Wildfire, Landscape Heterogeneity and Fauna in Fire-prone Forests

by

Evelyn K. Chia
B.Sc. (Env) (Hons) University of Sydney

Submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy

Deakin University
October, 2015
I am the author of the thesis entitled

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PREFACE

This study was part of a large collaborative project, the Faunal Fire Refuges Project, conducted by Deakin and La Trobe Universities, and funded by the (then) Victorian State Department of Sustainability and Environment. The project was initiated following the extensive and severe ‘Black Saturday’ wildfires in central Victoria in 2009. It aimed to understand the effects of the fire regime on biodiversity, and the potential role of unburnt forest, prior planned burning and topographic variation in creating faunal ‘refuges’ in the flammable foothill forests of Victoria, south-eastern Australia. Multiple taxa were examined including mammals, birds, invertebrates and plants. My project focused on mammal species. The core project team included principal scientists, Prof. Andrew Bennett and Prof. Michael Clarke; project officer Dr. Steve Leonard; and PhD students Natasha Robinson, Michelle Bassett, and myself. Extensive site mapping was conducted by Natasha Robinson. The overall study design and selection of ~90 sites, stratified by fire severity and fire history was conducted by the core team.

This thesis comprises eight chapters. Research chapters (3-6) were written with the intention of eventual publication in peer-reviewed journals, and contain a separate abstract, introduction, methods, and discussion. Chapter 3 has been published in Ecosphere, and Chapter 4 has been published in Forest Ecology and Management. These chapters are written with the plural pronoun (we) to acknowledge the contributions of all co-authors, whilst the remaining chapters of the thesis refer to the singular pronoun (I). Efforts were taken to minimize repetition in relation to description of the study area and methods in Chapters 5-7, by referring to the relevant parts of earlier chapters. References for all chapters are combined and included in a single section towards the end of the thesis.

This thesis presents my work, as part of the broader project, investigating the effects of large fires, fire regime components and landscape heterogeneity on mammals. My colleague, Michelle Bassett, and I worked as a team in collecting the data on mammals
for the overall project. We co-developed the study design specifically for native and introduced mammal species, and conducted field surveys and data entry for all mammals, including spotlight surveys, camera trap surveys and live trapping (Chapters 3-7). However, in preparing theses, we have each addressed different topics with different analyses in an independent manner.

In addition to collaborative study design and field survey work above, I undertook the following in this thesis independently:

- Reviewed the literature and theory on fire, mammals and lyrebirds
- Developed the study design specifically for arboreal mammals (Chapter 3)
- Conducted site selection for the isolation study for arboreal mammals (Chapter 3)
- Conducted all statistical analyses in this thesis
- Collated and prepared all tables and figures in this thesis
- Wrote initial drafts of all chapters in this thesis, and revised and collated contributions by co-authors for the two chapters submitted for publication.

The research chapters (Chapters 3-7) include aspects of work contributed by co-authors. For published or submitted manuscripts (Chapters 3-4), specific contributions from co-authors are outlined in two separate authorship statements (following). In addition, for Chapter 5, Euan Ritchie provided critical comments and input, and Dale Nimmo provided advice on statistical analysis. For Chapter 7, Steve Leonard conducted habitat surveys. Discussions about statistical methods included Andrew Bennett, Michelle Bassett, Dale Nimmo and Greg Holland. Andrew Bennett (as principal supervisor) provided scientific guidance and critically commented on the entire thesis for intellectual content.

During this research, I also contributed to two other published manuscripts, and a published brochure, as part of the Faunal Fire Refuges Project (see Appendices 1-3):


This research was conducted under Department of Sustainability and Environment permit (10005478) and Deakin animal welfare permit (A56-2010).
AUTHORSHIP STATEMENT A

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<td>Fire severity and fire-induced landscape heterogeneity affect arboreal mammals in fire-prone forests</td>
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This publication is one part of the larger collaborative Faunal Refuges Project. I contributed to the conception and design of the Project. For this publication, I am the primary contributor to the design of methodology and surveys, data collection, analysis and interpretation, as well as drafting the manuscript, collating contributions and revising it for critically important intellectual content.

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Michael F. Clarke, La Trobe University | Conception and design of the Faunal Refuges Project, and critically revising the manuscript for intellectual content.
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Andrew F. Bennett, La Trobe University and Arthur Rylah Institute | Conception and design of the Faunal Refuges Project, design and advice of methodology for this publication, project discussions, and critical and extensive revisions of the manuscript.

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<td>Advice on data analysis, project discussions, and critically revising the manuscript for intellectual content.</td>
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ACKNOWLEDGEMENTS

Someone once told me that completing a PhD was a bit like chipping away at one of those toy dinosaurs hidden inside a plaster egg. You start chipping away at the plaster. Slowly, slowly, patiently and persistently chipping away, piece by piece. Finally, without realising it, the last piece is chipped away, and there you have it. A complete dinosaur that was hidden away that whole time, waiting to appear. At the risk of sounding a little clichéd— I finally have my dinosaur! Thanks to the many who have helped me get there.

First I would like to thank my principal supervisor, Andrew Bennett, for sharing his wisdom, guidance and scientific excellence. He has been described as a person of integrity, both in his work and as a human being, and I must say that I agree! I feel privileged to have had the opportunity to work with him. I wish to thank Euan Ritchie for his supervision, constant encouragement and support throughout my candidature. His enthusiasm and ideas for science-based conservation is admirable.

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Field work could simply have not been completed without the help of many enthusiastic people. I would especially like to thank our excellent research assistants Mark Hall, Jemima Connell and Phil Rance. Our industry placement assistants were also invaluable: Jessica Collins, Karina Newnham, Matthew Goodie, Megan Osborn, Jenna Tregoweth, Dan Nugent, and Simon Verdon. I am also grateful for the help of our many volunteers. Thanks to Simon McKenzie for help in the field, as well as for working magic on our camera trap database.

The project was generously funded by the Department of Environment, Land, Water and Planning (DEWLP, then Department of Sustainability and Environment). Thanks to all the supportive staff at DELWP, Parks Victoria, Victorian State Forests and Melbourne Water.

My PhD was funded by an Australian Postgraduate Award scholarship. I appreciate funding from the School of Life and Environmental Sciences and the Centre for Integrative Ecology, Deakin University. In particular, funding from Deakin University gave me the opportunity to present at conferences for the Ecological Society of Australia, the Australian Mammal Society, and in conjunction with a travel grant from the British Ecological Society, at INTECOL in London 2013 (International Congress of Ecology). I am grateful for the mentorship and master class provided by the Wentworth Group of Concerned Scientists in their PhD scholarship program.

I appreciate the time and expertise of scientists who aided in the identification of mammal species in photos including Jenny Nelson, Greg Holland, Andrew Bennett, Fred Ford, Richard Loyn, Peter Menkorst, Euan Ritchie, Justine Smith and John White.
Thanks to all the members of the bushfire-affected communities we met along the way. Their stories and generosity are inspiring. In particular, I wish to thank Colin and Michelle French and Sean Adam from the Kinglake Ranges Adventure Park for providing accommodation during live-trapping.

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My fellow PhD colleagues have provided me much support. In particular, thanks to Michelle Bassett and Anna Flanagan-Moodie for being great colleagues and friends. Thanks in particular to Emma Carlos, Christine Connelly, Sarah Maclagan, Kate Stevens and Connie Warren for their positivity and encouragement. I appreciate my friends outside of my PhD world who were a great support. Thanks to Prue Addison for help with formatting my thesis.

To my family who have lead me to where I am today. I am forever grateful. I wish to thank my mum who is a constant source of inspiration, love and light. She is truly one of the most amazing women I know. Thanks to Dad for his good humour and for sparking my interest in nature as a child by teaching me the difference between a magpie and a currawong. Thanks to both Dad and Gloria for their support. I would like to thank my brother for sharing jokes and good food, and especially for his generosity and kindness throughout my PhD and my life. Thanks to Andrew for his patience, constant support and encouragement, and for always making me laugh.
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ABSTRACT

Fire is a primary disturbance process in forest ecosystems across the globe. The fire regime experienced in an ecosystem can have major impacts on biodiversity by influencing the occurrence of species, the composition of communities, and the process of species succession. Fire regimes can influence the distribution and abundance of faunal species at different spatial scales, by altering habitat suitability at a site and the spatial heterogeneity of habitat quality in the surrounding landscape. Altered fire regimes, climate change impacts on fire activity, and their synergies with other threatening processes such as introduced species, are likely to significantly affect the distribution and abundance of fauna in forest ecosystems. Hence, the effect of fire on biodiversity is an important theme in ecological research, and in the conservation and management of fire-prone ecosystems. Despite this, the effects of different components of the fire-regime and the influence of landscape heterogeneity on the occurrence of animal species are rarely examined together.

The aim of this research was to understand how large fires, fire regime components and landscape heterogeneity influence the occurrence of fauna in the temperate eucalypt forests of south-eastern Australia, one of the most fire-prone forest ecosystems in the world. This was achieved by investigating the relative influence of i) wildfire severity and the pre-wildfire burning history at individual sites, and ii) fire-created heterogeneity in the surrounding landscape, on the distribution and relative abundance of animal species. The study was undertaken in the foothill forests of the Central Highlands of Victoria, in the Kilmore-Murrindindi fire complex, in which ~250 000 ha of forest was burnt as part of the severe and extensive ‘Black Saturday’ wildfires of 2009. The occurrence of four groups of forest fauna were examined at 2-3 years after wildfire: arboreal mammals, native terrestrial mammals, introduced terrestrial mammals, and the superb lyrebird (*Menura novaehollandiae*), a ground-dwelling bird species regarded as an ecosystem engineer in moist eucalypt forests.

Spotlight surveys were conducted at night to investigate the occurrence of arboreal mammals: first, to examine the influence of topography, wildfire components and
landscape context at 24 sites; and second, at an additional 14 severely burnt sites, to test the effects on arboreal mammals of isolation from unburnt forest. Forested gully sites contained more arboreal mammals than forest slopes. Fire severity was the strongest driver of arboreal mammal abundance, with higher numbers recorded in unburnt than severely burnt sites. Fire interval had little influence. When considering severely burnt sites, landscape context was important: the number of arboreal mammals at severely burned sites was higher with increasing area of unburnt and understorey-only burnt forest within a 1 km radius. These results support the hypothesis that unburnt forest and moist gullies provide important habitat that enhances both the persistence and recolonisation of arboreal mammals, and hence are serving as refuges in the early post-fire environment.

Camera surveys were carried out at 80 sites, each of which comprised a gully and adjacent slope, stratified to represent different levels of fire severity and fire history. Thirteen species of native terrestrial mammals were detected, records of eight species were sufficient for analysis. Most species were widespread: seven species were recorded in all fire severity classes (unburnt, understorey burnt, severely burnt, reference). Whilst fire severity was the most influential variable at the site-level, for most species this effect was not strong. The amount of unburnt forest and the heterogeneity in fire severity in the surrounding landscape had limited influence on mammal occurrence at sites. It appears that mammal species have either survived in situ or they have recolonised rapidly within 2 years of a severe wildfire. Rapid regeneration of understorey vegetation following above-average, drought-breaking rains in 2010, has provided suitable habitat for most species.

Six species of introduced terrestrial mammal were detected by camera surveys, four of which were examined in detail. The house mouse (Mus musculus), black rat (Rattus rattus), red fox (Vulpes vulpes), and feral cat (Felis catus) were widespread and present in all classes of fire severity. Surprisingly, the black rat was the only species that was influenced by fire severity and topography at the site-level: higher recording rates were present in burnt (understorey and severely burnt) than unburnt sites, and in moist gullies than on drier slopes. Few associations were apparent between the spatial occurrence of introduced and native species. Fire and landscape heterogeneity had a
limited effect on the occurrence of introduced species at 2-3 years after fire, likely because of their ability to adapt to a variety of habitats, and in response to the rapid regeneration of understorey vegetation.

