Fire severity and fire-induced landscape heterogeneity affect arboreal mammals in fire-prone forests

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Abstract. In fire-prone regions, wildfire influences spatial and temporal patterns of landscape heterogeneity. The likely impacts of climate change on the frequency and intensity of wildfire highlights the importance of understanding how fire-induced heterogeneity may affect different components of the biota. Here, we examine the influence of wildfire, as an agent of landscape heterogeneity, on the distribution of arboreal mammals in fire-prone forests in south-eastern Australia. First, we used a stratified design to examine the role of topography, and the relative influence of fire severity and fire history, on the occurrence of arboreal mammals 2–3 years after wildfire. Second, we investigated the influence of landscape context on the occurrence of arboreal mammals at severely burnt sites. Forested gullies supported a higher abundance of arboreal mammals than slopes. Fire severity was the strongest influence, with abundance lower at severely burnt than unburnt sites. The occurrence of mammals at severely burned sites was influenced by landscape context: abundance increased with increasing amount of unburnt and understorey-only burnt forest within a 1 km radius. These results support the hypothesis that unburnt forest and moist gullies can serve as refuges for fauna in the post-fire environment and assist recolonization of severely burned forest. They highlight the importance of spatial heterogeneity created by wildfire and the need to incorporate spatial aspects of fire regimes (e.g., creation and protection of refuges) for fire management in fire-prone landscapes.

Key words: biodiversity; climate; dispersal; marsupial; metapopulation; refuge; wildfire.

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INTRODUCTION

Fire exerts a profound influence on the structure and function of ecosystems worldwide (Bond and Keeley 2005, Pausas et al. 2008). Fire-dependent ecosystems—those in which species have evolved in the presence of fire—encompass over 50% of the global terrestrial area and support a large proportion of the world's biota (Shlisky et al. 2007). In such ecosystems, large fires are a key influence on the creation and maintenance of landscape heterogeneity (Turner et al. 1994, Burton et al. 2008), with post-fire successional changes influencing vegetation

structure and biota for decades or even centuries (Schoennagel et al. 2008, Haslem et al. 2011). While many studies have investigated temporal changes in the occurrence and abundance of species in post-fire succession (e.g., Fox 1982, Briani et al. 2004, Kelly et al. 2011), less attention has been given to how fire-induced spatial heterogeneity, and the factors that determine such heterogeneity, affect the distribution of plant and animal species (but see e.g., Brotons et al. 2005, Fuhlendorf et al. 2006, Lindenmayer et al. 2013).

Landscape heterogeneity is influenced by multiple components of the fire regime (sensu Gill 1975), mediated by environmental variation (e.g., topography, climate; Noss et al. 2006, Bradstock et al. 2010, Mackey et al. 2012). Fire intensity, for example, varies within a fire boundary such that some patches of vegetation remain unburnt, some are burnt at low severity (e.g., understorey only is burnt), and others experience high severity fire (both understory and canopy are consumed; Burton et al. 2008, Schoennagel et al. 2008, Roman-Cuesta et al. 2009). In forested landscapes, these patterns are modified by topography: gullies and drainage lines are less likely to be severely burnt than slopes due to less flammable vegetation, protection from wind and higher moisture levels (Bradstock et al. 2010, Leonard et al. 2014, Berry et al. 2015a). Environmental variables that modify fire effects, such as topography or vegetation, can also influence resource availability (e.g., soil and water nutrients) which affects the distribution of biota (Soderquist and Mac Nally 2000, Keppel et al. 2012). The prior fire history of a landscape, such as the time since last fire, adds further complexity to spatial patterns (Turner et al. 1994, Avitabile et al. 2013).

Landscape heterogeneity from large fires influences the distribution of animal species in several ways. First, there may be a direct effect via mortality of species at different locations during, or shortly after, a major fire (Whelan et al. 2002). Second, indirect effects of fire on species distributions arise via spatial variation in the fire regime with consequent variation in the composition and structure of vegetation, which determine the availability of resources (shelter, refuge, foraging substrates) for species (Smucker et al. 2005, Fontaine et al. 2009, Nimmo et al. 2014).

Knowledge of the post-fire conservation status of species depends on understanding the relationship between the fire regime and occurrence of species across the landscape, and how this is moderated by environmental variation.

Third, landscape heterogeneity arising from large wildfires influences the spatial context of individual sites and the potential for species to persist or recolonize (Brotons et al. 2005, Watson et al. 2012, Lindenmayer et al. 2013). In particular, unburnt, or less severely burnt, vegetation may act as a refuge for fauna within large fires and have a strong influence on post-fire patterns of occurrence in the burnt landscape (Robinson et al. 2013). If such refuges do serve as a source for recolonization and faunal recovery, then the occurrence of species in burnt sites is likely to be influenced by the proximity and amount of unburnt vegetation. In contrast, if post-fire recovery is driven primarily by in situ survival rather than dispersal and recolonization (Banks et al. 2011a), then context effects are less likely.

