg, S., Thomson, J.R., Lada, H. & Clarke, R.H. (2014) Do frogs bounce, and if so, by how much? Responses to the ‘Big Wet’ following the ‘Big Dry’ in south-eastern Australia. *Global Ecology and Biogeography*, **23**, 223–234.
- Monamy, V. & Fox, B.J. (2000) Small mammal succession is determined by vegetation density rather than time elapsed since disturbance. *Austral Ecology*, **25**, 580–587.
- Nimmo, D.G., Kelly, L.T., Spence-Bailey, L.M., Watson, S.J., Haslem, A., White, J.G., Clarke, M.F. & Bennett, A.F. (2012) Predicting the century-long post-fire responses of reptiles. *Global Ecology and Biogeography*, **21**, 1062–1073.
- Nimmo, D.G., Kelly, L.T., Farnsworth, L.M., Watson, S.J. & Bennett, A.F. (2014) Why do some species have geographically varying responses to fire history? *Ecography*, **37**, 805–813.
- Paull, D. (1995) The distribution of the southern brown bandicoot (*Isodon obesulus obesulus*) in South Australia. *Wildlife Research*, **22**, 585–600.
- Pearce, J. & Ferrier, S. (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling*, **133**, 225–245.
- Potts, J.M. & Elith, J. (2006) Comparing species abundance models. *Ecological Modelling*, **199**, 153–163.
- R Core Development Team. (2013) R: a language and environment for statistical computing.
- Recher, H.F., Lunney, D. & Matthews, A. (2009) Small mammal populations in a eucalypt forest affected by fire and drought. I. Long-term patterns in an era of climate change. *Wildlife Research*, **36**, 143–158.
- Smith, A.L., Bull, C.M. & Driscoll, D.A. (2013) Successional specialization in a reptile community cautions against widespread planned burning and complete fire suppression. *Journal of Applied Ecology*, **50**, 1178–1186.
- Vamstad, M.S. & Rotenberry, J.T. (2010) Effects of fire on vegetation and small mammal communities in a Mojave Desert Joshua tree woodland. *Journal of Arid Environments*, **74**, 1309–1318.
- Watson, S.J., Taylor, R.S., Nimmo, D.G., Kelly, L.T., Haslem, A., Clarke, M.F. & Bennett, A.F. (2012) Effects of time since fire on birds: how informative are generalized fire response curves for conservation management? *Ecological Applications*, **22**, 685–696.
- Wood, S.N. (2006) *Generalized additive models: an introduction with R/Simon N. Wood*. Chapman and Hall/CRC Press, Boca Raton, FL.
- Wood, S.N. (2008) Fast stable direct fitting and smoothness selection for generalized additive models. *Journal of the Royal Statistical Society. Series B: Statistical Methodology*, **70**, 495–518.
- Wood, S.N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, **73**, 3–36.
- Wood, S.N. & Scheipl, F. (2015) gamm4: Generalized additive mixed models using mgcv and lme4. In: R package, version 0.2-3, <https://cran.r-project.org/web/packages/gamm4/gamm4.pdf>.
- Zuur, A., Ieno, E., Walker, N., Saveliev, A. & Smith, G. (2009) *Mixed effects models and extensions in ecology with R*. Springer New York, New York.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 R code for optimising geometric mean of abundances based on land types.

Table S1 Overall small mammal captures summary.

Table S2 Results of generalised additive mixed models describing the relationship between mammals and time since fire, climatic phase and NDVI for the linear term NDVI.

Table S3 Results of generalised additive mixed models describing the relationship between mammals and time since fire, climatic phase and NDVI for the linear term climatic phase.

Table S4 The number of surveys across the seven years of the study, in each of the distinct fire age classes during each climatic phase.

BIOSKETCH

The Grampians Fire and Biodiversity Project is a collaboration between Deakin University, Charles Sturt University and Parks Victoria. The team is interested in the ability of land management to enhance the capacity of the Grampians ecosystem to cope with and recover from changes in climate and disturbance regimes.

Author contributions: S.H. and D.N. led the writing. J.W., R.C. and G.H. contributed to the writing. D.N., S.J. and S.H. analysed the data. J.W., M.S. and R.C. conceived ideas. S.H., M.S., N.D.B., R.W., M.C., K.C., K.S., S.C., R.D. and B.H. collected data.

Editor: Alexandra Syphard