The distribution of the superb lyrebird, as revealed by camera surveys, was influenced by both the fire severity and fire history at sites; but with no evidence for an effect arising from fire-related patterns in the surrounding landscape. A higher recording rate was evident at unburnt sites compared with severely burnt sites. For sites burnt in the 2009 wildfire, there was a lower recording rate at those with recent prior fire (< 3 years) than those with a longer fire history (> 20 years). Topographic position moderated the effect of fire severity, with gullies favoured over slopes. Greater shrub cover (< 2 m) in gullies was the only habitat component that positively influenced the recording rate of this species. Unburnt patches and mesic gullies are valuable habitat for the superb lyrebird at 2-3 years after wildfire. They support the persistence of the superb lyrebird within the burnt landscape by providing important habitat and resources (e.g. foraging substrates, food, and cover) in the post-fire environment.

These results highlight the role of wildfire severity as an important driver of the occurrence of forest fauna at the site-level at 2-3 years post-fire, by its influence on the suitability of forest habitat. Unexpectedly, landscape heterogeneity generated by fire had limited effects on most species, probably because animals were responding to the rapid regeneration of vegetation. These results also have implications for the conservation and management of fire-prone ecosystems. First, during the development of fire management plans, it is important to consider individual responses and habitat requirements after fire. Second, fire management activities, such as strategic planned burns, that can increase the number of unburnt patches likely to occur after wildfire (particularly in valuable areas such as topographic gullies) will be of particular benefit to the persistence of fire-sensitive species. Third, longer intervals between fires to preserve habitat complexity at forest sites are recommended for species that are detrimentally influenced by fire severity and short fire intervals; and for species that rely on complex habitat structure or mature forest stands (e.g. with large hollow bearing trees). Fourth, management of introduced species is likely to be most effective immediately following wildfire when vegetative cover is greatly reduced, and could
be targeted in locations known to have important populations of native species, or in habitat areas that are valuable for native fauna after fire, such as unburnt forest patches.

This broad-scale survey has uniquely investigated the effects of fire regime components and landscape heterogeneity on multiple species at 2-3 years after a severe wildfire. Building from this study, further work could examine species succession over a longer time period (i.e. a longitudinal study) and recovery under different climatic circumstances (e.g. extended drought). In addition, further research is needed on the effects of fire and landscape heterogeneity on the mechanisms that underpin the responses of fauna; such as mortality and *in situ* survival at the time of the fire, recolonisation, demographic changes and species interactions (e.g. predation, competition). Such knowledge would build on the distributional patterns identified here, and further enhance the management and conservation of biodiversity in fire-prone landscapes.
CHAPTER 1 General Introduction

Severely burnt forest at 1.5 years after the 2009 wildfires
1-1 Impacts of large fires and the fire regime

Fire is a recurring natural disturbance that plays an important role in the ecology of many biomes around the world (Sousa, 1984; Pickett et al., 1989; Keeley et al., 1999; Stocks et al., 2002; Boer et al., 2008; de Groot et al., 2013; Smit et al., 2013; Moreno et al., 2014). Fires can shape and transform ecosystem structure and function by reducing plant biomass, and altering vegetation structure and composition; thereby influencing the distribution and abundance of animal species, and the composition of faunal communities (Fox, 1982; Bond & Keeley, 2005; Bond et al., 2005; Burton et al., 2008; Bowman et al., 2009; Hoffmann et al., 2012; Bowman et al., 2013). Important ecological processes, such as nutrient cycling and carbon fixation, are also affected by fire (Harden et al., 2000; Bond-Lamberty et al., 2007; Burton et al., 2008). Large fires may alter soil hydrology and sediment yields when the burning of vegetation increases surface runoff and erosion, which can lead to damaging debris flows (Cawson et al., 2012; Goode et al., 2012; Moody et al., 2013). There are also important social and economic consequences of large fires, including loss of human life, and impacts on infrastructure and built assets, water supply and agricultural production (Gill & Allan, 2008; Pausas et al., 2008; Bowman et al., 2009; Gill & Stephens, 2009; Bowman et al., 2011; Moritz et al., 2014).

Fire activity in fire-prone regions is predicted to change with climate change, threatening biodiversity in ecosystems around the world (Shlisky et al., 2007; Flannigan et al., 2009; Loarie et al., 2009; Moritz et al., 2012). Climbing temperatures, consequent drought, and increased fuel loads are predicted to lead to a greater frequency of large and severe fires, and initiate longer and more severe fire seasons in many areas of the globe (Flannigan et al., 2009; Wotton et al., 2010; Westerling et al., 2011; Attiwill & Binkley, 2013; Flannigan et al., 2013; Stephens et al., 2013; Williams, 2013). Decreases in fire activity may also occur in some ecosystems, but longer fire intervals could increase the susceptibility of fire-prone areas to severe wildfire (Moritz 2012). Climate change, fire and their synergies with other threatening processes such as invasive species, can pose a threat to biodiversity via declines in species’ abundance or the loss of species from ecosystems (Thomas et al., 2004;
Shlisky et al., 2007; Brook, 2008; Brook et al., 2008; Griffiths & Brook, 2014; Doherty et al., 2015). It is important, therefore, to understand the effects of fire and the fire regime on biodiversity, not only to advance ecological knowledge, but also for the effective management and conservation of the flora, fauna and ecosystems in fire-prone regions (Hammill & Bradstock, 2006).

A large fire can be considered as one that is extensive across a landscape (i.e. large in size) and usually includes areas of high fire intensity. Large fires are defined by the size of the area burnt in either absolute or relative terms, depending on the location and environment (Gill & Allan, 2008). Global examples of large fires in forest ecosystems include: the Solsones fire in 1998 which incinerated 27 000 ha of forest in north-eastern Spain (Roman-Cuesta et al., 2009); the 2013 Rim Fire in California, USA, which burnt over 104 000 ha of forest (Lydersen et al., 2014); the 2002 Biscuit fire in forests of south-west Oregon, USA, that burnt > 200 000 ha (Thompson et al., 2007); and the fires in 2003 in the Alpine region of south-eastern Australia which affected approximately 3 million ha (Williams et al., 2008). Other fires, although smaller in spatial area than the above, can also be considered ‘large’ depending on their context. For instance, in the Mediterranean region in Europe, large fires include those that are over 500 ha in size (San-Miguel-Ayanz et al., 2013). Large fires typically include areas of high intensity, spread quickly and may burn for long periods (Adams & Attiwill, 2011). If value is placed on the area burnt, by the community or land management agency, the fire may also be considered large (Song et al., 2001).

Large fires can have a long-lasting impact on ecosystems as they provide the foundation for the future fire regime of a landscape (Williams & Bradstock, 2008). Gill (1975) defined the fire regime to represent the pattern of fire associated with a particular area, including fire intensity, fire frequency, season and type of fire. Parameters associated with the conditions of fire occurrence or those that relate to the immediate effects of fire can also be considered as part of the fire regime (Krebs et al., 2010). Fire severity and extent (i.e. fuel consumption and fire spread), for example have also been identified as fire regime components (Bond & Keeley, 2005). Fire intensity is the rate of heat or energy released from the fire (Cheney, 1981), and is different from fire severity which is a measure of how much vegetation or organic
material is lost, in the vertical plane, after the fire event (Bradstock, 2008; Keeley, 2009). Fire severity describes the more immediate effects of fire on vegetation and is a useful concept for determining the effects of fire on ecosystems (Bond & Keeley, 2005; Krebs et al., 2010). The fire history of a fire regime refers to past fire events (Gill & Allan, 2008). Fire frequency (time between fire events) and season (time of year that a fire occurs) can have long-lasting effects on ecosystems (Gill, 1975). Fire type typically is classified according to the dominant vegetation burnt, such as a grass, peat or forest fire, and can be above or below ground (Gill, 1975; Cheney, 1981; Gill & Allan, 2008). Fire regimes are complex and they may vary across different scales in time and space (Krebs et al., 2010). Fire regimes influence the distribution of plants and animals in forests and other ecosystems (Bunnell, 1995; Gill & Catling, 2002; Whelan et al., 2002; Gill & Allan, 2008).

Large fires create spatial patterns of heterogeneity in the landscape which influence the distribution of species, the composition of communities and ecological processes (Turner et al., 1994; Pausas et al., 2002; Schoennagel et al., 2008; Roman-Cuesta et al., 2009; Williams & Baker, 2012). Spatial variation within the fire boundary is generated by patches of different fire severity, dependent upon fire intensity (Hammill & Bradstock, 2006; Bradstock, 2008). In turn, variation in fire intensity is determined by the combination of vegetation type, fuels, flammability, topography, and weather and climatic conditions that control fire behaviour (Cheney, 1981; Cruz et al., 2012; Sullivan et al., 2012). Vegetation acts as fuel for fire (e.g. trees, shrubs, bark, grasses), with large amounts of dry fuel increasing the flammability (Walker, 1981). Topographic variation in forested landscapes also influences fire intensity, with moist gullies being less likely to be severely burnt than upper slopes and ridges (Broncano & Retana, 2004; Bradstock et al., 2010). Commonly, large fires are driven by severe weather conditions of high temperature and high winds, low relative humidity and low fuel moisture (Bradstock, 2008). Large fires have also been associated with extended periods of drought in mesic forests, during which the vegetation and litter has dried (Gill & Allan, 2008). Variation in fire intensity creates spatial patterns in the landscape which can influence the survival, dispersal, recolonisation and persistence of plants and animals after fire.
The heterogeneity that can be observed in a landscape after the most recent fire event is considered to be the “visible mosaic”, while the temporal variation arising from different fire history in different parts of the landscape (e.g. the time since last fire, the between-fire interval) is the “invisible mosaic” (Gill et al., 2003; Bradstock et al., 2005). Variation in fire severity that creates the visible mosaic (Bradstock et al., 2005) is often classified into different categories, such as unburnt vegetation, vegetation in which only the understorey is burnt, and patches of vegetation in which both understorey and canopy are burnt (e.g. crown scorch, crown burnt) (Keeley, 2009; Price & Bradstock, 2012). Patches of unburnt, or less-severely burnt forest within the fire boundary (Bradstock, 2008) differ in shape and size, form different spatial configurations and vary in their degree of isolation from other unburnt patches (dependent on severity of a recent fire event) (Bradstock et al., 2005). Such unburnt or less severely burnt patches may serve as refuges for fauna, that mitigate the adverse effects of fire by enabling the survival, recovery, recolonisation or persistence of faunal populations in the post-fire environment (Robinson et al., 2013). However, specific attributes of refuge patches, as well as their spatial pattern and landscape context have rarely been identified for fauna (Robinson et al., 2013).

Ecological knowledge of the effects of spatial patterns of fire on species and populations is necessary for effective fire management and biodiversity conservation, but is not well understood (Driscoll et al., 2010; Spies et al., 2012; Griffiths & Brook, 2014; Griffiths et al., 2015). In particular, the impacts of fire on animal species and communities has received much less attention than for plants (Bradstock et al., 2002; Clarke, 2008). Fire has direct impacts on animals via mortality from radiant heat, and indirect effects by fire-induced changes in vegetation used as habitat (Gill & Catling, 2002; Whelan et al., 2002). However, understanding of how different components of the fire regime influence fauna at different spatial scales is limited (Driscoll et al., 2010). In recent years, more research has been conducted on the effects of time since fire on faunal groups (e.g. Langlands et al., 2011; Watson et al., 2012b; Chalmandrier et al., 2013; Kelly et al., 2014; Moranz et al., 2014; Nimmo et al., 2014; Pedersen et al., 2014). There has also been some attention to the effects of fire severity for different faunal groups, including for birds (e.g. Smucker et al., 2005; Hutto, 2008; Fontaine et al., 2009), mammals (e.g. Roberts et al., 2008; Diffendorfer et al., 2012; Doumas &
Koprowski, 2013a, b; Schuette et al., 2014), bats (e.g. Buchalski et al., 2013), and invertebrates (Wikars & Schimmel, 2001). However, with the exclusion of a few studies (e.g. Pons & Clavero, 2010; Lindenmayer et al., 2013), the relative influence on fauna of these different components, fire severity and fire history, at both the site level and landscape level is poorly known.