Here, we examine the influence of wildfire, as a driver of landscape heterogeneity, on the distribution of arboreal mammals in fire-prone eucalypt forests in south-eastern Australia. These are among the most fire-prone forests in the world (Adams and Attiwill 2011). The limited evidence available, particularly from tall wet forests (e.g., Lindenmayer et al. 2013), suggests that arboreal mammals are particularly vulnerable to wildfire. This study was undertaken in the lower altitude foothill forests within the boundary of the Kilmore East-Murrindindi fire complex, an extensive wildfire which started on "Black Saturday," February 2009, and resulted in ~250,000 ha of forest being burnt, the loss of 1780 houses and tragically, 159 human fatalities (Teague et al. 2010).

The study had two main components. First, we used a stratified design to investigate the effect of topography, wildfire severity and fire history on the occurrence of arboreal mammals two years after wildfire. We predicted that (1) forest gullies would support a greater abundance of arboreal mammals than adjacent slopes and (2) fire severity would be the primary influence on mammal occurrence after fire, such that severely burnt sites would support fewer animals than unburnt or less severely burnt sites. Second, we investigated the influence of landscape context

on the occurrence of arboreal mammals in severely burnt forest, by selecting sites with different levels of spatial isolation from unburnt forest. We hypothesized that isolation would have a detrimental effect on arboreal mammals because (a) mortality from the fire event, or (b) a reduction in habitat suitability, would limit the rate of recolonization of isolated sites in severely burnt forest. Hence, we predicted (3) that the abundance of arboreal mammals in severely burned forest would increase as the amount of surrounding unburnt forest increased.

MATERIAL AND METHODS

Study area

The study was undertaken in temperate eucalypt forests of central Victoria, south-east Australia (Fig. 1). Elevation ranges from ~150 to 1000 m, and the topography is varied, including steep gully systems and gentle slopes and hills. The climate is temperate with mild summers (mean daily maximum and minimum temperatures of 25°C and 12°C, respectively) and cool winters (9°C and 4°C, respectively). Mean annual rainfall is ~1300 mm. From 1997 to 2009, prior to the wildfire, the region experienced an extended and severe drought (van Dijk et al. 2013). Subsequently, above-average rainfall occurred in both 2010 and 2011, to end the drought.

The study area is dominated by foothill forests of Messmate Stringybark (*Eucalyptus obliqua*) and Broad and Narrow-leaf Peppermint (*E. dives* and *E. radiata*), with a canopy height of 25–30 m. In contrast to montane ash eucalypt forest (dominated by *E. regnans* or *E. delegatensis*), in foothills forest the overwhelming majority of eucalypts survive even high intensity fire, regenerating from epicormic shoots (Benyon and Lane 2013). Lower slopes commonly have a mid-understorey of trees and shrubs such as Blackwood Wattle (*Acacia melanoxylon*), Prickly Tea-tree (*Leptospermum continentale*), and Prickly Currant-bush (*Coprosma quadrifida*). The understorey often contains Austral Bracken (*Pteridium esculentum*) and a mixture of grasses and herbs. In gullies, Blue Gum (*E. globulus*) occurs along with understory species that prefer moister conditions (e.g., Rough Tree-fern (*Cyathea australis*) and Common Understorey-fern (*Calochlaena dubia*).

Site selection

Sites were selected in the western part of the Kilmore East-Murrindindi fire complex, mostly in managed forests or national parks (Fig. 1). In the first component of the study ("fire regime study"), we examined the relative influence of fire severity, fire history and time since fire on arboreal mammals. We selected 24 sites, stratified to represent combinations of fire severity (unburnt, understorey burnt, severely burnt) and fire history (not burnt for >20 yr before 2009, burnt within 3 yr prior to 2009), with four replicates of each of the six combinations. Sites were located with a fire severity layer, aerial photography and fire records from the Department of Environment and Sustainability, in a Geographic Information System (GIS). After selection, sites were inspected to verify fire severity and history. Each site encompassed a 5-ha area of forest of the same fire severity, and included a gully and slope (~100 m apart). Sites disturbed by logging in the last 50 years (clearfell and selected logging) were excluded. Sites were at least 100 m from roads or areas of different fire severity.

In the second component of the study ("isolation study"), we investigated the effect of isolation on the occurrence of arboreal mammals in severely burnt forest. We chose 14 sites that were severely burnt (i.e., both understorey and canopy were scorched/burnt), located either close to (<1 km) or far from (2–5 km) patches of unburnt forest or forest with understorey-only burn. We calculated the total amount of unburnt forest and forest with understorey-only burnt within a radius of 1 km. All sites from both studies were at least 2 km apart.

Spotlight surveys

In the fire regime study, spotlight surveys were undertaken ~2.5 years post-wildfire, with four survey rounds completed at 28 sites from August to November 2011. Surveys were conducted by two people simultaneously at each site: one along a gully transect and one along the adjacent slope (at least 100 m apart), both within forest vegetation. Observers moved in the same direction, remaining in communication to avoid counting the same animal. Each transect was 200 m and was searched for 20 mins using a handheld LED spotlight (LED Lenser M14).

