



Effects of the fire regime on mammal occurrence after wildfire: Site effects vs landscape context in fire-prone forests



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ABSTRACT

Wildfires have major impacts on ecosystems globally. Fire regimes (including fire frequency, intensity, season and type of fire) influence the status of species by altering habitat suitability at the site scale, and by creating heterogeneity at the landscape scale. The relative effects of site and landscape-scale fire attributes on animal species are rarely examined together. Such knowledge is important, given that fire regimes are sensitive to changing land management practices; and that fires are predicted to become larger and more frequent in some regions as a result of climate change. Here, we tested the relative influence of elements of the fire regime (fire severity, fire history) at the site-scale, and the landscape context (extent of surrounding unburnt forest, fire heterogeneity) on the occurrence of native terrestrial mammals after severe wildfire in south-eastern Australia. We conducted surveys by using automatically triggered, infrared cameras at 80 sites in fire-prone eucalypt forests, 2–3 years post-wildfire. Thirteen native mammal species were recorded, eight of which were detected with sufficient frequency for analysis. Most species were widespread (35–90% of sites) and recorded in all fire severity classes. Fire effects at the site-level were more influential than landscape context effects arising from heterogeneity in the fire regime (e.g. extent of surrounding unburnt forest). Fire severity was the most influential of the fire-regime elements investigated, but it affected different species in different ways. This study highlights three main points relevant to conservation of terrestrial mammals after wildfire. First, spatial variation in fire severity associated with wildfire (ranging from unburned to severely burned stands) is an important contributor to the post-fire status of species. Second, post-fire environmental conditions are significant: here, rapid regeneration of vegetation following drought-breaking rains greatly influenced the suitability of post-fire habitats. Third, it is valuable to consider the effects of the fire regime at multiple scales, including both the site (forest stand) and its landscape context. Insights from short-term surveys, such as this, will be enhanced by complementary longitudinal studies, especially where they encompass environmental variation through the post-fire succession.

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1. Introduction

Fire has an important role in determining the distribution and abundance of species in fire-prone regions globally (Bond et al.,

2005; Bowman et al., 2013). Multiple components of the fire regime (*sensu* Gill, 1975), including fire frequency, intensity, season and type of fire, can influence biodiversity (Gill, 1975; Gill and Allan, 2008). The intensity of a large wildfire, for example, influences the composition and spatial pattern of plant communities (Pausas et al., 2008; Roman-Cuesta et al., 2009; Turner et al., 1994). While knowledge of the relationship between fire regimes and plant communities is growing (Driscoll et al., 2010; Whelan et al., 2002), much less is known about the components of the fire regime and their influence on fauna and ecosystems (Clarke, 2008; Fontaine and Kennedy, 2012). Fire regimes are expected to change in future decades as a consequence of climate change (Krawchuk et al., 2009; Moritz et al., 2012); wildfires are predicted to increase

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in size, occurrence and frequency over a longer fire season in some fire-prone areas (Clarke et al., 2011; McKenzie et al., 2004; Wotton et al., 2010). Fire regimes are also altered by changes in land management practices, including the use of planned burning for ecological or fuel reduction purposes (Moritz et al., 2012; Parks et al., 2015).

The fire regime can influence the occurrence of animal species at two spatial scales: (a) at the site-level via its influence on the suitability of habitat at a particular location; and (b) at the landscape-level via its influence on the landscape context of a site. At the site-level, fire intensity and the time between fires are important components of the fire regime. Fire intensity relates to the amount of energy emitted during the fire, whilst fire severity relates to the amount of vegetation or organic matter lost after a fire event (Keeley, 2009). Here, we refer to fire severity. A high severity fire may result in complete incineration of ground and canopy vegetation; whereas in a low severity fire the understorey may burn in a patchy manner and the canopy remains largely unburnt. Consequently, fire severity will have marked effects on the availability of resources such as shelter, foraging substrates and food for animal species post-fire (Fontaine et al., 2009; Keith et al., 2002; Smucker et al., 2005). The effect of fire severity on fauna after wildfire has rarely been quantified (but see Lindenmayer et al., 2013). Fire history (including the time between fire events), can also influence the suitability of a site by affecting vegetation successional stage and associated habitat structure (Bradstock et al., 2005). Sequential fires at short or longer intervals can have differing outcomes for structural features that provide habitat resources for animal species (Haslem et al., 2011). For instance, in semi-arid mallee vegetation in Australia, long fire intervals (at least >40 years) are required for tree hollows to develop and be suitable for hollow-nesting animals, whereas leaf litter can accumulate quickly within shorter fire intervals to provide habitat for other species (Haslem et al., 2011).

At the landscape-level, spatial variation in components of the fire regime contribute to landscape heterogeneity. Large fires vary spatially in their intensity, leading to a post-fire landscape of vegetation patches of differing fire severity (Leonard et al., 2014; Roman-Cuesta et al., 2009; Schoennagel et al., 2008). Animal populations potentially are influenced by the way in which such fire-induced heterogeneity determines the landscape context at a particular site. For instance, a patchy mosaic of burnt and unburnt vegetation may benefit species that move between fire age-classes to obtain different resources (e.g. shelter, food) (Buchalski et al., 2013; Doumas and Koprowski, 2013b). Unburnt patches within the landscape may act as refuges for species which otherwise are eliminated from, or are scarce in, severely burnt areas (Robinson et al., 2013). The extent and proximity of refuges may influence the rate of population recovery at severely burned sites (Bradstock et al., 2005; Robinson et al., 2013).

Environmental attributes, such as topographic variation in soils and moisture, also influence landscape heterogeneity and may mitigate the effects of fire by enabling survival of animals during or after a fire event (Bradstock et al., 2010; Garvey et al., 2010; Leonard et al., 2014). Understanding the effects of the fire regime and environmental attributes on mammal species at multiple scales can improve ecological knowledge of species responses, and is valuable for applied management.