In Australia, mammals are one of the better understood faunal groups in relation to fire, with knowledge of small mammals in forest systems progressing over the last two decades (Sutherland & Dickman, 1999; Griffiths & Brook, 2014). Succession and changes in abundance of small mammals after fire in relation to changes in vegetation have been studied in dry sclerophyll forests and coastal heathland in south-eastern Australia (Newsome et al., 1975; Catling & Newsome, 1981; Fox & McKay, 1981; Fox, 1982; Friend, 1993). Less is known of the effects of large fires and different fire regime components on arboreal mammals and larger terrestrial species. There is also limited knowledge of the response to fire of keystone species, such as predators and ecosystem engineers, species which are likely to have widespread influence on other species and ecosystems. Mammals in Australia have suffered from large declines and species extinctions, with further extinctions imminent (Woinarski et al., 2015).

Extensive (large spatial scales) and less patchy fires can pose a threat to small mammal species (Lawes et al., 2015). Hence, in this fire-prone continent, it is important to understand the ecological effects of fire on mammals both for effective management of fire and for biodiversity conservation (Spies et al., 2012; Griffiths & Brook, 2014).

1-2 Large fires in Australia

Australia is a fire-prone continent, with large fires common in multiple ecosystems which span across many climate zones in the northern tropical savannas, central deserts, southern temperate forests and alpine regions (Woinarksi et al., 2004; Williams et al., 2008; Letnic & Dickman, 2010; Adams & Attiwill, 2011; Lawes et al., 2015; Murphy et al., 2015). South-eastern Australia is particularly vulnerable to severe wildfires (Cruz et al., 2012), with the state of Victoria being subject to some of the most intense fires in the world (Attiwill & Adams, 2013). The eucalypt forests of
this region are exceptionally flammable and susceptible to large fires due to the 
vegetation type, topography, weather and climatic conditions (Gill & Catling, 2002; 
Cruz et al., 2012; Sullivan et al., 2012; Murphy et al., 2013). Eucalypt forests generate 
substantial amounts of combustible fuel, such as leaf litter and fibrous bark, which can 
ignite and spread over large distances by spotting and firebrands (ignition at multiple 
points beyond the fire front) (Gill, 1981a; Cruz et al., 2012).

Dry eucalypt forests are more likely to burn than wet forest or rainforest (Leonard et 
al., 2014a). These forests occur in topographically varied landscapes; topographic 
location can determine fire intensity dependent on fire weather, because moist gullies 
have a lower likelihood of severe burns (Bradstock et al., 2010; Sullivan et al., 2012). 
Extreme weather conditions of high temperatures and winds, low relative humidity 
and low fuel moisture are common in south-eastern Australia, which increases the 
probability of crown fires occurring (Bradstock, 2008; Bradstock et al., 2010; Sullivan 
et al., 2012). Drought, often associated with El Niño periods, is frequent in south-
eastern Australia, which also contributes to increased amounts of dry and flammable 
fuel in forests and the occurrence of large fires (Bradstock, 2008; Gill & Allan, 2008; 
Sullivan et al., 2012; Murphy et al., 2013). Alternatively, during periods of La Niña 
years of high rainfall, vegetation flourishes and can later act as fuel that supports the 
ignition and spread of large fires (Gill & Allan, 2008).

Severe fires in south-eastern Australia are not unusual, with both historic and 
prehistoric records of large fires occurring (Pyne, 1991; Bradstock, 2008). Aboriginal 
burning practices have a long history in Australia, with charcoal records indicating 
that deliberate burning took place as early as 40 000 years ago (Nicholson, 1981; 
Kershaw et al., 2002). Indigenous communities used fire as a tool for different 
purposes, including hunting and food collection, and for social, ritualistic and domestic 
reasons (Nicholson, 1981; Gott, 2005). For example, burning was applied to create 
paths for easier access through thick vegetation, and was used as a means of flushing 
out animals during a hunt (Nicholson, 1981). Aboriginal fire regimes, including the 
season and frequency of burning, and applying a mosaic of patchy burns, have helped 
shape the Australian landscape and its biota (Pyne, 1991; Gott, 2005; Trauernicht et 
al., 2015).
Since European settlement in 1788 in Australia, fire regimes throughout the continent have changed. Early settlers in Victoria cleared land for agriculture, and then burnt the area to clear up the debris (Gill, 1975, 1981a). The incidence of large fires in south-eastern Australia increased early in the 20th century, most likely from a combination of higher ignition rates from unregulated use of fire by early European settlers and severe weather (Bradstock, 2008). Later, large fires were less frequent in the late 20th century due to fire suppression from fire management practices (Bradstock, 2008).

Fire events have been systematically documented in south-eastern Australia over the last century, but major wildfires are also known to have occurred prior to 1900 (Gill, 1981b; Teague et al., 2010). Major fires include those that have caused loss of human life, have burnt large amounts of land or have caused the substantial loss of property (Teague et al., 2010). There are records of over 70 major fires that have burned in south-eastern Australia since the 1930’s (Teague et al., 2010). Victoria is particularly fire-prone with 52 major fires recorded since 1851, and two-thirds of these occurring in the last 70 years (Teague et al., 2010). Several large wildfires considered to be ‘catastrophic’, because they have had long-lasting social, environmental and economic consequences, have occurred in south-eastern Australia including the 1939 Black Friday fires, the 1983 Ash Wednesday fires, the 2003 Alpine fires, the 2003 Canberra fires, and the 2009 Black Saturday fires (Williams et al., 2008; Teague et al., 2010; Cruz et al., 2012). All of these wildfires, except for the 2003 Canberra fires, occurred in or partly within Victoria. The 1939 Black Friday fires, for instance, tragically claimed 71 lives and burnt 1.5-2 million ha; and in 1983, the Ash Wednesday wildfires killed 47 people, destroyed 2080 houses and burnt 210 000 ha of land (Gill, 1981a; Adams, 2013).

The Black Saturday wildfires that occurred on the 7th February 2009, are some of the largest and most devastating wildfires to have occurred in south-eastern Australia (Cruz et al., 2012). They burned more than 430 000 ha in south-eastern Australia and resulted in the tragic losses of 173 lives and 2133 houses (Teague et al., 2010; Adams, 2013). The economic costs were estimated to be more than $4 billion (Teague et al., 2010). Many wildfires occurred on Black Saturday, but among the largest and most significant were the Kilmore-Murrindindi fires which combined to burn a total of ~228
000 ha of forest, and caused the loss of 159 human lives and 1780 houses (Teague et al., 2010). Further details about the Kilmore-Murrindindi fires are given in Chapter 2.

1-3 Project origin

This project arose after the large and extensive ‘Black Saturday’ wildfires in February 2009. The Kilmore-Murrindindi fires together burned a large region across the Central Highlands of Victoria and provided a unique opportunity to study the effects of a large wildfire on the fauna, and the influence of components of the fire regime and landscape heterogeneity arising from the fires. The Victorian Department of Environment, Land, Water and Planning (previously Department of Sustainability and Environment at the beginning of the project) provided funding for a project designed to investigate the value of fire ‘refuges’ for fauna in this fire-prone region. Hence the Faunal Fire Refuge Project, a collaboration between Deakin and La Trobe Universities was born. The project aimed to identify the occurrence, function and attributes of fire refuges for fauna. It was based on a ‘snapshot’ view of the landscape 2-4 years after wildfire. The overarching project questions were:

1. To what extent does recent burning moderate the impact on fauna and flora of a large wildfire event through the creation of unburnt, or less severely burnt, areas?
2. How important is the extent of natural and transient (fuel reduced) refuge areas in maintaining the diversity of organisms in the landscape and how does it differ between taxonomic groups?
3. What are the characteristics of potential refuge areas that enhance their value for maintaining the diversity and abundance of different taxa?

The project team studied multiple taxa at ~ 90 sites, including plant species and vegetation structure, birds, mammals, invertebrates, and bryophytes. The outcomes of this study are intended to provide knowledge to enhance fire management. This thesis focuses on the response of native and introduced mammals to fire, as well as that of an ecosystem engineer, the superb lyrebird (Menura novaehollandiae).
1-4 Study Area

The study was based in the foothill eucalypt forests of the Central Highlands, Victoria, Australia. An extended description of the study area is given in Chapter 2.

1-5 Overview of the objectives and structure of this thesis

The aim of the research in this thesis is to understand how large fires, fire regime components and landscape heterogeneity influence the occurrence of forest fauna in the foothill eucalypt forests of south-eastern Australia. The two main goals of this thesis are:

i) to determine the effects on fauna of fire severity and fire history at the site-level, and

ii) to investigate the influence of fire-created heterogeneity at the landscape-level on the distribution and abundance of forest fauna.

In this thesis, I focus on four components of the forest fauna: terrestrial native mammals; introduced mammals; arboreal native mammals; and an ecosystem engineer, the superb lyrebird (descriptions in Chapter 2, 6). A brief overview of the thesis structure is given below.

Chapter 2 describes the study area and vegetation, provides a brief background to the fire history and management of the region, and includes a description of mammal species known to occur in the study area and their responses to fire. This provides a setting for the remainder of the thesis.

Chapter 3 presents an investigation of the influence of the fire regime and landscape context on the distribution and occurrence of arboreal mammals. First, I examined the influence of topography, fire severity and fire history on arboreal mammal occurrence at two years after wildfire. Second, I determined the effect of isolation from unburnt
forest on the occurrence of arboreal mammals at severely burnt sites in the post-fire environment.

**Chapter 4** examines the effects of fire regime components on terrestrial native mammal species at two spatial scales. I tested the relative influence of fire severity and fire history at the site level, and fire-induced heterogeneity at the landscape level, on the distribution and abundance of ground-dwelling mammals at 2-3 years after wildfire.

**Chapter 5** determines the relative impacts of a large fire on introduced mammal species, in three parts. First, I tested the relative effects of fire severity, fire history and landscape context on the distribution and abundance of introduced terrestrial species. Next, I determined whether there were patterns in their occurrence after wildfire related to topography. Finally, I considered whether there were correlative patterns of occurrence between introduced and native mammals species based on potential ecological interactions (e.g. predator/prey or competitors) in the post-fire environment.

**Chapter 6** examines the effects of fire, topographic location, and habitat on an ecosystem engineer, the superb lyrebird. I tested the relative influence of fire severity, fire history, and landscape context on the distribution and abundance of this species after wildfire. I analysed whether topography moderated the effect of fire severity on the occurrence of the superb lyrebird. Vegetation and habitat attributes in different topographic locations (gullies and slopes) were examined to see whether they were correlated with the occurrence of the superb lyrebird.

**Chapter 7** provides a summary of a study designed to test whether fire severity and fire history influenced the demography of small mammal species after wildfire. Study design was undertaken and field surveys were initiated, but planned analysis and further interpretation was not followed through due to limitations with insufficient data. A brief summary of the study is presented.
Chapter 8 provides a synthesis of the results from the overall thesis. I summarise key findings and outcomes, implications for the conservation of native mammal species in this region, and identify areas of research that need further investigation.