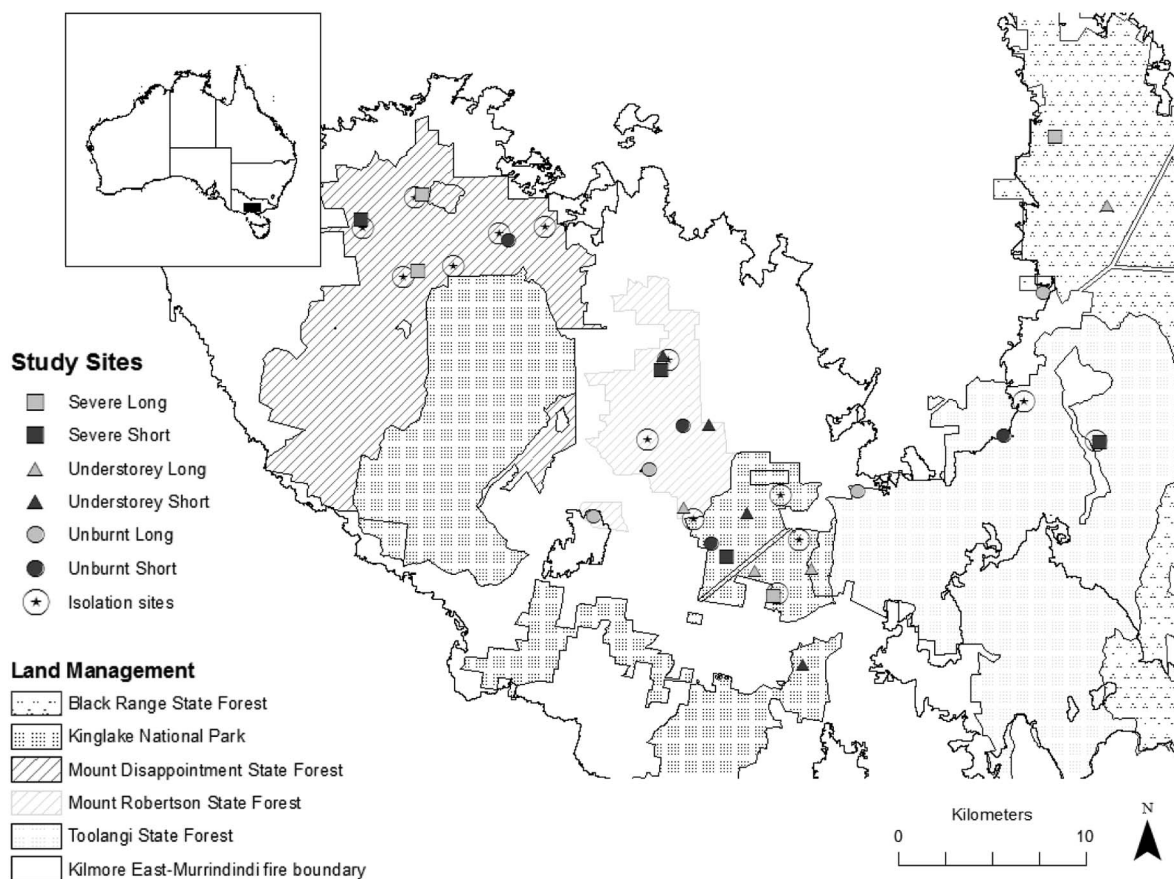For the isolation study, spotlight surveys were

Fig. 1. Location of study sites within the boundary of the Kilmore East-Murrindindi wildfire. For the "fire regime" study, sites were stratified by severity (unburnt, understorey-only burnt and severe) and fire history before the wildfire (long > 20 yr, or short < 3 yr). For the "isolation study," sites were in severely burnt forest and were surrounded by different amounts of unburnt and understorey-only burnt forest in a 1 km radius.

carried out ~3.5 years post-wildfire, with four survey rounds at 14 sites from August to November 2012. At each site, two observers simultaneously moved away (opposite directions) from the site midpoint, walking slowly along a forest track, searching the forest on both sides of the track along a 400 m transect (800 m in total) for 30 min. Observers used a handheld spotlight (50-watt, 12-V battery pack).

In each study, observers recorded all arboreal mammals seen or heard and the distance (with a rangefinder). Surveys commenced at least an hour after sunset (for animals to leave their dens) and nights with strong wind or rain were avoided.

Statistical analyses

Response and predictor variables.—We used regression modeling to examine: (1) the effects of topography (gullies and slopes) on the abundance of arboreal mammals; (2) the effect of fire severity, fire history and time since fire on the number of arboreal mammals seen or heard; and (3) the effect of isolation on the number of arboreal mammals recorded in severely burnt forest.

Response variables for the fire regime study included the total number of arboreal mammals and of the Greater Glider (*Petauroides volans*), and the species richness of arboreal mammals, over four surveys combined. For the isolation study, four response variables were included: total number of arboreal mammals, Greater Gliders

Table 1. Description of predictor variables used in the fire regime and isolation studies with the first level for each categorical variable used as the reference level.