Here, we examine the effects of an extensive wildfire on the occurrence of native terrestrial mammals in foothill eucalypt forests of south-eastern Australia. These are some of the most fire-prone forests worldwide (Adams and Attiwill, 2011). We surveyed the mammal assemblage 2–3 years after wildfire, at sites stratified in relation to two components of the fire regime, fire severity and fire history (interval since last fire). The overall aim was to test the relative influence on native mammals of components of the fire

regime operating: (a) at the site-level (i.e. site specific wildfire severity and fire history); and (b) at the landscape-level (i.e. amount of unburnt forest and heterogeneity of fire severity within the surrounding landscape). We predicted that site level effects, particularly wildfire severity, would be the primary influence on the distribution of mammal species; but that landscape context would also influence the occurrence of species, in particular via unburnt forest functioning as a refuge and providing a source of colonising individuals for nearby burnt sites.

2. Methods

2.1. Study area

The study was based in the foothills of the central highlands of Victoria, Australia (Fig. 1), where elevation ranges from ~150 to 1000 m. The climate is temperate with cool winters (mean monthly minimum 4 °C) and mild summers (mean monthly maximum 23 °C), and a mean annual rainfall of ~1200 mm (BOM, 2013). From 1997 to 2009, a severe drought occurred in south-eastern Australia (van Dijk et al., 2013). The drought broke in 2010, with above-average annual rainfall recorded in both 2010 and 2011 (BOM, 2013). These rainfall events formed part of the wettest years on record in south-eastern Australia (Chowdhury et al., 2015), and were associated with an extreme La Niña that had impacts globally (Heffernan, 2013).

Vegetation of the foothills comprises eucalypt forest (~25–35 m canopy height) dominated by messmate stringybark (*Eucalyptus obliqua*), narrow and broad-leaf peppermint (*Eucalyptus dives* and *Eucalyptus radiata*) and blue gum (*Eucalyptus globulus*) in moist gullies. The mid-storey contains species such as blackwood (*Acacia melanoxylon*), silver wattle (*Acacia dealbata*), prickly tea-tree (*Leptospermum continentale*) and prickly currant-bush (*Coprosma quadrifida*). The ground layer has sparse to dense cover of austral bracken (*Pteridium esculentum*), and a variety of grasses and herbs, particularly tall rush (*Juncus procerus*) and wattle mat rush (*Lomandra filiformis*). Moist gullies typically include an understorey of rough tree-fern (*Cyathea australis*), common understorey-fern (*Calochlaena dubia*), and musk daisybush (*Olearia argophylla*).

On the 7th February 2009 ('Black Saturday'), two intense wildfires joined to form the Kilmore–Murrindindi fire complex, which burned ~228,000 ha of forest through the study area. Less than 1% of forest within the fire boundary remained as unburnt patches (Leonard et al., 2014).

2.2. Site selection

A series of study sites were selected across the Kilmore East–Murrindindi fire complex, primarily in reserves or national parks. Sites were stratified in relation to two main attributes: the severity of the 2009 wildfire (i.e. unburnt, understorey burnt, severely burnt) (see Table 1 for descriptions); and fire history before the 2009 wildfire (i.e. unburnt >20 years prior to 2009, burnt within 3 years prior to 2009). Unburnt reference sites outside but near the fire boundary were also selected. Trees in these foothill eucalypt forests generally are not killed by high severity fire, but are able to regenerate via epicormic growth. The set of 80 sites represented eight combinations of fire severity and fire history, with 4–12 replicates of each (Fig. 1). Sites were selected by using aerial photography and fire severity layers from the Department of Sustainability and Environment within a Geographic Information System (GIS); and then examined in the field to ground-truth fire severity and fire history. Each site comprised a 5 ha stand of forest of consistent fire severity, which included a gully and adjacent slope (~100 m apart). Sites were at least 100 m from forest patches