During this study, I have also contributed to an additional two research papers, and a brochure, which are included as Appendices.

Appendix 1. This paper reviews the concept of fire refuges for fauna, and identifies knowledge gaps and key areas that require research.


Appendix 2. This paper examines the relative effects of fire severity, fire history and topography on the distribution of coarse woody debris in forests. These fire regime components interacted with topography, with implications for the quality of habitat for fauna.


Appendix 3. This brochure contains a summary of the key findings of the Faunal Fire Refuges Project. It outlines the effects of fire severity, fire history, and the value of fire refuges for mammals, birds, invertebrates and plants.

Leonard, S.W.J., Robinson, N.M., Bassett, M., Chia, E.K., Ritchie, E., Buckingham, S., Murphy, N., Gibb, H., Schofield, J., Gibson, M, Bennett, A.F. & Clarke, M.F.
CHAPTER 2  Fire and forest-dwelling mammals in eucalypt foothill forests of central Victoria

Foothills forest, Kinglake National Park.
This chapter provides a background to the study area, an overview of the fire history and fire management in the study area, records of mammal species that occur in the study area and their previous or expected responses to fire.

2-1 Study area

This study was undertaken in the eucalypt foothill forests within the boundary of the Kilmore-Murrindindi fire complex of the Black Saturday fires, in the Central Highlands of the Great Dividing Range, approximately 85 km north of Melbourne (location: 37.285° S, 145.29° E), Victoria, south-east Australia (Figure 2.1). Elevation ranges from ~150-1500 m, but most of the study is conducted at 600-1000 m. Topography is varied, ranging from steep gullies and mountainous ridges, to wide drainage lines surrounded by gentle rising slopes.
Chapter 2: Fire and forest-dwelling mammals in eucalypt foothill forests

The climate is temperate with cool winters (mean monthly minimum 4°C) and mild summers (mean monthly maximum 23°C) (Toolangi, elevation 595 m; Bureau of Meteorology, 2013). Long-term average annual rainfall is ~1200 mm (Figure 2.2; Kinglake West Wallaby Creek, elevation 488 m; Bureau of Meteorology, 2013). Severe drought affected the study area from 1997 to 2009 (van Dijk et al., 2013), and was part of the worst drought on record for south-eastern Australia (Chowdhury et al., 2015). In central Victoria, the average rainfall during this time was 10-20% less than the 1961-1990 average (Cruz et al., 2012). In the study area, the drought ended in 2010 with two consecutive years of above-average rainfall of ~1600 mm in 2010, and ~1400 mm in 2011 (Fig. 2.2; Kinglake West Wallaby Creek; Bureau of Meteorology, 2013). The unusually heavy rainfall in 2010-2012 caused by successive La Niña episodes and sea surface temperatures formed part of the wettest years on record in south-eastern Australia (Chowdhury et al., 2015).

The majority of the study area comprises forested land managed by government agencies, including four national parks (Big River, Kinglake, Lake Eildon, Yarra Ranges), and five state forests (Black Range, Mount Disappointment, Mt Robertson, Toolangi, and Marysville). One site was located on privately-managed land. Townships such as Kinglake and Marysville are near the study area. The state forests of the region are harvested for timber, mostly by single tree selection. However, in this study we avoided areas that were known to have clear felling or areas that had experienced logging within the last 30 years.
Figure 2.2  Average annual rainfall (mm) in the study area during the drought in 1997-2009 was lower than the long-term mean of ~1200 mm. The drought was broken with above average rainfall in the years 2010 and 2011 (Kinglake West Wallaby creek; Bureau of Meteorology, 2013).

2-2  Vegetation of the study area

Vegetation of the study area comprises temperate eucalypt foothill forests, primarily of two Ecological Vegetation Classes, as classified by the Department of Land Water, Environment and Planning (DSE, 2005): Herb-rich Foothill Forest and Damp Forests. Herb-rich Foothill Forest is commonly present in gullies and lower slopes on medium-well drained soils in locations with moderate-high levels of rainfall, and Damp Forests...
are often found on colluvial soils. Herb Rich Foothill Forest vegetation in the study area is characterized by medium to tall forest (up to 25 m), including the dominant tree species messmate stringybark (*Eucalyptus obliqua*), and narrow and broad-leaf peppermint (*E. radiata* and *E. dives*). The sub-canopy contains smaller trees commonly including species of Australian blackwood and silver wattle (*Acacia melanoxylon* and *A. dealbata*). The understorey consists of a sparse to dense layer of shrubs and ferns, commonly including austral bracken (*Pteridium esculentum*), and a dense ground layer of herbs and grasses. Blue gum (*E. globulus*) is a dominant tree species of Damp Forest, and the understorey typically contains tree ferns (*Dicksonia antarctica* and *Cyathea* spp.). Mesic gullies also contain a dense mix of other species such as prickly currant-bush (*Coprosma quadrifida*), musk daisybush (*Olearia argophylla*) and hazel pomaderris (*Pomaderris aspera*) (DSE, 2005).

### 2-3 Fire history and fire management of the study area

Several wildfires have burned in the study area before 2009, including the severe 1939 Black Friday wildfires. Other wildfires that burnt smaller portions of the study area occurred in 1962, 1969, 1983 and 2006. In addition, planned management burns have also been conducted within the study area for fuel reduction, ecological and silvicultural objectives (Leonard *et al.*, 2014a).

In the eucalypt forests of southern Australia, prescribed burning has been conducted since the 1950’s to control fuel loads (McCaw, 2013). Contemporary management practices apply prescribed burning as the main fire management tool to moderate and control unplanned fires by reducing fuel levels and hence the rate of fire spread and the fire intensity (Bradstock *et al.*, 1998; Penman *et al.*, 2014). Prescribed burns can sometimes regulate fire severity (Fernandes & Botelho, 2003) and wildfire occurrence (Boer *et al.*, 2009). Currently, most fire management agencies in Australia are required by law to protect the safety of human life and property from wildfire (Clarke, 2008; McCaw, 2013). As a result, prescribed burning focuses on reducing fuel loads and associated risk in case of a wildfire event, and this is commonly implemented in forests in or around urban areas (Bradstock *et al.*, 1998). Fire management agencies also have
the concurrent goal of conserving biodiversity, ecological communities and ecosystem processes (Clarke, 2008).

Eucalypt foothill forests in south-eastern Australia are subject to repeated prescribed burning for fire management (Adams & Attiwill, 2011). Generally, planned burning can reduce the chance of crown fires (high intensity) for up to five years after burns in southern Australian forests (McCaw, 2013). However, for foothill forests in south-eastern Australia specifically, the recommended tolerable fire interval is a minimum of 10 years for low intensity patchy fires, a minimum of 25 years for high severity fires, and a maximum tolerable fire interval of 100 years (Cheal, 2010). Prescribed burning could reduce wildfire intensity for up to 5-10 years in foothill forests (Price & Bradstock, 2012). In addition, prescribed burns of low intensity creates patchiness and refuges for some species, and allows some patches of vegetation to escape burning at frequent intervals (Penman et al., 2007; Cheal, 2010). Even so, under extreme weather conditions, pre-emptive burning that reduces fuel loads is unlikely to prevent the occurrence of wildfire (Price & Bradstock, 2012).

State and federal inquiries after major fires are a common occurrence in Australia and can spur changes in how fire management in fire-prone landscapes is conducted (Adams & Attiwill, 2011; McCaw, 2013). After the 2009 Black Saturday fires, the State Government established a Royal Commission to understand and respond to the major social, economic and environmental impacts of the wildfires (Teague et al., 2010). Sixty-seven recommendations were made by the Commission, seven of which related to land and fuel management, and one for research and evaluation (Teague et al., 2010). One fire management recommendation was that the amount of planned burning on public land be increased from 1.7% to 5% of the public land area as an annual rolling target, which increased the area of land to be burnt from 130 000 to 385 000 ha in the state per year (Teague et al., 2010). This has affected fire management practices throughout the state, with eucalypt foothill forests being subject to increased prescribed burning. However, the consequences of increased prescribed burning, in addition to the effects of large wildfires, on flora and fauna in foothills forests is unknown. Further understanding of the effects of prescribed burning and wildfire on
biodiversity was also recommended, to improve science-based management (Teague et al., 2010).

2-4 Kilmore-Murrindindi Fires, Black Saturday 2009

In 2009, the Kilmore-Murrindindi fires were some of the largest and most damaging of the Black Saturday wildfires. Extreme fire weather conditions prevailed in the lead up to, and during, the Kilmore-Murrindindi fires. South-eastern Australia had experienced extended drought with below-average rainfall for over a decade, as well as 12 years of above average temperature before 2009 (Teague et al., 2010; Timbal & Fawcett, 2013). In the lead up to the 2009 fires there were two record-breaking heatwaves, from 27-31st January and 6-7 February (Cruz et al., 2012). The first heatwave consisted of temperatures reaching over 43° C for three successive days, whilst the second consisted of temperatures in the mid-40s (Teague et al., 2010). On the 7th February, two separate fires ignited in Kilmore East and Murrindindi (Fig. 2.3), which later merged to form the Kilmore-Murrindindi fire complex (Teague et al., 2010; Cruz et al., 2012). These wildfires were driven by high forest fuel loads with low moisture, on a day of very high temperature (> 45° C) and low humidity (9%), and strong north-westerly winds (afternoon averages of 48-68 km h⁻¹ and gusts of up to 91 km h⁻¹) (Cruz et al., 2012; Price & Bradstock, 2012). This fire complex spread rapidly with average speeds higher than 70 m min⁻¹, and a maximum of 150 m min⁻¹, via short (500 m) and long (> 5 km) range spotting, including up to 33 km ahead of the fire front (Cruz et al., 2012). Severe fire weather was the predominant influence on fire severity, and it generated extreme fire intensities of 70 000- 88 000 kW m⁻¹; high winds also resulted in fire plumes and increased fire spread (Cruz et al., 2012; Price & Bradstock, 2012).
The Kilmore-Murrindindi fire complex burnt a large area of ~228 000 ha of forest, with less than 1% of forest within the fire boundary remaining unburned (Leonard et al., 2014a). Forest vegetation was burnt at different fire intensities resulting in different fire severities. In this study, sites were chosen based on fire severity and fire history. The fire severity of a site was attained by severity mapping from Landsat or SPOT imagery (DSE, 2009b) (Figure 2.3), and further assessment of unburnt and understorey burnt sites was conducted with aerial photographs (DSE, 2009a) (Figure 2.4). Fire severities were grouped into categories describing the amount of vegetation that burnt within the fire boundary: a) unburnt, both the understorey and canopy levels showed no evidence of fire, b) understorey burnt, the ground or shrub layer was burnt but the canopy was unburnt, c) severely burnt, evidence of both understorey burn and crown scorch and/or crown burn (Figure 2.5). Reference sites were located outside of the fire boundary and hence were unburnt during the 2009 wildfire (Figure 2.5). The site selection process also considered the fire history prior to the 2009 wildfire, identifying
sites from two categories: a) long unburnt (burnt > 20 years before 2009 wildfires), and b) short (recent burns < 3 years before 2009) (Figure 2.6). Fire history before 2009 was retrieved from fire records of planned burns and wildfires from (then) Department of Sustainability and Environment. Classifications of fire severity and fire history were confirmed via visual inspection of all sites at 16-18 months after wildfire.