Variable	Level	Description
Fire regime study		
Topography	Gully	Topographic location
	Slope	
Severity	Unburnt	Not burnt in 2009 wildfire
	Understorey	Ground and/or understorey burnt
	Severe	Canopy scorched or completely burnt
History	Long	Unburnt ≥20 yr before 2009 wildfire
	Short	Burnt ≤3 yr before 2009 wildfire
Time since fire	20 yr	> 20 yr since the last fire
	3 yr	<3 yr since the last fire
	0 yr	Burnt in the 2009 wildfires
Tree	Continuous	Number of large trees >60 cm diameter
Isolation study		
Area unburnt	Continuous	Area (ha) of unburnt forest within 1 km radius
Area understorey	Continuous	Area (ha) of unburnt and understorey burnt forest combined within 1 km radius
Tree	Continuous	Number of large trees >60 cm diameter
Reserve	NA	Geographic location of sites based on land management (random factor in all models)

and Common Ringtail Possums (*Pseudocheirus peregrinus*), and species richness, all over four surveys. Other species were not modeled due to insufficient records (i.e., less than 10 records per species).

Predictor variables for each component of the study are given in Table 1. We included the number of large trees as a measure of habitat suitability as these are more likely to contain hollows used as den sites by arboreal mammals (Gibbons and Lindenmayer 1997). For the fire regime study, we counted the number of large trees (diameter > 60 cm) on each gully and slope transect (100 × 20 m). A linear mixed model revealed no significant difference in the number of large trees between fire severity classes. For the isolation study, we counted large trees on four transects (10 × 50 m), all within severely burnt forest, on opposite sides of the road at even distances.

For the isolation study, continuous predictor variables were centered and scaled, by subtracting the mean from each observation and dividing by their standard deviations, to allow comparisons. Log transformation (with a constant of 0.001 added) of predictor variables was modeled if there was evidence of improved model fit (i.e., AIC > 2).

Model selection.—We used generalized linear mixed models (GLMM) to relate response variables to predictor variables, appropriate when response variables are not normally distributed and there is potential for temporal or spatial auto-correlation (Zuur et al. 2009). A Poisson distribution (for count data) and a log-link function were specified for all response variables. Site groups based on geographic location of reserves (reserve) were added as a random effect to account for spatial correlation (Table 1). If models were overdispersed (>1.5) using Pearson's residuals, an observation-level random effect was included to account for additional variance (Zuur et al. 2009).

We used model selection within an information theoretic framework to compare competing hypotheses on the relative effect of predictor variables on mammal response variables. A model set was chosen for each study component, based on conceivable ecological scenarios (see Appendix: Table A1; Burnham and Anderson 2002). Model structures were fitted to each response variable with GLMM. Models were ranked for model fit and complexity using Akaike's information criterion corrected for small sample size (AIC_c), differences in AIC_c (ΔAIC_c), and Akaike weights (w_i). All models with ΔAIC_c < 2 from the top model (lowest AIC) were considered to have substantial support (Burnham and Anderson 2002). Parameter estimates were examined for models with substantial support. Predictor variables were considered to have an important influence on the response variable if the 95% confidence interval for the parameter coefficient did not overlap with zero (i.e., $z < -1.96$ or $z > 1.96$; Burnham and Anderson 2002). If a predictor variable was

important, then model predictions were generated with the univariate model. Additional assumptions of models were checked by plotting the residuals of the predictor variables. R^2 was quantified as a measure of model fit for marginal (fixed factors) and conditional (fixed and random factors) values (Nakagawa and Schielzeth 2013).

All statistical analyses were conducted in the R statistical package version 3.1.1 (R Core Team 2014). GLMMs and predictions were run with lme4, MuMIn and AICcmodavg packages (Bartoń 2014, Bates et al. 2014, Mazerolle 2014). R^2 values were calculated with the rsquared.glmm function (Lefcheck and Casallas 2014).

RESULTS

Species recorded and topography

In the fire regime study, six species of arboreal mammal (all marsupials) were recorded: the Greater Glider was the most common (28 observations), then Mountain Brushtail Possum (*Trichosurus cunninghami*), Common Brushtail Possum (*T. vulpecula*), Common Ringtail Possum, Sugar Glider (*Petaurus breviceps*), and Koala (*Phascolarctos cinereus*; Appendix: Table A2). Overall, 57 observations were made at 24 sites on 192 spotlight transects. Most animals were observed at unburnt sites (50.9% of total) and less in understory (38.6%) and severely burnt sites (10.5%; equal number of sites in each fire severity class).

The number of observations were too few to generate a robust detection function to examine differential detectability using distance sampling (Buckland et al. 2001). To test for differences in detectability in forest of different fire severity, we used a linear model to compare the distance from observer to (1) any arboreal mammal and (2) a Greater Glider (species with sufficient observations), in relation to three classes of fire severity (unburnt, understorey burnt, severely burnt). The Greater Glider response was log-transformed to meet assumptions of normality. There was no difference in mean sighting distance amongst fire severity classes for total arboreal mammals ($F_{2,44} = 0.537$, $P = 0.588$) or for the Greater Glider ($F_{2,25} = 0.472$, $P = 0.629$). Therefore, we assumed no difference in detection amongst severity classes.

More observations of arboreal mammals (all species combined) occurred in gullies than on slopes (Appendix: Table A2; GLMM, estimate = -0.54 ± 0.27 SE, $z = -1.96$). There was no difference in the number of Greater Gliders (estimate = -0.44 ± 0.39, $z = -1.13$) or in species richness (estimate = -0.57 ± 0.35, $z = -1.64$) between gullies and slopes.