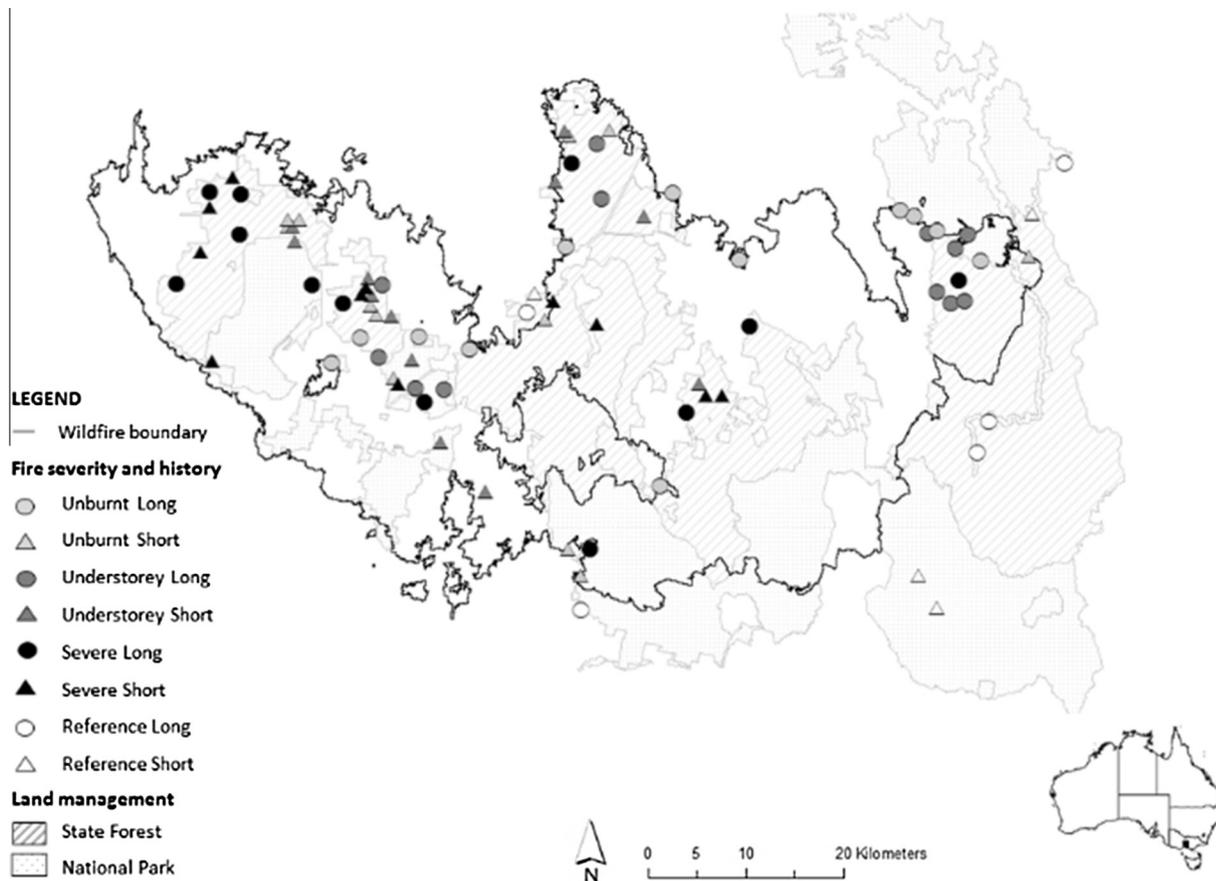


Fig. 1. Location of study area within the Kilmore–Murrindindi fire complex in south-east Australia. Sites were stratified by fire severity and fire history, and situated in reserves and national parks.

Table 1
Description of predictor variables used in models; GLMMS tested the relative influence of fire severity, fire history, and landscape-level variables on response variables of individual native mammal species. The first level for each categorical variable was treated as the reference level.

Variable	Site/landscape level	Variable description	Level	Level description
Severity	Site	Fire severity of forest within boundary of 2009 wildfire	Unburnt	Unburnt forest
			Understorey	Understorey and/or ground burnt
			Severe	Canopy scorched or canopy completely burnt
			Reference	Unburnt and located outside the wildfire boundary
History	Site	Fire interval before 2009	Long	Unburnt ≥ 20 years before wildfire
			Short	Burnt ≤ 3 years before wildfire
Landscape unburnt area ^a	Landscape	Unburnt forest in surrounding landscape	Continuous	Area of unburnt forest within a 1 km radius of site (ha)
Heterogeneity ^b	Landscape	Heterogeneity of fire severity in surrounding landscape	Continuous	Heterogeneity of fire severity classes within 1 km radius of site, calculated by Shannon's diversity index
Waterways ^c	Landscape	Waterways in surrounding landscape	Continuous	Total length of waterways within a 1 km radius of site (m)
Reserve	NA	Geographic location of sites based on land management	NA	Random effect
Season	NA	Surveys undertaken in three seasons: Summer, Autumn, Winter	NA	Random effect

^a Log transformed for the mountain brushtail possum.

^b Log transformed for the agile antechinus, bush rat, swamp wallaby and mountain brushtail possum.

^c Log transformed for the bush rat.

with different severities, and from roads. Sites disturbed by logging in the last 50 years were excluded.

2.3. Fauna surveys and species identification

Surveys were conducted from January–August 2011 using remote sensor cameras (Scout Guard 550, ScoutGuard IR Cameras,

Australia). Each study site was surveyed on a single occasion to gain a “snapshot” of mammal abundance at ~ 2 –3 years post-wildfire. In any given survey round (total = 9), sites were carefully chosen to include different combinations of fire severity and history. Six cameras were set at each site: three in a gully at 0 m, 100 m, and 200 m along a transect; and similarly, three along a parallel transect on the adjacent slope (~ 100 m from the gully

transect). On each transect, two cameras targeted small native mammals and were set facing downwards on steel posts from a height of 1.3 m (De Bondi et al., 2010). The third camera targeted larger native and introduced mammals, faced outwards, and was set on an aluminium post at 0.5 m height. Cameras were activated by motion sensors and used an infrared flash to take three photos within six seconds (30 s delay).

Camera plots were baited with scented lures, placed inside a section of PVC pipe with steel mesh ('cowl vent'), and pegged to the ground at a measured distance within the camera's field of view. Lures for small native mammals contained peanut butter, honey, peanut oil, vanilla essence and truffle oil; and for larger mammals, tuna and truffle oils, and were soaked into absorbent cloth (Paulu et al., 2011). Vegetation within the camera's field of view was removed to reduce false triggers (all for downwards-facing cameras, and within 2 m for outwards-facing cameras), and cameras were set for 14 consecutive nights.

For all photos of animal 'captures', the site, location, time and date were recorded. We identified species with the aid of reference photos from the study area and a field guide (Menkhorst and Knight, 2010). Important characteristics for species identification included body size, head-body and tail length ratios (using the bait holder as a known size reference), the presence of fur on tail and feet. A selection of 50 photos, comprising the range of species encountered, was checked by scientists with extensive experience in identifying mammals. Inconsistencies primarily related to small mammal species (i.e. agile antechinus *Antechinus agilis* and house mouse *Mus musculus*), and so we re-examined photos of all small mammal species to confirm identification. Any photos with persistent ambiguity were excluded from analysis.

2.4. Statistical analyses

2.4.1. Detection probability

Detection probability was calculated for each species to help distinguish true absence at a site from a lack of detection (i.e. false absence). Data for both gully and slope transects were combined. We used a single season occupancy model at the site level to calculate detection probability; and assumed constant detection, constant occupancy and independence of sites (MacKenzie et al., 2006). The minimum number of survey nights (N) required to detect a true absence was estimated by:

$$N = \frac{\log_{10}(1 - \frac{a}{100})}{\log_{10}(1 - p)}$$

where (a) is the level of confidence and (p) the detection probability (Kery, 2002). The detection probability was calculated with the 'Unmarked' package (Fiske et al., 2013) in the R statistical program 3.02 (R Development Core Team, 2014). We calculated the minimum number of nights required for 80%, 90% and 95% confidence intervals to indicate whether a lack of detection was likely to be a true absence.