Figure 2.4  An example of an aerial photograph (chlorophyll based) taken after the 2009 wildfires showing unburnt patches of vegetation (red-patches show high chlorophyll) surrounded by a severely burnt landscape (brown/black indicates low chlorophyll).
Figure 2.5  Typical sites in foothill forest in the study area at the time of surveys (2011) representing different fire severity classes a) unburnt, b) understorey, c) severe (crown scorch and crown burn) d) reference and fire history categories (long > 20yrs, short < 3yrs).
Figure 2.6  Fire history classes (short < 3 years, long > 20 years) within the Kilmore-Murrindindi fire complex prior to the 2009 wildfires.

2-5 Mammal species and fire

There have been no systematic studies of the relative effects of fire regime components and landscape heterogeneity on native mammals in foothill forests of the Central Highlands, even though these foothill forests are frequently subject to prescribed burning. General surveys of the mammal fauna have been conducted in the foothill forests of the Central Highlands: specifically surveys in Kinglake National Park (located within the study area) between 1967-1975 (Nicol 1978); surveys conducted from 1966-1980 which included the Central Highlands as part of a state wide overview (Hampton et al., 1982); and an extensive census of the vertebrate fauna in 1991 based in the Central Highlands and beyond, including the coastal areas of the Mornington Peninsula and Western Port regions of Victoria (Lumsden et al., 1991). More recently in 2010, a survey targeting threatened fauna species was conducted in association with the construction of the Sugarloaf pipeline, which included Toolangi State Forest (Sugarloaf Pipeline Alliance, 2010).
A small number of studies on mammals have been conducted within the Kilmore-Murrindindi fire complex since the Black Saturday wildfires 2009. These include studies by the state environment department that a) examined the effectiveness of poison baiting for the introduced red fox (*Vulpes vulpes*) on native terrestrial mammals in the eastern side of the Kilmore-Murrindindi fire complex in 2010 (Robley *et al.*, 2012); b) investigated the distribution of the white-footed dunnart (*Sminthopsis leucopus*) or common dunnart (*S. murina*) in relation to burnt and unburnt sites 2012, in the Cathedral Ranges State Forest and Lake Eildon National Park, both of which occur in the study area (Nelson & Jemison, 2012, and c) in conjunction with local community groups, studied the response of terrestrial mammals to fire history in the Black Range state forest (Macak *et al.*, 2012). In 2012, the state environment department conducted a survey throughout the Central Highlands region to understand the distribution and habitat requirements of threatened species of mammals, birds and fish, including the Leadbeater’s possum (*Gymnobelidus leadbeateri*) in wet forests, smoky mouse (*Pseudomys fumeus*), greater glider (*Petauroides volans*), and yellow-bellied glider (*Petaurus australis*) (Lumsden *et al.*, 2013). The occupancy and abundance of the introduced sambar deer (*Cervus unicolor*) in Kinglake National Park after wildfire has also been investigated (Forsyth *et al.*, 2011; Forsyth *et al.*, 2012). However, no study has examined the effects of fire severity, fire history and landscape context on the native and introduced mammal fauna at large spatial scales across the fire region.

In this study, I examined the response of mammals to components of the fire regime and landscape heterogeneity after wildfire in this fire-prone region, 2-3 years after the Black Saturday event in 2009. Three focal groups of mammals were chosen for study: a) arboreal mammals, b) terrestrial, ground-dwelling mammal species (hereafter referred to as terrestrial), and c) introduced mammal species. Species in each of these groups are likely to be affected by fire severity, fire history and landscape heterogeneity, depending upon their habits, habitat requirements, dispersal and recolonisation abilities, and flexibility to disturbance.
Eleven species of arboreal mammal (all marsupials) have been recorded in the foothill/damp forests of the study area (Table 2.1) (Lumsden et al., 1991). These arboreal species vary in size and weight, ranging from the feathertail glider (*Acrobates pygmaeus*) weighing only 10 g, up to 14 kg for the koala (*Phascolarctos cinereus*). One arboreal species, the Leadbeater’s possum is listed as Critically Endangered under the federal Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act). Two species are listed as threatened under the Flora and Fauna Guarantee Act (FFG) 1988 of Victoria, including the Leadbeater’s possum, and the brush-tailed phascogale (*Phascogale tapoatafa*) The Leadbeater’s possum is generally restricted to the taller mountain ash (*E. regnans*) forests of the Central Highlands (Lumsden et al., 1991); and hence was not part of the focal group for this study. The brush-tailed phascogale occurs in the study area. Several species are uncommon, including the uncommon but widespread feathertail glider, the uncommon but moderately distributed eastern pygmy-possum (*Cercartetus nanus*), and the yellow-bellied glider. The remaining arboreal species that are focal to this study are widespread and common (Figure 2.7).
Table 2.1  Mammal species (excluding bats) that occur in Foothill/Damp forests of the Central Highlands (Lumsden et al., 1991).

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arboreal mammals</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acrobatidae</td>
<td>Acrobates pygmaeus</td>
<td>Feathertail glider</td>
</tr>
<tr>
<td>Burramyidae</td>
<td>Cercartetus nanus</td>
<td>Eastern pygmy-possum</td>
</tr>
<tr>
<td>Dasyuridae</td>
<td>Phascogale tapoataf</td>
<td>Brush-tailed phascogale</td>
</tr>
<tr>
<td>Petauridae</td>
<td>Gymnobelideus leadbeateri</td>
<td>Leadbeater’s possum</td>
</tr>
<tr>
<td>Petauridae</td>
<td>Petaurus australis</td>
<td>Yellow-bellied glider</td>
</tr>
<tr>
<td>Petauridae</td>
<td>Petaurus breviceps</td>
<td>Sugar glider</td>
</tr>
<tr>
<td>Petauridae</td>
<td>Petauroides volans</td>
<td>Greater glider</td>
</tr>
<tr>
<td>Phascolarctidae</td>
<td>Phascolartos cinereus</td>
<td>Koala</td>
</tr>
<tr>
<td>Pseudocheiridae</td>
<td>Pseudocheirus peregrinus</td>
<td>Common ringtail possum</td>
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<td>Phalangeridae</td>
<td>Trichosurus cunninghami</td>
<td>Mountain brushtail possum</td>
</tr>
<tr>
<td>Phalangeridae</td>
<td>Trichosurus vulpecula</td>
<td>Common brushtail possum</td>
</tr>
<tr>
<td>Terrestrial native mammals</td>
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<tr>
<td>Dasyuridae</td>
<td>Antechinus agilis</td>
<td>Agile antechinus</td>
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<td>Dasyuridae</td>
<td>Antechinus swainsonii</td>
<td>Dusky antechinus</td>
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<td>Dasyuridae</td>
<td>Dasyurus maculatus</td>
<td>Tiger quoll (Spot-tailed quoll)</td>
</tr>
<tr>
<td>Dasyuridae</td>
<td>Dasyurus viverrinus*</td>
<td>Eastern quoll</td>
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<td>Dasyuridae</td>
<td>Sminthopsis leucopus</td>
<td>White-footed dunnart</td>
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<td>Muridae</td>
<td>Mastacomys fuscus</td>
<td>Broad-toothed rat</td>
</tr>
<tr>
<td>Muridae</td>
<td>Pseudomys fumeus</td>
<td>Smoky mouse</td>
</tr>
<tr>
<td>Muridae</td>
<td>Rattus fuscipes</td>
<td>Bush rat</td>
</tr>
<tr>
<td>Muridae</td>
<td>Rattus lutreolus</td>
<td>Swamp rat</td>
</tr>
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<td>Macropodidae</td>
<td>Wallabia bicolor</td>
<td>Swamp wallaby</td>
</tr>
<tr>
<td>Macropodidae</td>
<td>Macropus giganteus</td>
<td>Eastern grey kangaroo</td>
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<td>Long-nosed bandicoot</td>
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<td>Vombatus ursinus</td>
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<td>Introduced mammal species</td>
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<td>Red fox</td>
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<td>Cervidae</td>
<td>Cervus unicolor</td>
<td>Sambar deer</td>
</tr>
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<td>Family</td>
<td>Species</td>
<td>Common Name</td>
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</tr>
<tr>
<td>Felidae</td>
<td><em>Felis catus</em></td>
<td>Feral cat</td>
</tr>
<tr>
<td>Leporidae</td>
<td><em>Oryctolagus cuniculus</em></td>
<td>European rabbit</td>
</tr>
<tr>
<td>Muridae</td>
<td><em>Mus musculus</em></td>
<td>House mouse</td>
</tr>
<tr>
<td>Muridae</td>
<td><em>Rattus rattus</em></td>
<td>Black rat</td>
</tr>
</tbody>
</table>

*Extinct species

Studies examining the response of arboreal mammals to fire in south-eastern Australia have primarily been based in the wet montane forests of Victoria and the dry sclerophyll forests of NSW (Newsome et al., 1975; Lunney, 1987; Catling, 1991; Catling et al., 2001; Russell et al., 2003; Matthews et al., 2007; Banks et al., 2011a; Collins, 2012; Lindenmayer et al., 2013; Berry et al., 2015a) (Table 2.2). None of these studies occurred in the foothill forests of the Central Highlands, and none have tested the relative effects of fire severity, fire history, and landscape heterogeneity on arboreal mammals.

Arboreal mammal species in foothill forests are likely to respond negatively to increasing fire severity, particular to high intensity fire that affects tree canopy and tree hollows. This is because many of these arboreal species feed on foliage in the canopy or on tall shrubs, and tree hollows are essential habitat for nesting (e.g. greater glider (Strahan, 1995; Hume, 1999). Fire that burns the ground or understorey levels may have less of an impact on arboreal mammals because most species essentially use the middle-upper parts of the canopy.

I examine the response of arboreal mammals to fire regime components and landscape heterogeneity in Chapter 3.
Chapter 2: Fire and forest-dwelling mammals in eucalypt foothill forests

Authors and sources:

Figure 2.7  Arboreal mammal species known to occur in the study area including a) brush-tailed phascogale, b) sugar glider, c) mountain brushtail possum, d) common brushtail possum, e) common ringtail possum, f) greater glider, and e) koala.
Table 2.2  Description of arboreal mammal species that are focal to this study, and references to studies of their responses to fire in forests of southeastern Australia. No studies have been conducted in the foothill forests of the Central Highlands, Victoria.

<table>
<thead>
<tr>
<th>Species</th>
<th>Vegetation type occupied in region</th>
<th>Weight range (g)</th>
<th>Habit, Habitat</th>
<th>Diet</th>
<th>Fire research in wet montane forest, Victoria</th>
<th>Fire research in dry sclerophyll forest, NSW</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sugar glider (&lt;i&gt;Petaurus breviceps&lt;/i&gt;)</td>
<td>Foothill forest, damp forest</td>
<td>95-160</td>
<td>Arboreal. Associated with Acacias&lt;sup&gt;5&lt;/sup&gt;. Present in all forest levels, and often observed on the trunk or major branches&lt;sup&gt;6&lt;/sup&gt;. Nests in tree hollows&lt;sup&gt;4&lt;/sup&gt;.</td>
<td>Arthropods, insect and plant exudates including eucalypt sap, Acacia gums, nectar, pollen, honeydew&lt;sup&gt;3,5&lt;/sup&gt;.</td>
<td>Lindenmayer et al., (2013)</td>
<td>Lunney, (1987)</td>
</tr>
<tr>
<td>Mountain brushtail possum (&lt;i&gt;Trichosurus cunninghami&lt;/i&gt;)</td>
<td>Foothill forest, damp forest</td>
<td>2500-4500</td>
<td>Arboreal/terrestrial. Uses all levels of forest strata, including lower-mid levels and ground&lt;sup&gt;6&lt;/sup&gt;. Dens primarily in tree hollows, branches, logs&lt;sup&gt;1&lt;/sup&gt;.</td>
<td>Fruit, buds, seeds, mesophytic shrubs, lichen, fungi, bark&lt;sup&gt;5,1&lt;/sup&gt;.</td>
<td>Banks et al., (2011a)</td>
<td>Catling, (2011)</td>
</tr>
<tr>
<td>Species</td>
<td>Vegetation type occupied in region</td>
<td>Weight range (g)</td>
<td>Habit, Habitat</td>
<td>Diet</td>
<td>Fire research in wet montane forest, Victoria</td>
<td>Fire research in dry sclerophyll forest, NSW</td>
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</tr>
<tr>
<td>Common brushtail possum <em>(Trichosurus vulpecula)</em></td>
<td>Foothill forest, damp forest</td>
<td>1200-4500</td>
<td>Arboreal/terrestrial. Uses all levels of forest strata, including mid-canopy levels, bole and ground. Similar use of dens to mountain brushtail possum.</td>
<td>Mostly foliage, also flowers and fruit.</td>
<td>Newsome et al., (1975)</td>
<td>Catling, (1991)</td>
</tr>
</tbody>
</table>

*Scansorial, detected during terrestrial surveys.*

2-5-2 Native terrestrial mammal species

There are fourteen native mammal species that are predominantly ground-dwelling that have been recorded in the foothill/damp forests of the study area (Table 2.1) (Lumsden et al., 1991). These species range from small to large in size including the agile antechinus (*Antechinus agilis*; 16 g body weight) to the eastern grey kangaroo (*Macropus giganteus*; up to 66 kg). The eastern quoll (*Dasyurus viverrinus*) once occurred but has been regionally extinct from the mainland since the 1940’s.