In the isolation study, four species were recorded: Greater Glider, Mountain Brushtail Possum, Common Ringtail Possum and Sugar Glider (Appendix: Table A2). In total, 44 animals were recorded at 14 sites on 112 transects.

Fire regime study

We tested the relative influence of fire severity, fire history, time since fire and number of large trees for each response variable: overall, fire severity had the greatest influence (Table 2). There were no "best" models for which $w_i > 0.90$, hence we considered models with substantial support ($\Delta AIC_c < 2$) and examined their parameter estimates.

For the total number of arboreal mammals, three models including (1) fire severity, (2) large trees, and (3) fire severity plus fire history had substantial support (Table 2). Upon examination of the parameter estimates, the abundance of arboreal mammals was most strongly influenced by fire severity (Table 3). In both the severity model, and the severity plus history model, fewer individuals were observed in severely burnt sites than at unburnt sites (Fig. 2). There was no difference in the number of individuals between understorey burnt and unburnt sites, nor with sites with a different number of large trees (Table 3).

For the abundance of the Greater Glider, two models had substantial support, namely (1) fire severity plus large trees, and (2) fire severity plus fire history plus large trees (Table 2). Fire severity and the number of large trees were important variables in both models (Table 3). Fewer individuals were observed in severely burnt than in unburnt sites, and Greater Gliders were positively associated with sites containing more large trees (Fig. 2).

Species richness had three plausible models including (1) fire severity plus fire history, (2) large trees, and (3) fire severity (Table 2). The parameter estimates of these models showed that

Table 2. Models with the most support (ΔAIC < 2) for each response variable in the fire regime and isolation studies including AIC values presented for each alternative model and model fit represented by R^2m (variance explained by fixed predictors) and R^2c (variance explained by both fixed and random predictors).

Response variable	Model structure	df	Log likelihood	AIC$_c$	ΔAIC$_c$	Akaike weight	R^2m	R^2c
Fire regime study								
All arboreal mammals	Severity	5	−45.29	103.9	0.00	0.39	0.33	0.33
	Tree	4	−47.38	104.9	0.96	0.24	0.13	0.13
	Severity + History	6	−44.37	105.7	1.77	0.16	0.38	0.38
Greater Glider	Severity + Tree	5	−28.14	69.6	0.00	0.59	0.62	0.86
	Severity + History + Tree	6	−27.10	71.1	1.54	0.28	0.61	0.90
Species richness	Severity + History	5	−31.43	76.2	0.00	0.34	0.35	0.35
	Tree	3	−34.79	76.8	0.59	0.25	0.07	0.07
	Severity	4	−33.74	77.6	1.38	0.17	0.20	0.20
Isolation study								
All arboreal mammals	Area understory†	4	−26.76	66.2	0.00	0.68	0.65	0.75
Greater Glider	Area understory + Tree	4	−15.52	43.5	0.00	0.49	0.40	0.65
	Area unburnt + Tree	4	−15.79	44.0	0.55	0.38	0.27	0.64
Common Ringtail Possum	Area understory† + Tree	4	−15.06	42.6	0.00	0.35	0.60	0.85
	Tree	3	−17.26	42.9	0.36	0.29	0.16	0.76
	Area understory	3	−17.32	43.0	0.48	0.28	0.64	0.84
Species richness	Area understory	3	−16.86	42.1	0.00	0.65	0.60	0.60

† Log transformed.

Table 3. Model parameters and coefficients for models with substantial support (i.e., ΔAIC$_c$ < 2) in the fire regime study.

Response variable and model structure	Variable	Parameter	Coefficient	SE	Z
All arboreal mammals					
Severity	Severity	Intercept	1.00	0.34	2.98
	Severity	Understorey	−0.17	0.46	−0.37
	Severity	Severe	−1.49*	0.58*	−2.59*
Tree	Tree	Intercept	−0.69	0.77	−0.90
	Tree	Tree	0.15	0.09	1.74
Severity + history	Severity	Intercept	1.29	0.43	2.96
	Severity	Understorey	−0.21	0.50	−0.42
	Severity	Severe	−1.54*	0.65*	−2.38*
	History	Short	−0.57	0.44	−1.31
Greater Glider					
Severity + tree	Severity	Intercept	−2.06	1.26	−1.64
	Severity	Understorey	0.43	0.48	0.90
	Severity	Severe	−2.52*	1.06*	−2.38*
	Tree	Tree	0.28*	0.11*	2.51*
Severity + history + tree	Severity	Intercept	−2.31	1.14	−1.63
		Understorey	0.39	0.51	0.76
		Severe	−2.80*	1.09*	−2.58*
	History	Short	−0.75	0.52	−1.44
	Tree	Tree	0.35*	0.13*	2.70*
Species richness					
Severity + history	Severity	Intercept	0.88	0.29	3.00
	Severity	Understorey	−0.15	0.39	−0.39
	Severity	Severe	−0.85	0.49	−1.74
	History	Short	−0.79*	0.38*	−2.07*
Tree	Tree	Intercept	−0.29	0.52	−0.56
	Tree	Tree	0.08	0.06	1.22
Severity	Severity	Intercept	0.56	0.27	2.09
	Severity	Understorey	−0.15	0.39	−0.39
	Severity	Severe	−0.85	0.49	−1.74