2.4.2. Response and predictor variables

We used regression modelling to examine the relative influence of site and landscape-level attributes on the occurrence of native terrestrial mammals. Eight species for which sufficient data were obtained were used as response variables. Data for the two transects at a site were combined. We defined the 'recording rate' as the proportion of total camera nights (max. = 84; i.e. 6 cameras per site by 14 nights = 84 camera-nights) on which a species was recorded at a site. On average, there were 76 (91%) of a possible 84 camera/nights per site, across the 80 sites (lower values typically resulted from camera failure). Both outwards and downwards

facing cameras were used for analysis of native mammal occurrence.

We selected five variables representing fire regime and landscape context as predictors likely to influence the distribution and abundance of terrestrial mammals (Table 1). Fire severity (i.e. unburnt, understorey-only burnt, severely burnt, reference), and fire history (i.e. long, short) were categorical variables (Table 1). Three continuous variables were used to represent the landscape within a 1 km radius of each site: (1) the heterogeneity of fire severity classes; (2) the total area of unburnt forest; and (3) and the total length of waterways. Waterways represent the extent of topographic variation and gully systems in the surrounding landscape. These landscape variables were extracted in a GIS. Heterogeneity in fire severity was calculated with Shannon's diversity index based on four severity classes: unburnt, understorey burn, crown scorch (both understorey burnt and canopy scorched) and crown burn (understorey and canopy completely burnt). A fire severity GIS layer from the Department of Environment, Land, Water and Planning was used to determine the levels of fire severity, whilst unburnt patches of forest were mapped with aerial photography.

We checked for collinearity between continuous predictor variables with Spearman's rank correlation; all correlation coefficients were <0.22. Continuous predictor variables were centred and scaled (subtracting the mean from each observation and dividing by the standard deviation) to allow direct comparison of variable coefficients. Linear relationships between continuous predictor variables and response variables were checked by using scatterplots, and by comparing models with and without transformed predictor variables (by using Akaike's Information Criterion (AIC)). If there was support for improved linearity with a transformation, then the transformed variable was used (Table 1).

2.4.3. Model selection

We used generalized linear mixed models to test the relationship of response variables to predictor variables. This modelling approach facilitates the inclusion of random effects to account for non-independent error structures (Zuur et al., 2009). Here, sites were grouped based on their geographic location (i.e. into one of nine 'reserves'), and the time of year in which the survey was conducted (three 'seasons'). Consequently, two variables, 'reserve' and 'season', were included in models as random effects to account for potential spatial and temporal correlation (Table 1). Since the response variables represent proportions, a proportional binomial distribution using a log-link function was employed in all cases.

We used an information theoretic approach to compare a set of competing hypotheses (A.1). Eight models were built for each species, with combinations of predictor variables and interactions (A.1) selected based on ecological knowledge (Burnham and Anderson, 2002). Models within a set were ranked and compared by using AIC corrected for small sample size (AICc). Differences in AICc ($\Delta AICc$) were calculated, as were Akaike weights (w_i). Models with $\Delta AICc < 2$ were considered to have substantial support. If there was no single best model (i.e. all AICc weights < 0.90), model averaging was performed on all models for which $\Delta AICc < 6$ because these models have some support (Burnham et al., 2011). Model-averaged coefficients and standard errors were estimated for each parameter, and coefficients were defined as important if the 95% confidence interval did not cross zero (i.e. if $z < -1.96$ or $z > 1.96$) (Burnham and Anderson, 2002). We also considered parameters to have some influence ('trend') at the 90% confidence interval (i.e. if $z < -1.645$ or $z > 1.645$) to avoid an underestimate of fire effects, which can be difficult to detect for faunal species conducted over smaller time scales or samples (Smith et al., 2013). The global model was assessed for overdispersion for all response variables and, where present, an additional observation-level random term was added to all eight

models in the set to account for additional variance (Zuur et al., 2012). Residuals from global models were also inspected to ensure adequate fit. A measure of the variance explained by models was determined by calculating the marginal R^2 (i.e. from fixed predictor variables) and the conditional R^2 (i.e. from fixed and random effects) (Nakagawa and Schielzeth, 2013). After model averaging, predictions were generated from models (GLMM) that only included variables that were identified as influential.

Statistical analyses were conducted in the R statistical package 3.1.1 (R Development Core Team, 2014). GLMMs were run using the 'lme4' package (Bates et al., 2014) while model averaging was performed using the 'MuMIn' package (Bartoń, 2014). Model predictions were generated with the 'AICcmodavg' (Mazerolle, 2014) and 'boot' (Canty and Ripley, 2014) packages. R^2 values were calculated with the 'rsquared.glm' function (Lefcheck and Casallas, 2014).

3. Results

3.1. Species recorded and detection probability

From January–August 2011 we surveyed a total of 6084 camera trap-nights. From this effort, 13 species of native mammals were detected, eight of these were examined further (Table 2). Five species (mostly arboreal) were detected at fewer than seven sites (<9%) and were excluded from analyses. These included the common brushtail possum (*Trichosurus vulpecula*) recorded at 6 sites (8%), the koala (*Phascolarctos cinereus*) detected at 2 sites (3%), whilst the remaining three species were rare and were only at one site each (1%) (i.e. common ringtail possum (*Pseudocheirus peregrinus*), brush-tailed phascogale (*Phascogale tapoatafa*), and dusky antechinus (*Antechinus swainsonii*). Of the remaining eight species, six had high detection probabilities, with 14 survey nights being sufficient to have >80% confidence that lack of detection was a true absence at a site (Table 2). Two smaller sized mammal species were widespread in the post-fire environment, agile antechinus was recorded at 41 sites (51%) and bush rat (*Rattus fuscipes*) at 57 sites (71%). The other two small mammal species were less common; the long-nosed bandicoot (*Perameles nasuta*) was detected at 9 sites (11%), and echidna (*Tachyglossus aculeatus*) at 20 sites (25%). The semi-arboreal mountain brushtail possum (*Trichosurus cunninghami*) was detected at 31 sites (39%). Two of the medium-large sized mammal species were the most common out of all the mammal species including the common wombat (*Vombatus ursinus*) at 59 sites (74%) and swamp wallaby (*Wallabia bicolor*) at 72 sites (90%). The largest species, the eastern grey kangaroo (*Macropus giganteus*) occurred at one third of all sites (28 sites; 35%). Despite lower detection probabilities (Table 2), the long-nosed bandicoot and short-beaked echidna were also included in analyses.