Currently, two species are listed as Endangered under the federal EPBC Act and threatened under the State FFG Act: the spotted-tailed quoll (*Dasyurus maculatus*; South-east mainland population), and the smoky mouse (*Pseudomys fumeus*). The broad-toothed rat (*Mastacomys fuscus*) is also threatened under the State FFG Act. The remaining terrestrial mammal species in the study area are widespread and common, with the exception of the swamp rat (*Rattus lutreolus*), white-footed dunnart, long-nosed bandicoot (*Perameles nasuta*) and the eastern grey kangaroo. The bush rat (*R. fuscipes*) is considered abundant (Figure 2.8) (Lumsden et al., 1991).
Figure 2.8  Terrestrial native mammal species known to occur in the study area including a) dusky antechinus, b) agile antechinus, c) bush rat, d) long-nosed bandicoot, e) short-beaked echidna, f) common wombat, g) swamp wallaby, h) eastern grey kangaroo.
Chapter 2: Fire and forest-dwelling mammals in eucalypt foothill forests

Research designed to identify the effects of fire on terrestrial native mammals in south-eastern Australian forests (aside from community-based surveys), has mainly occurred in the dry sclerophyll forests of coastal NSW, with few studies in Victoria, mostly in wet montane forest of the Central Highlands (Table 2.3). Studies conducted in the dry forests of NSW focused on the initial effects of fire (including clearing and burning) and time since fire on the abundance of mammal species at different times in the post-fire succession, often in relation to changes in habitat structure (Newsome et al., 1975; Recher et al., 1975b; Fox & McKay, 1981; Fox, 1982; Lunney et al., 1987; Catling, 1991; Catling et al., 2001; Recher et al., 2009; Arthur et al., 2012), whilst one study tracked the movements of the swamp wallaby (Wallabia bicolor) shortly after prescribed burns and wildfire (Garvey et al., 2010). In the wet montane forests of Victoria, the agile antechinus and bush rat were examined in unburnt compared with severely burnt sites (not understorey burnt), and the effect of distance to unburnt forest, with evidence of in situ survival of these species (Banks et al., 2011b). In Victoria, one study examined the effects of clearing and burning in sclerophyll eucalypt forests of Gippsland, Victoria, (Friend, 1979). No study has investigated the effects of fire severity, fire history and landscape heterogeneity on native terrestrial mammals in foothill forests of the Central Highlands.

Terrestrial native mammal species in foothill forests are likely to respond in different ways to fire components, most likely due to the indirect effects of fire via changes in vegetation that provides habitat for species (Fox, 1982). These species are likely to be affected in different ways in relation to fire severity (i.e. where the understorey is burnt, or both the ground layer and canopy layers are burnt). Spatial isolation to unburnt forest is also likely to influence species recovery after fire (Banks et al., 2011b).

I examine the response of terrestrial native mammals to fire regime components and landscape heterogeneity in Chapter 4.
Table 2.3 Description of terrestrial native mammal species that are focal to this study, and references to studies of their responses to fire in different forest types of south-eastern Australia. No studies have been conducted in the foothill forests of the Central Highlands, Victoria.

<table>
<thead>
<tr>
<th>Species</th>
<th>Vegetation Type</th>
<th>Weight ranges (g)</th>
<th>Habit, Habitat</th>
<th>Diet</th>
<th>Fire research in wet montane forest or dry sclerophyll forest, Victoria</th>
<th>Fire research in dry sclerophyll forest, NSW</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>Vegetation Type</td>
<td>Weight ranges (g)</td>
<td>Habit, Habitat</td>
<td>Diet</td>
<td>Fire research in wet montane forest or dry sclerophyll forest, Victoria</td>
<td>Fire research in dry sclerophyll forest, NSW</td>
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<td>---------------------------------------------</td>
</tr>
</tbody>
</table>

2-5-3 Introduced mammal species

Numerous mammal species were introduced into Victoria from Europe in the 1900’s motivated by settlers wanting familiar surroundings from their homeland (Lumsden et al., 1991). Many introduced mammal species have become successful in expanding their range throughout Australia. Seven introduced mammal species have been recorded in the region (Table 2.1) (Lumsden et al., 1991). The feral cat (Felis catus), red fox, European rabbit (Oryctolagus cuniculus), and sambar deer are all listed as threats for native species and plants under the federal EPBC Act. In addition, threat abatement plans have been created specifically for predation by the feral cat and red fox, and for competition and land degradation by the European rabbit. Predation of native animals by the feral cat and red fox, and reduction in biodiversity of native vegetation by sambar deer have also been recognised as potentially threatening processes under the Victorian State FFG Act. All of the introduced mammal species in this study are widespread and common, except for the black rat (R. rattus) (Lumsden et al., 1991).

Research in south-eastern Australian forests specifically examining the response of introduced mammals to fire has been primarily in dry sclerophyll forests of coastal NSW (Table 2.4). In dry forests of NSW, introduced species have shown mixed responses to fire, with fluctuations in abundance during the post-fire succession (Newsome et al., 1975; Recher et al., 1975b; Fox & McKay, 1981; Fox, 1982; Lunney et al., 1987; Catling, 1991; Catling et al., 2001; Recher et al., 2009; Arthur et al., 2012). One study has been conducted in foothill forests within the study area: this study reported that the abundance of the sambar deer was reduced in areas of high severity burns (Forsyth et al., 2012). No study has examined the relative effects of fire severity, fire history and landscape context on a suite of terrestrial introduced mammal species in foothill forests in the Central Highlands.

Introduced species are a threat to populations of native fauna (Vitousek et al., 1997b). Therefore it is important to understand how introduced species are influenced by fire. Introduced mammal species in foothill forests are likely to respond in different ways
to fire components; most likely from indirect effects associated with changes in vegetation that influences their habitat components, as well as by species interactions such as predator/prey and competition (Arthur et al., 2012).

I examine the response of terrestrial introduced mammals to fire regime components and landscape heterogeneity in Chapter 5.
Table 2.4 Description of focal introduced terrestrial mammal species and references to studies that have examined the response of mammals to fire in dry sclerophyll forests, south-eastern Australia.

<table>
<thead>
<tr>
<th>Species</th>
<th>Vegetation Type</th>
<th>Weight range (kg)</th>
<th>Habitat[1]</th>
<th>Diet</th>
<th>Fire research in dry sclerophyll forest, NSW</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Mus musculus)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black rat</td>
<td>Damp forest</td>
<td>0.095 - 0.340</td>
<td>First entry into Australia may have been with the First Fleet in 1988. Present in coastal regions, with more found close to urban areas.</td>
<td>Omnivorous with a wide ranging diet[1].</td>
<td></td>
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<tr>
<td>(Rattus rattus)</td>
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<td></td>
<td></td>
<td></td>
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<tr>
<td>(Vulpes vulpes)</td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Feral Cat</td>
<td>Foothill forest, damp forest</td>
<td>2.5-6.2</td>
<td>Possibly introduced before European settlement. Present in all ecosystems in Australia.</td>
<td>Predator. Feeds on native small-medium sized vertebrates, including amphibians, reptiles, birds, and mammals, and invertebrates[1].</td>
<td></td>
</tr>
<tr>
<td>(Felis catus)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>Vegetation Type</td>
<td>Weight range (kg)</td>
<td>Habitat¹</td>
<td>Diet</td>
<td>Fire research in dry sclerophyll forest, NSW</td>
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</tr>
<tr>
<td>European rabbit</td>
<td>Foothill forest, damp forest</td>
<td>0.96-2.42</td>
<td>Deliberately brought into south-eastern Australia in 1858 from England. Associated with water sources.</td>
<td>Grazes primarily on grasses and herbs, and also feeds on bark, leaves, roots, shrubs¹.</td>
<td>Newsome et al., (1975) Catling, (1991)</td>
</tr>
</tbody>
</table>

CHAPTER 3 Fire severity and fire-induced landscape heterogeneity affect arboreal mammals

This chapter has been published as:


Koala (Phascolarctos cinereus), and Kinglake National Park.
3-1 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 recolonisation 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.
Chapter 3: Fire severity and fire-induced landscape heterogeneity affect arboreal mammals

3-2 Introduction

Fire exerts a profound influence on the structure and function of ecosystems worldwide (Bond & 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 understorey 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., 2014a; Berry et al., 2015b). 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 & 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).
Chapter 3: Fire severity and fire-induced landscape heterogeneity affect arboreal mammals

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 recolonise (Brotons et al., 2005; Watson et al., 2012a; 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 recolonisation 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 recolonisation (Banks et al., 2011b), 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 & 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 recolonisation 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.

3-3 Material and Methods

3-3-1 Study area

The study was undertaken in temperate eucalypt forests of central Victoria, south-east Australia (Figure 3.1). Elevation ranges from ~150-1000 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.
Figure 3.1 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 > 20yrs, or short < 3yrs). 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 1km radius.

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 & 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 understorey...
species that prefer moister conditions (e.g. rough tree-fern (*Cyathea australis*) and common understorey-fern (*Calochlaena dubia*). 

3-3-2 Site selection

Sites were selected in the western part of the Kilmore East-Murrindindi fire complex, mostly in managed forests or national parks (Figure 3.1). 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 yrs before 2009, burnt within 3 yrs prior to 2009), with four replicates of each of the six combinations. Sites were located with a fire severity layer, aerial photography and fire history data 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.

3-3-3 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-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 carried out ~3.5 years post-wildfire, with four survey rounds at 14 sites from August-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 mins. 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.

3-3-4 Statistical analyses

Response and predictor variables. We used regression modelling to examine: a) the effects of topography (gullies and slopes) on the abundance of arboreal mammals; b) the effect of fire severity, fire history and time since fire on the number of arboreal mammals seen or heard; and c) 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 and common ringtail possum (*Pseudocheirus peregrinus*), and species richness, all over four surveys. Other species were not modelled due to insufficient records (i.e. less than 10 records per species).
Predictor variables for each component of the study are given in Table 3.1. 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 & Lindenmayer, 1997). For the fire regime study, we counted the number of large trees (diameter > 60 cm) on each gully and slope transect (100 m x 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 x 50 m), all within severely-burnt forest, on opposite sides of the road at even distances.