Note: Reference categories for categorical variables were unburnt (fire severity), and long > 20 years (fire history).
* Parameters are considered important if the 95% confidence limits of the coefficient do not overlap zero (i.e., Z values of > 1.96 or < −1.96).
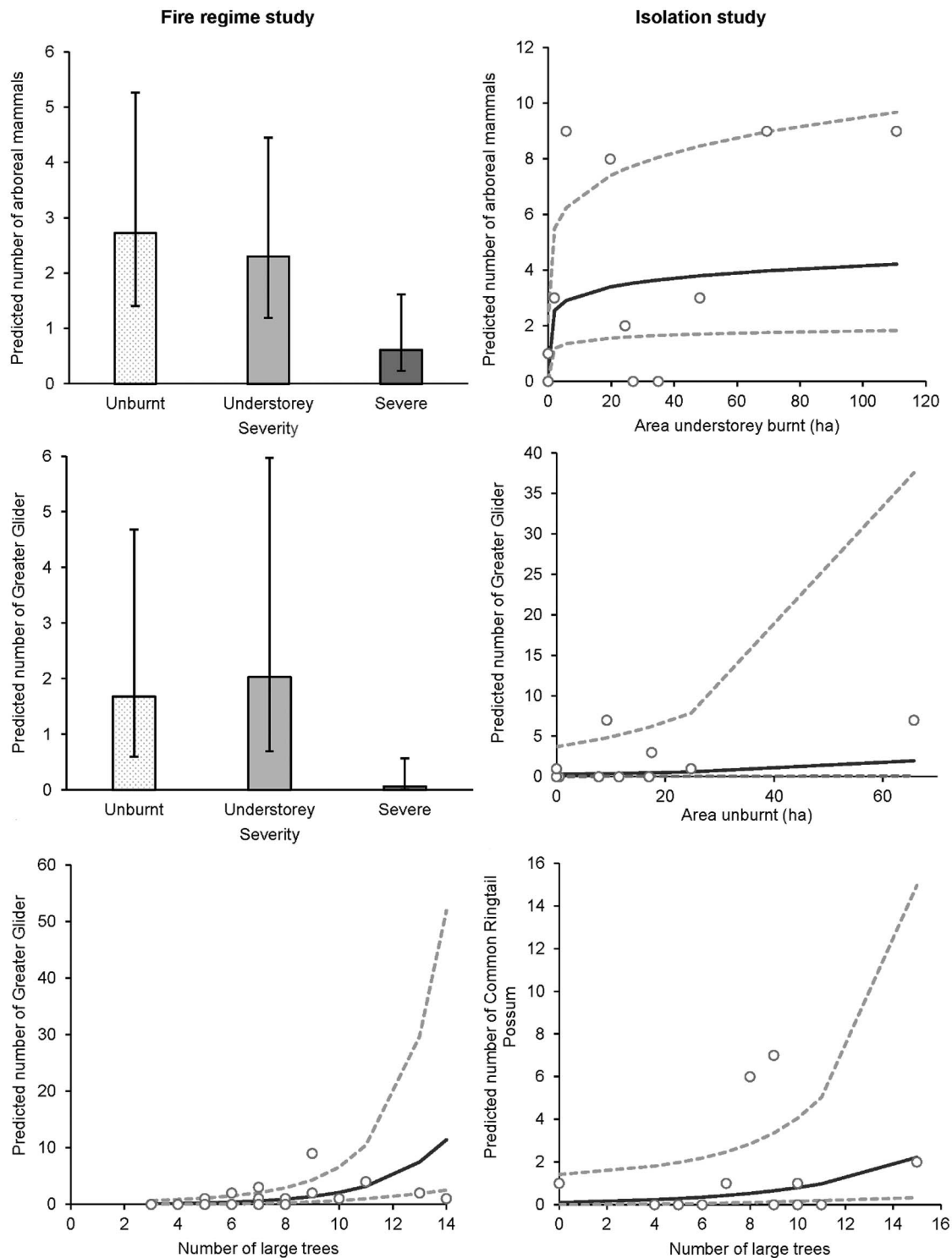
Fig. 2. Predicted values with 95% CI from univariate models of important variables and response variables for the fire regime study and the isolation study including total number of arboreal mammals, number of Greater Gliders, and number of Common Ringtail Possums.

Table 4. Model parameters and coefficients for models with substantial support (i.e., $\Delta AIC_c < 2$) in the isolation study.