3.2. Relative influence of site and landscape-level variables

Seven of the eight species analysed were recorded in all site-level fire severity classes; except for the long-nosed bandicoot which was not detected in reference sites.

The agile antechinus and bush rat, two of the most common small mammal species, were the only species to be influenced by fire severity and fire history at the site-level, and by landscape-level variables (Table 3). For the agile antechinus, the only model to have substantial support ($\Delta AICc < 2$) included all five variables at both the site-level and landscape-level (Table 3). The Akaike weight for this model was <0.9, and therefore we conducted model averaging. Three variables were influential (95% confidence intervals of estimates did not overlap zero): fire severity (site-level), fire history (site-level) and the area of surrounding unburnt forest in

the landscape (landscape-level) (Fig. 2). The recording rate of the agile antechinus was lower at sites exposed to an understorey burn compared with unburnt sites (Fig. 3). Recording rates were higher at sites with a short fire interval (<3 years) than a long fire interval (≥ 20 years; Fig. 3), and lower at sites surrounded by more unburnt forest (Fig. 2). Additionally, there was a trend (coefficients did not cross zero at the 90% confidence interval) for a lower recording rate at severely burnt compared with unburnt sites (Fig. 2).

For the bush rat, four models had substantial support in explaining the recording rate (Table 3). Model averaging revealed the recording rate of the bush rat to be influenced by three variables: fire severity (site-level), fire history (site-level), and length of waterways in the surrounding landscape (landscape-level) (Fig. 2). The recording rate was higher at sites that were severely burnt in the wildfire than at unburnt sites, lower at sites with a short fire interval than a long fire interval (Fig. 3), and there was a negative relationship with the length of waterways in the surrounding landscape (Fig. 2).

In contrast to the smaller mammal species, the three medium-large sized species were less influenced by fire severity and history at the site-level, and none were influenced by any landscape-level variable. For the common wombat and eastern grey kangaroo, the null model had the most support for explaining the recording rate of both these species, indicating that neither site nor landscape-level variables influenced these species (Table 3). Model averaging confirmed this result, with no evidence of a strong influence of any variable on the recording rate of common wombat or kangaroo (Fig. 2). However, for the common wombat there was a trend (coefficients did not cross zero at the 90% confidence interval) for an influence of fire severity at the site-level, with lower recording rate at severely burnt compared with unburnt sites (Figs. 2 and 3). Unlike the previous two species, the swamp wallaby was influenced by site-level fire regime components. There was initial support from three models ($\Delta AICc < 2$) (Table 3). After model averaging, the recording rate of the swamp wallaby was influenced by the fire severity and history interaction (Fig. 2). There was a higher recording rate at sites that were severely burnt with a long fire history (not burnt for >20 years before wildfire), than at unburnt sites with a long fire history (Fig. 3).

For the only semi-arboreal species, the mountain brushtail possum, two models had support: the null model and the model of an interaction between fire severity and history (Table 3). Results of model averaging showed no influence of any variable at the 95% CI (i.e. 95% confidence intervals overlap zero). However, there was a trend (important at the 90% confidence interval) for an influence of fire severity and the interaction between severity and history; indicating a lower recording rate at severely burnt sites with a long fire history (>20 years) compared with unburnt sites with a long fire history.

For the final two species, the long-nosed bandicoot and echidna, there were mixed responses. The recording rate for the long-nosed bandicoot was accounted for by a single 'best' model (i.e. AIC weight > 0.9) which included fire severity plus fire history at sites (Table 3). The recording rate was higher in severely burnt compared with unburnt sites (estimate = 2.30, SE = 1.13, $z = 2.03$), and greater in sites with a short fire interval (<3 years) than a long fire interval (estimate = 2.72, SE = 1.09, $z = 2.51$). The recording rate of echidna did not respond to any of the fire regime and landscape-level components examined, as the single best model with support (Akaike weight > 0.9) was the null model (Table 3).

4. Discussion

Understanding how fire regimes influence fauna at different scales can improve ecological knowledge for fire management

Table 2

Species recorded during camera surveys, the number of sites at which they were detected, and the number of survey nights required for 80%, 90% and 95% confidence intervals. The number of nights was rounded up to the nearest integer.

Scientific name	Number of sites present	Detection probability (<i>P</i>)	SE (<i>P</i>)	Number of nights for 80%CI (1.96SE)	Number of nights for 90%CI (1.96SE)	Number of nights for 95%CI (1.96SE)
<i>Antechinus agilis</i>	41	0.21	0.02	3 (2.62–3.27)	5 (3.74–4.68)	6 (4.87–6.09)
<i>Rattus fuscipes</i>	57	0.42	0.02	3 (2.91–3.26)	5 (3.75–4.67)	6 (4.88–6.07)
<i>Vombatus ursinus</i>	59	0.08	0.01	10 (7.94–10.63)	14 (11.35–15.22)	17 (14.78–19.80)
<i>Wallabia bicolor</i>	72	0.35	0.02	4 (3.36–4.15)	6 (4.80–5.94)	7 (6.25–7.73)
<i>Macropus giganteus</i>	28	0.13	0.02	12 (8.61–16.38)	17 (12.32–23.43)	22 (16.03–30.49)
<i>Trichosurus cunninghami</i>	31	0.18	0.02	9 (6.61–10.85)	12 (9.45–15.53)	16 (12.30–20.20)
<i>Perameles nasuta</i> ^a	9	0.10	0.03	16 (9.36–46.44)	23 (13.39–66.43)	30 (17.43–86.44)
<i>Tachyglossus aculeatus</i> ^a	20	0.05	0.02	33 (19.10–106.69)	47 (27.32–152.64)	62 (35.54–198.59)

^a Species with insufficient detection probability for 80% confidence intervals.