Table 3.1 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.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Level</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Fire regime study</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Topography</td>
<td>Gully</td>
<td>Topographic location</td>
</tr>
<tr>
<td></td>
<td>Slope</td>
<td></td>
</tr>
<tr>
<td>Severity</td>
<td>Unburnt</td>
<td>Not burnt in 2009 wildfire</td>
</tr>
<tr>
<td></td>
<td>Understorey</td>
<td>Ground and/or understorey burnt</td>
</tr>
<tr>
<td></td>
<td>Severe</td>
<td>Canopy scorched or completely burnt</td>
</tr>
<tr>
<td>History</td>
<td>Long</td>
<td>Unburnt ≥20 years before 2009 wildfire</td>
</tr>
<tr>
<td></td>
<td>Short</td>
<td>Burnt &lt;3 years before 2009 wildfire</td>
</tr>
<tr>
<td>Time since fire</td>
<td>20yrs</td>
<td>&gt; 20 years since the last fire</td>
</tr>
<tr>
<td></td>
<td>3yrs</td>
<td>&lt; 3 years since the last fire</td>
</tr>
<tr>
<td></td>
<td>0yrs</td>
<td>Burnt in the 2009 wildfires</td>
</tr>
<tr>
<td>Tree</td>
<td>Continuous</td>
<td>Number of large trees &gt; 60 cm diameter</td>
</tr>
<tr>
<td><strong>Isolation study</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Area unburnt</td>
<td>Continuous</td>
<td>Area (ha) of unburnt forest within 1 km radius</td>
</tr>
<tr>
<td>Area understorey</td>
<td>Continuous</td>
<td>Area (ha) of unburnt and understorey burnt forest combined within 1 km radius</td>
</tr>
<tr>
<td>Tree</td>
<td>Continuous</td>
<td>Number of large trees &gt; 60 cm diameter</td>
</tr>
<tr>
<td>Reserve</td>
<td>NA</td>
<td>Geographic location of sites based on land management (random factor in all models)</td>
</tr>
</tbody>
</table>
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 modelled 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 3.1). 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 Table S3.1) (Burnham & 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 (AICc), differences in AICc (ΔAICc), and Akaike weights (w_i). All models with ΔAICc < 2 from the top model (lowest AIC) were considered to have substantial support (Burnham & 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 & 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 & Schielzeth, 2013).
Chapter 3: Fire severity and fire-induced landscape heterogeneity affect arboreal mammals

All statistical analyses were conducted in the R statistical package version 3.1.1 (R Development Core Team, 2014). GLMMs and predictions were run with ‘lme4’, ‘MuMIn’ and ‘AICcmodavg’ packages (Bartoń, 2014; Bates et al., 2014; Mazerolle, 2014). R² values were calculated with the ‘rsquared.glmm’ function (Lefcheck & Casallas, 2014).

3-4 Results

3-4-1 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) (Table S3.2). 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 understorey (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 a) any arboreal mammal and b) 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 (F₂:44, =0.537, P=0.588) or for the greater glider (F₂:25, =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 (Table S3.2) (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 (Table 3.2). In total, 44 animals were recorded at 14 sites on 112 transects.

3-4-2 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 3.2). There were no “best” models for which \( w_i > 0.90 \), hence we considered models with substantial support (\( \Delta AICc < 2 \)) and examined their parameter estimates.

For the total number of arboreal mammals, three models including a) fire severity, b) large trees, and c) fire severity plus fire history) had substantial support (Table 3.2). Upon examination of the parameter estimates, the abundance of arboreal mammals was most strongly influenced by fire severity (Table 3.3). In both the severity model, and the severity plus history model, fewer individuals were observed in severely-burnt sites than at unburnt sites (Figure 3.2). 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 3.3).

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 3.2). Fire severity and the number of large trees were important variables in both models (Table 3.3). Fewer individuals were observed in severely burnt than in unburnt sites, and greater gliders were positively associated with sites containing more large trees (Figure 3.2).
### Table 3.2 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 R²m (variance explained by fixed predictors) and R²c (variance explained by both fixed and random predictors). *†Log transformed.*

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Model structure</th>
<th>df</th>
<th>Log likelihood</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Akaike weight</th>
<th>R²m</th>
<th>R²c</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Fire regime study</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All arboreal mammals</td>
<td>Severity</td>
<td>5</td>
<td>-45.29</td>
<td>103.9</td>
<td>0.00</td>
<td>0.39</td>
<td>0.33</td>
<td>0.33</td>
</tr>
<tr>
<td></td>
<td>Tree</td>
<td>4</td>
<td>-47.38</td>
<td>104.9</td>
<td>0.96</td>
<td>0.24</td>
<td>0.13</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td>Severity + History</td>
<td>6</td>
<td>-44.37</td>
<td>105.7</td>
<td>1.77</td>
<td>0.16</td>
<td>0.38</td>
<td>0.38</td>
</tr>
<tr>
<td>Greater glider</td>
<td>Severity + Tree</td>
<td>5</td>
<td>-28.14</td>
<td>69.6</td>
<td>0.00</td>
<td>0.59</td>
<td>0.62</td>
<td>0.86</td>
</tr>
<tr>
<td></td>
<td>Severity + History + Tree</td>
<td>6</td>
<td>-27.10</td>
<td>71.1</td>
<td>1.54</td>
<td>0.28</td>
<td>0.61</td>
<td>0.90</td>
</tr>
<tr>
<td>Species richness</td>
<td>Severity + History</td>
<td>5</td>
<td>-31.43</td>
<td>76.2</td>
<td>0.00</td>
<td>0.34</td>
<td>0.35</td>
<td>0.35</td>
</tr>
<tr>
<td></td>
<td>Tree</td>
<td>3</td>
<td>-34.79</td>
<td>76.8</td>
<td>0.59</td>
<td>0.25</td>
<td>0.07</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>Severity</td>
<td>4</td>
<td>-33.74</td>
<td>77.6</td>
<td>1.38</td>
<td>0.17</td>
<td>0.20</td>
<td>0.20</td>
</tr>
<tr>
<td><strong>Isolation study</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All arboreal mammals</td>
<td>Area understorey†</td>
<td>4</td>
<td>-26.76</td>
<td>66.2</td>
<td>0.00</td>
<td>0.68</td>
<td>0.65</td>
<td>0.75</td>
</tr>
<tr>
<td>Greater glider</td>
<td>Area understorey + Tree</td>
<td>4</td>
<td>-15.52</td>
<td>43.5</td>
<td>0.00</td>
<td>0.49</td>
<td>0.40</td>
<td>0.65</td>
</tr>
<tr>
<td></td>
<td>Area unburnt + Tree</td>
<td>4</td>
<td>-15.79</td>
<td>44.0</td>
<td>0.55</td>
<td>0.38</td>
<td>0.27</td>
<td>0.64</td>
</tr>
<tr>
<td>Common ringtail possum</td>
<td>Area understorey† + Tree</td>
<td>4</td>
<td>-15.06</td>
<td>42.6</td>
<td>0.00</td>
<td>0.35</td>
<td>0.60</td>
<td>0.85</td>
</tr>
<tr>
<td></td>
<td>Tree</td>
<td>3</td>
<td>-17.26</td>
<td>42.9</td>
<td>0.36</td>
<td>0.29</td>
<td>0.16</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>Area understorey</td>
<td>3</td>
<td>-17.32</td>
<td>43.0</td>
<td>0.48</td>
<td>0.28</td>
<td>0.64</td>
<td>0.84</td>
</tr>
<tr>
<td>Species richness</td>
<td>Area understorey</td>
<td>3</td>
<td>-16.86</td>
<td>42.1</td>
<td>0.00</td>
<td>0.65</td>
<td>0.60</td>
<td>0.60</td>
</tr>
</tbody>
</table>
Table 3.3  Model parameters and coefficients for models with substantial support (i.e. $\Delta$AICc < 2) in the fire regime study.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Model structure</th>
<th>Variable</th>
<th>Parameter</th>
<th>Coefficient</th>
<th>SE</th>
<th>Z</th>
</tr>
</thead>
<tbody>
<tr>
<td>All arboreal mammals</td>
<td>Severity</td>
<td>Severity</td>
<td>Intercept</td>
<td>1.00</td>
<td>0.34</td>
<td>2.98</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Understorey</td>
<td>-0.17</td>
<td>0.46</td>
<td>-0.37</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Severe</td>
<td>-1.49*</td>
<td>0.58*</td>
<td>-2.59*</td>
</tr>
<tr>
<td>Tree</td>
<td>Tree</td>
<td>Tree</td>
<td>Intercept</td>
<td>-0.69</td>
<td>0.77</td>
<td>-0.90</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Severe</td>
<td>-1.49*</td>
<td>0.58*</td>
<td>-2.59*</td>
</tr>
<tr>
<td></td>
<td>Severity + History</td>
<td>Severity</td>
<td>Intercept</td>
<td>1.29</td>
<td>0.43</td>
<td>2.96</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Understorey</td>
<td>-0.21</td>
<td>0.50</td>
<td>-0.42</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Severe</td>
<td>-1.54*</td>
<td>0.65*</td>
<td>-2.38*</td>
</tr>
<tr>
<td>Greater glider</td>
<td>Severity + Tree</td>
<td>Severity</td>
<td>Intercept</td>
<td>-2.06</td>
<td>1.26</td>
<td>-1.64</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Understorey</td>
<td>0.43</td>
<td>0.48</td>
<td>0.90</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Severe</td>
<td>-2.52*</td>
<td>1.06*</td>
<td>-2.38*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tree</td>
<td>Intercept</td>
<td>0.28*</td>
<td>0.11*</td>
<td>2.51*</td>
</tr>
<tr>
<td></td>
<td>Severity + History + Tree</td>
<td>Severity</td>
<td>Intercept</td>
<td>-2.31</td>
<td>1.14</td>
<td>-1.63</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Understorey</td>
<td>0.39</td>
<td>0.51</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Severe</td>
<td>-2.80*</td>
<td>1.09*</td>
<td>-2.58*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>History</td>
<td>Short</td>
<td>-0.75</td>
<td>0.52</td>
<td>-1.44</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tree</td>
<td>Intercept</td>
<td>0.35*</td>
<td>0.13*</td>
<td>2.70*</td>
</tr>
<tr>
<td>Species richness</td>
<td>Severity + History</td>
<td>Severity</td>
<td>Intercept</td>
<td>0.88</td>
<td>0.29</td>
<td>3.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Understorey</td>
<td>-0.15</td>
<td>0.39</td>
<td>-0.39</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Severe</td>
<td>-0.85</td>
<td>0.49</td>
<td>-1.74</td>
</tr>
<tr>
<td></td>
<td></td>
<td>History</td>
<td>Short</td>
<td>-0.79*</td>
<td>0.38*</td>
<td>-2.07*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tree</td>
<td>Intercept</td>
<td>-0.29</td>
<td>0.52</td>
<td>-0.56</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Tree</td>
<td>0.08</td>
<td>0.06</td>
<td>1.22</td>
</tr>
<tr>
<td>Severity</td>
<td>Severity</td>
<td>Intercept</td>
<td>0.56</td>
<td>0.27</td>
<td>2.09</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Understorey</td>
<td>-0.15</td>
<td>0.39</td>
<td>-0.39</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Severe</td>
<td>-0.85</td>
<td>0.49</td>
<td>-1.74</td>
<td></td>
</tr>
</tbody>
</table>

*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).
Figure 3.2  Predicted values with 95% CI from univariate models of important variables and response variables for the fire regime study and the isolation study including a) total number of arboreal mammals, b) number of greater gliders, and c) number of common ringtail possums.
Species richness had three plausible models including 1) fire severity plus fire history, 2) large trees, and 3) fire severity (Table 3.2). The parameter estimates of these models showed that fire history was the only influential variable (Table 3.3). Species richness was lower at sites with a short fire history where there had been a recent burn (< 3 years) prior to the wildfires.