Response variable and model structure	Variable	Coefficient	SE	Z
All arboreal mammals				
Area understorey	Intercept	0.28	0.51	0.56
	Area understorey†	1.35*	0.57*	2.35*
Greater Glider				
Area understorey + tree	Intercept	−0.83	0.84	−0.99
	Area understorey	0.89*	0.40*	2.21*
	Tree	−1.02*	0.33*	−3.10*
Area unburnt + tree	Intercept	−0.80	0.96	−0.84
	Area unburnt	0.69*	0.29*	2.36*
	Tree	−0.84*	0.31*	−2.75*
Common Ringtail Possum				
Area understorey + tree	Intercept	−1.32	1.07	−1.23
	Area understorey†	1.72	1.22	1.41
	Tree	0.63	0.35	1.79
Tree	Intercept	−0.61	0.86	−0.72
	Tree	0.75*	0.38*	1.98*
	Intercept	−1.15	1.09	−1.05
	Area understorey†	1.88	1.30	1.45
Species richness				
Area understorey	Intercept	−0.22	0.38	−0.57
	Area understorey†	0.99*	0.49*	2.01*

  † Log transformed.
  * Parameters are considered important if the 95% confidence limits of the coefficient do not overlap zero (i.e., Z values of > 1.96 or < −1.96).

fire history was the only influential variable (Table 3). Species richness was lower at sites with a short fire history where there had been a recent burn (<3 yr) prior to the wildfires.

Isolation study

Isolation of severely burnt sites from unburned forest within the wildfire boundary influenced the abundance of arboreal mammals. For total arboreal mammals, only the top model had substantial support (Table 2). The number of mammals increased with the combined area of surrounding unburnt and understorey-only burnt forest (Table 4, Fig. 2).

The abundance of Greater Gliders was supported by two models: (1) the combined area of surrounding unburnt and understorey burnt forest plus large trees, and (2) the area of surrounding unburnt forest plus large trees (Table 2). There was a positive association between Greater Glider abundance and area of surrounding unburnt forest (Fig. 2), and combined unburnt and understorey-only burnt forest (Table 4). Surprisingly, there was also a negative relationship with the number of large trees (Table 4).

For the Common Ringtail Possum, three models had substantial support including (1) area of combined unburnt and understorey-burnt forest plus large trees, (2) large trees, and (3) area of combined unburnt and understorey-burnt forest (Table 2). The number of large trees was the only important parameter, with a positive relationship between the number of Common Ringtail Possums and abundance of large trees at a site (Table 4, Fig. 2).

Species richness of arboreal mammals had one model with support (the top model), the combined area of unburnt and understory-only burnt forest (Table 2). Species richness increased with the surrounding area of both unburnt and understorey burnt forest (Table 4).

Discussion

In this study, we used the opportunity arising from a major wildfire to investigate how arboreal mammals are affected by fire-induced landscape heterogeneity and landscape context in a rarely studied forest type. The study has three key findings. First, the abundance of arboreal mammals was influenced by topography, with higher abundance in forest gullies than on adjacent slopes (pooled across all fire severity classes). Second, fire severity was an important factor in the abundance of arboreal mammals at 2.5 years

post-wildfire. Severely burnt forest supported fewer animals than unburnt forest. Third, in a separate study at 3.5 years after fire, the abundance of arboreal mammals in severely burnt forest was influenced by landscape context: the number of arboreal mammals was positively related to the amount of surrounding unburnt or understorey-burnt forest. Together, these findings highlight the importance of environmental variation and fire-induced landscape heterogeneity in the aftermath of major wildfires. They are consistent with the view that mesic forest gullies and patches of unburnt or less-severely burnt forest (understory only burnt) have a role as refuges for arboreal mammals in severely burnt landscapes, and that such refuges assist the recovery of mammal populations after wildfire.

We recorded six species of arboreal mammal, all of which occurred in relatively low abundance (in both burned and unburned forest) compared with other studies in south-eastern Australia (e.g., Lunney 1987, Bennett et al. 1991). Two additional species potentially occur in the region (Yellow-bellied Glider *Petaurus australis*, Feather-tailed Glider *Acrobates pygmaeus*) but were not detected. The low abundance of arboreal mammals is likely due, at least in part, to the study occurring shortly after the end of a decade of drought, the worst drought on record in south-eastern Australia (van Dijk et al. 2013). In the nearby wet forests of the central highlands, the Greater Glider has declined at a yearly rate of 8.8% in the 12 years prior to 2010 in part due to low rainfall (Lindenmayer et al. 2011*a*). Other species in these forests are also vulnerable to low rainfall, for example the Sugar Glider (Lindenmayer et al. 2011*b*). Similarly, drought caused a decrease in arboreal mammals in coastal forests of New South Wales, Australia (Lunney 1987). The paucity of records means that the clearest results relate to pooled data for all arboreal mammal species rather than for individual species.

Topographic influence

Mesic gullies supported a greater abundance of arboreal mammals (all species) than slopes. Other studies have also reported a greater abundance of arboreal mammals in gullies in forests in southern Australia (e.g., Lindenmayer et al. 1990, Pausas et al. 1995), including after

wildfire (Lunney 1987, Berry et al. 2015*b*). The topographic location of gullies, their high moisture content and fire resistant vegetation reduce exposure to high severity fires (or even multiple fires), allowing them to maintain structural complexity, including trees with hollows (Collins et al. 2012). Gullies not only are important for the recovery of arboreal mammal populations and other species shortly after fire, but also provide valuable habitats in the long term (Collins et al. 2012, Diffendorfer et al. 2012, Bassett et al. 2015).