Table 3

Models with substantial support ($\Delta AIC < 2$) out of the model set for each response variable (individual mammal species). Model structures are shown with corresponding df, Log likelihood, AICc, the difference in AICc from the best model (ΔAIC) and the Akaike weight. Model fit is represented by R^2m – the variance from fixed predictors, and R^2c – the variance explained by both fixed and random predictors.

Response variable	Model structure	df	Log likelihood	AICc	$\Delta AICc$	Akaike weight	R^2m	R^2c
<i>Antechinus agilis</i>	Severity + History + Landscape unburnt area + Heterogeneity + Water	11	–128.66	283.2	0	0.60	0.15	0.44
<i>Rattus fuscipes</i>	Severity + Landscape unburnt area + Heterogeneity + Water	10	–219.63	462.4	0	0.35	0.12	0.29
	Severity + History	8	–222.48	463.0	0.55	0.27	0.09	0.19
	Severity	7	–224.04	463.6	1.20	0.19	0.08	0.21
	Severity + History + Landscape unburnt area + Heterogeneity + Water	11	–219.09	464.1	1.63	0.16	0.12	0.26
<i>Vombatus ursinus</i>	Null model	4	–164.66	337.9	0	0.71	0	0.17
<i>Wallabia bicolor</i>	Severity	7	–218.85	453.3	0	0.36	0.03	0.03
	Null model	4	–222.41	453.4	0.1	0.35	0	0.04
	Severity + History	8	–218.20	454.4	1.17	0.20	0.03	0.03
<i>Macropus giganteus</i>	Null model	4	–94.36	197.3	0	0.75	0	0.11
<i>Trichosurus cunninghami</i>	Null model	4	–115.25	239.0	0	0.55	0	0.003
	Severity * History	11	–107.33	240.5	1.51	0.26	0.55	0.57
<i>Perameles nasuta</i> [*]	Severity + History	7	–31.68	78.9	0	0.94	0.89	0.91
<i>Tachyglossus aculeatus</i> [*]	Null model	3	–53.90	114.1	0	0.90	0	0.29

^{*} Species with insufficient detection probability for 80% confidence intervals.

(Driscoll et al., 2010; Di Stefano et al., 2011). In the aftermath of a severe wildfire, we had a unique opportunity to investigate how native terrestrial mammals were influenced by fire-regime components at multiple scales, in one of the most fire-prone forests in the world. At 2–3 years post-fire, fire effects at the site-level exerted more influence on the occurrence of terrestrial mammal species than did fire effects at the landscape-level. Fire severity, an important component of the fire regime, was more influential than any other variable examined. Different species responded to the post-wildfire environment in different ways. Surprisingly, there was little evidence of wildfire having an effect at the landscape-level, suggesting either survival *in situ*, or rapid recolonization of the burnt forest environment from unburnt refuges (see below).

4.1. Fire regime effects at the site-level

Different species responded differently to fire severity, consistent with other studies (e.g. Buchalski et al., 2013; Dumas and Koprowski, 2013a; Fontaine and Kennedy, 2012; Roberts et al., 2008; Robinson et al., 2014; Smucker et al., 2005). The response of species to fire severity can be related to the way in which fire affects the availability of resources, such as vegetation, food and shelter (Catling et al., 2001; Sutherland and Dickman, 1999). Positive relationships of species to fire severity, as shown for the bush rat and long-nosed bandicoot, are likely a consequence of the rapid and dense regeneration of vegetation that occurred shortly after

the wildfire, associated with above-average rainfall in both 2010 and 2011. In particular, there was mass regeneration of eucalypts and shrubs (e.g. Hop goodenia *Goodenia ovata*), resulting in dense cover below 1.5 m height, which provided shelter for many mammal species. The bush rat is often associated with dense understorey (Holland and Bennett, 2007); whilst the long-nosed bandicoot is linked with dense understorey for nesting and open areas for foraging (Chambers and Dickman, 2002), both of which were available in the post-fire environment. Other studies have also shown fauna to respond to regeneration of vegetation after fire: for example, the long-nosed bandicoot and southern brown bandicoot (*Isodon obesulus*) were both associated with regrowth of shrub cover after wildfire in heathland (Arthur et al., 2012). The rapid regeneration of ground and shrub vegetation at burnt sites appears to diminish any adverse effects of high fire severity within just a few years post-fire, at least for some terrestrial species.

Animal species may also be negatively influenced by the effects of fire severity on the post-fire environment. There was a lower recording rate for the agile antechinus in understorey burnt compared with unburnt sites, and also a trend for a lower recording rate at severely burnt sites. These negative effects of fire likely reflect the reduced availability of habitat components at ground-level for this species, including food resources such as ground-invertebrates and a reduction in habitat structural components such as logs (Bassett et al., 2015). The agile antechinus was simi-

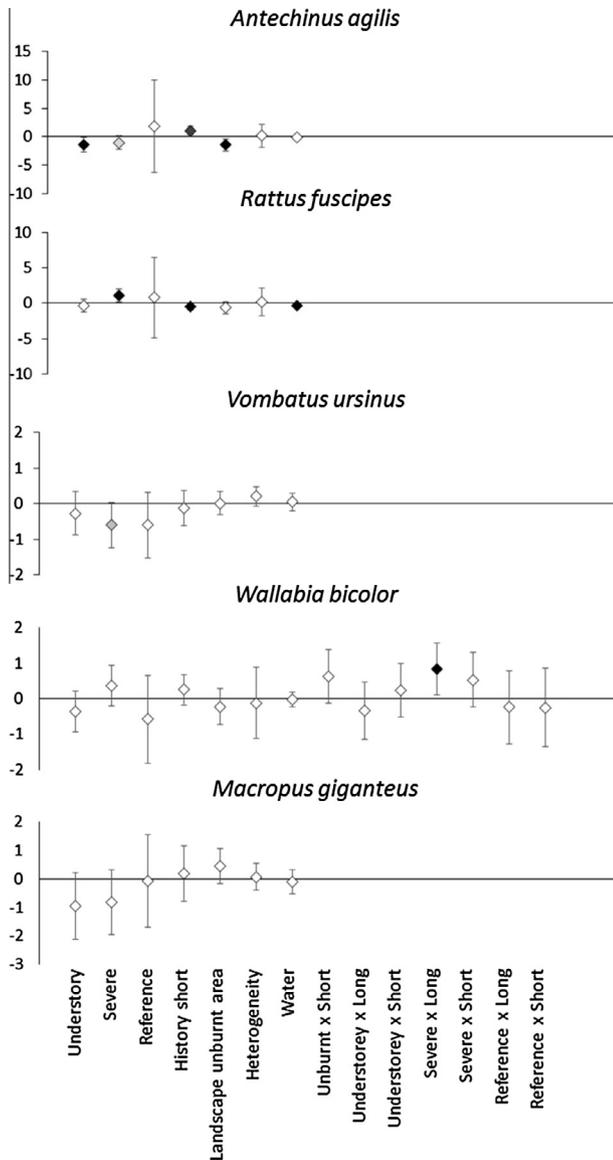


Fig. 2. Model-averaged estimates and associated confidence intervals of predictor variables for five mammal species. The reference category includes sites with an unburnt fire severity and long fire history (>20 years). Parameters are considered to be important if confidence intervals do not cross zero at the 95% confidence interval (black diamonds), and to have some influence ('trend') at the 90% confidence intervals (grey diamonds).

larly negatively affected by wildfire in nearby wet montane forest (Banks et al., 2011).

Different subsets of animal species rely on different strata of the forest vegetation, and hence respond differently to fire severity. Arboreal mammals were more negatively affected by high fire severity, with their abundance in severely burned forest related to the extent of nearby unburnt or lightly burnt forest (Chia et al., 2015). For these species, unburnt areas appear to serve as refuges that assist recolonization into the forest as it recovers after wildfire. Although other studies have found unburnt refuges to assist in recolonization (Lunney et al., 2008; Recher et al., 2009), there was little evidence that this is the case for terrestrial mammals in this study, at least at this stage in the post-fire succession, as species occurred at sites in all categories of fire severity and their occurrence at burnt sites did not depend on the amount of nearby unburnt forest. The rapid regeneration of vegetation in ground and shrub layers provides shelter and cover for terrestrial

mammals, allowing them to occupy sites that were blackened and bare of living vegetation immediately after the wildfire.

Fire history at a site did not appear to have a consistent influence on native mammal species, with different mammal species responding differently to fire history. Frequent fire can inhibit the re-growth of appropriate habitat for some species (Hobbs, 2002) and multiple, low intensity burns can reduce structural complexity (Gill and Catling, 2002). In this study, however, the effects of fire severity in the 2009 wildfire combined with rapid regeneration of vegetation after above-average, drought-breaking rainfall, apparently overrode the effect of previous fire history on vegetation structure for most species. Fire history is likely to have greatest influence on species that depend on structural features that can be markedly depleted by fire, such as dead trees, logs and tree hollows (Haslem et al., 2011).

4.2. Fire regime effects at the landscape-level

Contrary to our predictions, the landscape context of a site did not have a strong effect on the recording rate of mammal species. Only two out of eight mammal species, the agile antechinus and bush rat, were influenced by a landscape context variable. Surprisingly, unburnt forest in the surrounding landscape did not appear to have large influence on the occurrence of any mammal species. We anticipated that unburnt patches of vegetation might act as refuges for fauna in the post-fire environment, and that their spatial configuration and degree of isolation might influence species recovery after fire (Robinson et al., 2013). However, our results show, at least for those species for which there were sufficient data for analysis, that at 2–3 years post fire in this study most terrestrial mammals do not rely on unburnt forest patches as refuges.

The limited influence of fire heterogeneity at the landscape-level is likely for two reasons. First, the widespread occurrence of most species across all fire severity classes at 2–3 years post fire may be a consequence of survival of sufficient individuals *in situ*, even though some sites were severely burnt and isolated from unburnt sites. *In situ* survival of small mammal species was proposed for wet montane forests after this same wildfire (Banks et al., 2011), facilitated by retreating to micro-refuges during or after the fire, such as wombat burrows, large unburnt moist logs, adjacent moist gullies, or floodplains (Lunney et al., 2008; Banks et al., 2011; Bradstock et al., 2005; Garvey et al., 2010). Second, the limited effects of fire-induced landscape heterogeneity may be associated with rapid regeneration of vegetation in the first three years post-fire, allowing rapid re-occupation of burnt areas. Individuals may have survived in unburnt sites during or immediately after the wildfire, and then emigrated to nearby burnt sites as vegetation cover rapidly re-established (Fox, 1982). For example, species that have high mobility and generalist habitat requirements are able to access multiple habitat patches affected by different fire severities (Pastro et al., 2011; Whelan et al., 2002). For such species, rapid regeneration of ground cover provides suitable habitat, and also facilitates dispersal and recolonization across the landscape after fire.