Relative influence of fire severity

Wildfire severity was the most important component of the fire regime driving arboreal mammal abundance in these foothill forests. Several factors contribute to reduced abundance in severely burned forest. First, injury or mortality during, or immediately after, a fire is likely to be higher in severely burnt forest compared with forest burnt at low severity. Animals often survive in less intense fires or unburnt areas (Garvey et al. 2010, Banks et al. 2011*b*). Arboreal mammals are less able to escape than more mobile taxa such as birds (Whelan et al. 2002). The lower abundance in severely burned forest at the time of this survey (2.5 years post-fire) may reflect fire mortality, with insufficient time for populations to recover.

Second, lower abundance in severely burnt forest is likely associated with habitat less suitable to sustain populations. At the time of the study, severely burned forest was in the early stages of recovery after incineration or death of canopy foliage. Even though the canopy was re-sprouting, this may not have been sufficient to support arboreal mammal populations. Post-fire shortage of foliage as food for folivores, such as the Greater Glider, would severely affect local populations (Lindenmayer et al. 2013). Loss of canopy and vegetation structural complexity also equates to less cover for possums and gliders (Catling et al. 2001, van der Ree and Loyn 2002). Other structural changes, such as reduced availability of tree hollows for nesting (Inions et al. 1989, Banks et al. 2011*b*) also limit populations. Severe fire can exacerbate the collapse of large hollow-bearing trees, and reduce the number of den sites for arboreal mammals (Inions et al. 1989, Banks et al. 2011*b*, Collins et al. 2012). It is interesting to note that the relationship of

arboreal mammal abundance to fire severity is comparable to that described by Lindenmayer et al. (2013) in montane ash eucalypt forest at a similar time post-fire, despite the difference in post-fire canopy structure between foothills and ash forests (i.e., regenerating canopy versus largely absent canopy). This suggests that resources for arboreal mammals, including the foothill forest canopy, has not recovered sufficiently to allow restoration of arboreal mammal populations at 2–3 years after wildfire.

Third, arboreal mammal populations can be affected by predator activity; animals that survive fire may be more vulnerable to predation in burnt forest than in unburnt stands (Russell et al. 2003, Wayne et al. 2006) due to reduced cover and refuge. There is a need for better understanding of the relative roles of resource limitation, competition and predation in the persistence of individuals and populations after fire.

Spatial isolation

In severely burnt forest, sites that were more isolated from unburnt or understory-only burnt forest supported a lower abundance of arboreal mammals. There are two main options for population recovery in burned environments: survival in situ of some individuals, or recolonization by individuals dispersing into the burned environment from unburned forest (Banks et al. 2011a). In many situations, both processes are likely. Evidence for an isolation effect in this study lends support to the hypothesis that the status of populations in severely burned forest is influenced, at least in part, by recolonization from nearby unburned areas.

Little is known of the processes of faunal dispersal and (re)colonization following fire (Robinson et al. 2013). It is likely to depend on distance from source populations, size of source populations and the relative mobility of the taxa involved (Brotons et al. 2005, Banks et al. 2011a, Watson et al. 2012, Lindenmayer et al. 2013). This study indicates that recovery of the arboreal mammal assemblage remains incomplete at 3.5 years post fire, although there may be differences between taxa. While an isolation effect was detected for total arboreal mammals and the Greater Glider, it was not evident for the Common Ringtail Possum, although records were sparse.

Implications for conservation

Fire creates spatial heterogeneity in forest landscapes by variation in fire severity within a single fire, and by the combined effects of multiple fires over decades. This study in foothill eucalypt forests, together with work in nearby montane forests (Lindenmayer et al. 2013), demonstrates that arboreal mammals are particularly sensitive to fire severity even in forests with re-sprouting canopy, being less abundant in severely burned forest within the post-fire environment. Further, the positive influence of surrounding unburnt forest is consistent with the hypothesis that post-fire population recovery is assisted by recolonization from nearby source areas. Thus, scarce patches of unburnt forest within and adjacent to the fire boundary (<1% of the total areal Leonard et al. 2014) have important conservation value as refuges, at least in the short term.

The presence of unburnt patches in foothill forests was determined primarily by topography, fire intensity and time since last fire (Leonard et al. 2014). Such refuges were more likely to occur in less severe fire conditions, and be located in moister gullies or areas recently burned (<3 years) prior to the wildfire. Thus, planned burning has potential to contribute to refuge habitat for arboreal mammals in the face of subsequent wildfire, by strategically reducing fuel loads to reduce the likelihood of high-severity fire in important areas such as moist gullies and drainage lines, and forest stands of high quality habitat for arboreal mammals and other forest fauna (e.g., mature forest with high density of large old trees).

While this study has identified fire severity and fire-induced landscape heterogeneity as important influences on arboreal mammals in foothills forest, the fauna of this extensive system is also under pressure from other disturbances, such as introduced predators and competitors, logging, expanding human settlement, and climatic extremes such as drought. Targeted studies, along with long-term monitoring, will be important to understand the interactions between fire and these other stressors; particularly in the context of a changing climate expected to increase the size, frequency and intensity of

wildfire (McKenzie et al. 2004, Wotton et al. 2010).

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

The Appendix is available online at: http://dx.doi.org/10.1890/ES15-00327.1.sm