4.3. Implications for management and conservation

Our results highlight three main points relevant to management and conservation. First, fire severity is a particularly important component of the fire regime, with different effects on different species. A single fire regime is not appropriate for all species. The spatial variation in fire severity associated with a major wildfire (from unburnt to severely burned stands) is an important contributor to the post-fire status of species, and warrants inclusion in studies that attempt to understand fire effects on terrestrial mammals in other fire-prone systems. Second, post-fire environ-

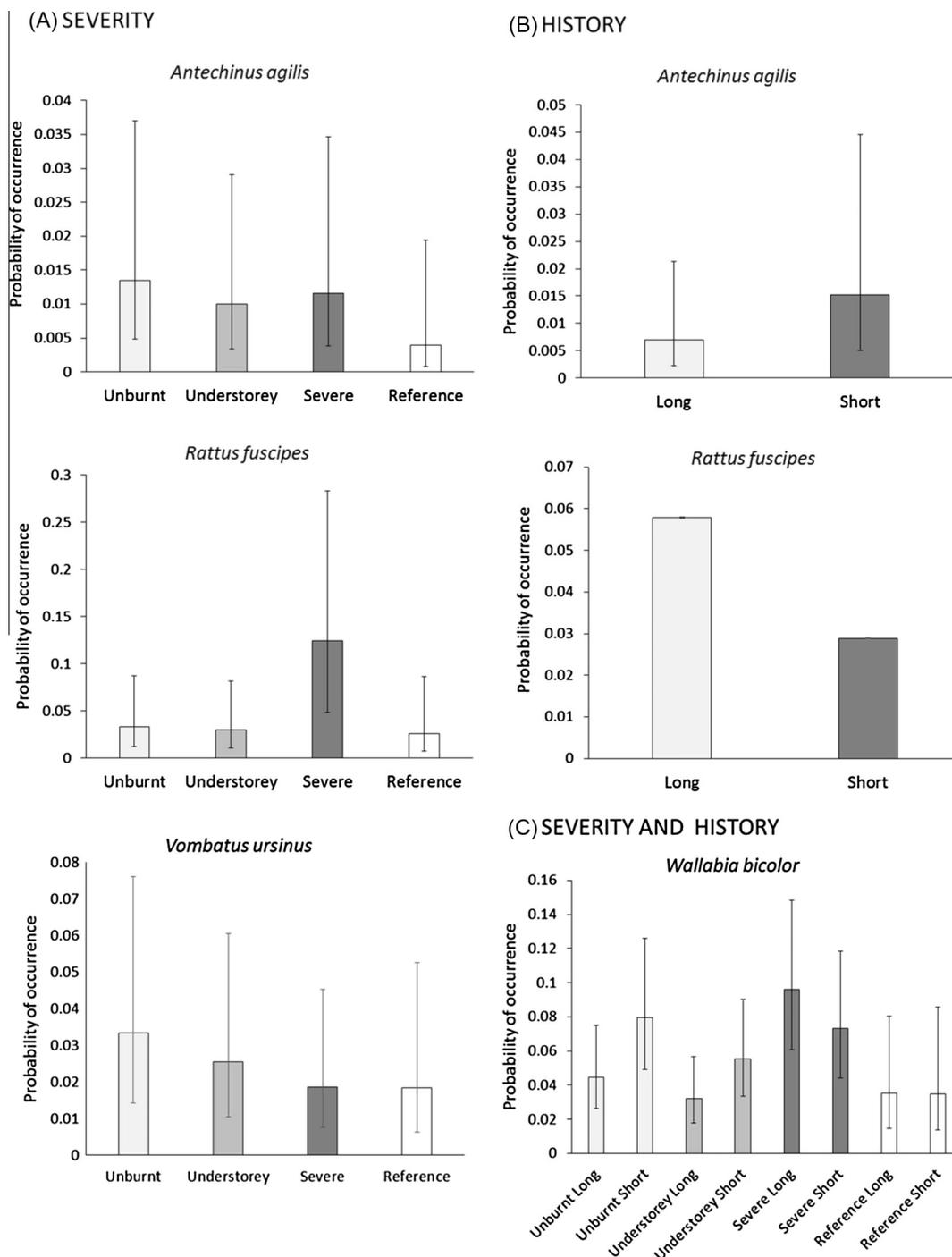


Fig. 3. The predicted values and 95% confidence intervals generated from fire-regime variables considered to be an important influence for mammal species, and 90% CI for one species, the common wombat. Bars represent the probability of recording a species at a site for (a) fire severity for the agile antechinus, bush rat and common wombat, (b) fire history for agile antechinus and bush rat, and (c) the interaction between fire severity and fire history for the swamp wallaby.

mental conditions must be considered. In this case, above-average, drought-breaking rains following the wildfire and the subsequent rapid regeneration of vegetation highlighted the importance of the interaction between fire regime and environmental conditions. If the drought had continued, it is likely a more severe post-fire outcome would have eventuated including delayed recoveries (Lunney et al., 1987; Recher et al., 2009). In harsh climatic conditions after wildfire, such as drought, it is likely that refuges of high quality habitat (e.g. unburnt patches, moist gullies) will be valuable for fire-sensitive fauna and a conservative approach that pro-

ducts such areas in the landscape will be beneficial. Third, there is value in examining the effects of fire regimes across multiple scales, including both the site scale and the wider landscape. Although landscape-scale effects were limited for terrestrial mammals in this study, landscape context was important for the occurrence of arboreal mammals (Chia et al., 2015) at a subset of these same sites. Finally, this study was a ‘snapshot’ of the occurrence of species at 2–3 years post-fire, and could be complemented with longitudinal studies that track changes in the biota from immediately after fire, through the post-fire succession.

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Appendix A.

A1. Model set selected for each response variable (i.e. individual mammal species). Models in the set contained different combinations of predictor variables fitted to each response variable with GLMM. All models included “reserve” and “season” as random effects. An additional random effect “Site” (observation level effect) was included for response variables when models were overdispersed.

Model set
 Null model
 Severity
 Severity + History
 Severity * History
 Severity + Landscape unburnt area + Heterogeneity
 + Waterways
 Severity + History + Landscape unburnt area + Heterogeneity
 + Waterways
 (Severity * History) + Landscape unburnt area
 + Heterogeneity + Waterways
 Landscape unburnt area + Heterogeneity + Waterways

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