### 3.4.3 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 3.2). The number of mammals increased with the combined area of surrounding unburnt and understorey-only burnt forest (Table 3.4; Figure 3.2).

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 3.2). There was a positive association between greater glider abundance and area of surrounding unburnt forest (Figure 3.2), and combined unburnt and understorey-only burnt forest (Table 3.4). Surprisingly, there was also a negative relationship with the number of large trees (Table 3.4).

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 3.2). 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 3.4, Figure 3.2).
Table 3.4  Model parameters and coefficients for models with substantial support (i.e. $\Delta$AICc < 2) in the isolation study.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Model structure</th>
<th>Variable</th>
<th>Coefficient</th>
<th>SE</th>
<th>Z</th>
</tr>
</thead>
<tbody>
<tr>
<td>All arboreal mammals</td>
<td>Area understorey</td>
<td>Intercept</td>
<td>0.28</td>
<td>0.51</td>
<td>0.56</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Area understorey</td>
<td>1.35*</td>
<td>0.57*</td>
<td>2.35*</td>
</tr>
<tr>
<td>Greater glider</td>
<td>Area understorey + Tree</td>
<td>Intercept</td>
<td>-0.83</td>
<td>0.84</td>
<td>-0.99</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Area understorey</td>
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<td>0.40*</td>
<td>2.21*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tree</td>
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<td>0.33*</td>
<td>-3.10*</td>
</tr>
<tr>
<td></td>
<td>Area unburnt + Tree</td>
<td>Intercept</td>
<td>-0.80</td>
<td>0.96</td>
<td>-0.84</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Area unburnt</td>
<td>0.69*</td>
<td>0.29*</td>
<td>2.36*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tree</td>
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<td>0.31*</td>
<td>-2.75*</td>
</tr>
<tr>
<td>Common ringtail possum</td>
<td>Area understorey + Tree</td>
<td>Intercept</td>
<td>-1.32</td>
<td>1.07</td>
<td>-1.23</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Area understorey</td>
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<td>1.22</td>
<td>1.41</td>
</tr>
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<td>0.35</td>
<td>1.79</td>
</tr>
<tr>
<td></td>
<td>Tree</td>
<td>Intercept</td>
<td>-0.61</td>
<td>0.86</td>
<td>-0.72</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tree</td>
<td>0.75*</td>
<td>0.38*</td>
<td>1.98*</td>
</tr>
<tr>
<td>Species richness</td>
<td>Area understorey</td>
<td>Intercept</td>
<td>-1.15</td>
<td>1.09</td>
<td>-1.05</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Area understorey</td>
<td>1.88</td>
<td>1.30</td>
<td>1.45</td>
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<tr>
<td></td>
<td></td>
<td>Area understorey</td>
<td>0.99*</td>
<td>0.49*</td>
<td>2.01*</td>
</tr>
</tbody>
</table>

†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).

Species richness of arboreal mammals had one model with support (the top model), the combined area of unburnt and understorey-only burnt forest (Table 3.2). Species richness increased with the surrounding area of both unburnt and understorey burnt forest (Table 3.4).

3-5 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 (understorey 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., 2011a). Other species in these forests are also vulnerable to low rainfall, for example the sugar glider (Lindenmayer et al., 2011b). 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.

3-5-1 **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., 2015a). 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).

3-5-2 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., 2011a). 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 & Loyn, 2002). Other structural changes, such as reduced availability of tree hollows for nesting (Inions et al., 1989; Banks et al., 2011a) 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., 2011a; 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.

3-5-3 Spatial isolation

In severely burnt forest, sites that were more isolated from unburnt or understorey-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 recolonisation by individuals dispersing into the burned environment from unburned forest (Banks et al., 2011b). 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 recolonisation 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., 2011b; Watson et al., 2012a; 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.

3-5-4 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 recolonisation from nearby source areas. Thus,
scarce patches of unburnt forest within and adjacent to the fire boundary (< 1% of the
total area: Leonard et al., 2014a) 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., 2014a). 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 are 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).

3-6 Acknowledgements

This study is part of the Faunal Fire Refuges Project, funded by the Department of Sustainability and Environment, Victoria. We appreciate the support of Parks Victoria, Victorian State Forests, and associated staff. We thank Natasha Robinson for contributions to the project and surveys; Mark Hall, Jemima Connell, Phil Rance, Megan Osborn and volunteers for field assistance; and Greg Holland for advice on statistical models. Comments from an anonymous reviewer improved the final version of this manuscript. EKC and MB were supported with Australian postgraduate research awards. Research was conducted under DEPI permit (10005478) and Deakin animal welfare permit (A56-2010).
3-7 Supplementary material

Table S3.1  Model structures of GLMMs fitted to each response variable for the fire regime and isolation studies with the inclusion of ‘reserve’ as a random effect in all models, and in the fire regime study an additional observational level random effect was included for the total number of all arboreal mammals as a response variable.

<table>
<thead>
<tr>
<th>Fire regime study</th>
<th>Isolation study</th>
</tr>
</thead>
<tbody>
<tr>
<td>Severity</td>
<td>Area unburnt</td>
</tr>
<tr>
<td>Time Since Fire</td>
<td>Area understorey</td>
</tr>
<tr>
<td>Tree</td>
<td>Tree</td>
</tr>
<tr>
<td>Severity + History</td>
<td>Area unburnt + Tree</td>
</tr>
<tr>
<td>Severity + Tree</td>
<td>Area understorey + Tree</td>
</tr>
<tr>
<td>Time Since Fire + Tree</td>
<td></td>
</tr>
<tr>
<td>Severity + History + Tree</td>
<td></td>
</tr>
<tr>
<td>Severity* History</td>
<td></td>
</tr>
<tr>
<td>(Severity* History) + Tree</td>
<td></td>
</tr>
</tbody>
</table>

Table S3.2  Number of arboreal mammals recorded in the fire regime and isolation studies.

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
<th>Fire regime study</th>
<th>Isolation study</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Gully</td>
<td>Slope</td>
</tr>
<tr>
<td>Greater Glider</td>
<td><em>Petauroides volans</em></td>
<td>17</td>
<td>11</td>
</tr>
<tr>
<td>Mountain Brushtail Possum</td>
<td><em>Trichosurus cunninghami</em></td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>Common Brushtail Possum</td>
<td><em>Trichosurus vulpecula</em></td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Common Ringtail Possum</td>
<td><em>Pseudocheirus peregrinus</em></td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Sugar Glider</td>
<td><em>Petaurus breviceps</em></td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Koala</td>
<td><em>Phascolarctos cinereus</em></td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Unidentified</td>
<td></td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Total number</td>
<td></td>
<td>36</td>
<td>21</td>
</tr>
</tbody>
</table>
CHAPTER 4 Effects of the fire regime on mammal occurrence after wildfire: site effects vs landscape context in fire-prone forests

This chapter is published as:


Severely burnt foothills forest, Kinglake National Park.
4-1 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.
4-2 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 (\textit{sensu} Gill, 1975), including fire frequency, intensity, season and type of fire, can influence biodiversity (Gill, 1975; Gill & Allan, 2008). The intensity of a large wildfire, for example, influences the composition and spatial pattern of plant communities (Turner et al., 1994; Pausas et al., 2008; Roman-Cuesta et al., 2009). While knowledge of the relationship between fire regimes and plant communities is growing (Whelan et al., 2002; Driscoll et al., 2010), much less is known about the components of the fire regime and their influence on fauna and ecosystems (Clarke, 2008; Fontaine & 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 in size, occurrence and frequency over a longer fire season in some fire-prone areas (McKenzie et al., 2004; Wotton et al., 2010; Clarke et al., 2011). 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 (Keith et al., 2002; Smucker et al., 2005; Fontaine et al., 2009). 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 (Schoennagel et al., 2008; Roman-Cuesta et al., 2009; Leonard et al., 2014a). 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 & 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., 2014a). 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 & 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: 1) at the site-level (i.e. site specific wildfire severity and fire history); and 2) 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.

4-3 Methods

4-3-1 Study area

The study was based in the foothills of the Central Highlands of Victoria, Australia (Figure 4.1), where elevation ranges from ~150 – 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 (Bureau of Meteorology, 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 (Bureau of Meteorology, 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 (*E. dives* and *E. radiata*) and blue gum (*E. globulus*) in moist gullies. The mid-storey contains species such as blackwood (*Acacia melanoxylon*), silver wattle (*A. 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*) (DSE, 2005).

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., 2014a).

4-3-2 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 4.1 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 (Figure 4.1). Sites were selected by using aerial photography and fire severity layers from the Department of Sustainably 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 with different severities, and from roads. Sites disturbed by logging in the last 50 years were excluded.

4-3-3 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 second 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 (Paull 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 & 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.

### 4-3-4 Statistical analyses

#### 4.3.4.1 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:

\[
N = \frac{\log_{10}(1 - a/100)}{\log_{10}(1 - p)}
\]

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.

### 4.3.4.2 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 4.1). Fire severity (i.e. unburnt, understorey-only burnt, severely burnt, reference), and fire history (i.e. long, short) were categorical variables (Table 4.1). 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 and Sustainability 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 4.1).

**4.3.4.3. 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 4.1). Since the response variables represent proportions, a proportional binomial distribution using a log-link function was employed in all cases.
### Table 4.1 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.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Site/Landscape level</th>
<th>Variable Description</th>
<th>Level</th>
<th>Level Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Severity</td>
<td>Site</td>
<td>Fire severity of forest within boundary of 2009 wildfire</td>
<td>Unburnt</td>
<td>Unburnt forest</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Understorey</td>
<td>Understorey and/or ground burnt</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Severe</td>
<td>Canopy scorched or canopy completely burnt</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Reference</td>
<td>Unburnt and located outside the wildfire boundary</td>
</tr>
<tr>
<td>History</td>
<td>Site</td>
<td>Fire interval before 2009</td>
<td>Long</td>
<td>Unburnt&gt;20 years before wildfire</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Short</td>
<td>Burnt &lt; 3 years before wildfire</td>
</tr>
<tr>
<td>Landscape unburnt area</td>
<td>Landscape</td>
<td>Unburnt forest in surrounding landscape</td>
<td>Continuous</td>
<td>Area of unburnt forest within a 1 km radius of site (ha)</td>
</tr>
<tr>
<td>Heterogeneity</td>
<td>Landscape</td>
<td>Heterogeneity of fire severity in surrounding landscape</td>
<td>Continuous</td>
<td>Heterogeneity of fire severity classes within 1 km radius of site, calculated by Shannon’s diversity index.</td>
</tr>
<tr>
<td>Waterways</td>
<td>Landscape</td>
<td>Waterways in surrounding landscape</td>
<td>Continuous</td>
<td>Total length of waterways within a 1 km radius of site (m).</td>
</tr>
<tr>
<td>Reserve</td>
<td>NA</td>
<td>Geographic location of sites based on land management</td>
<td>NA</td>
<td>Random effect</td>
</tr>
<tr>
<td>Season</td>
<td>NA</td>
<td>Surveys undertaken in three seasons: summer, autumn, winter</td>
<td>NA</td>
<td>Random effect</td>
</tr>
</tbody>
</table>

Log transformed for the mountain brushtail possum, the agile antechinus, bush rat, swamp wallaby and mountain brushtail possum, and for the bush rat.
We used an information theoretic approach to compare a set of competing hypotheses (Table S4.1). Eight models were built for each species, with combinations of predictor variables and interactions (Table S4.1) selected based on ecological knowledge (Burnham & Anderson, 2002). Models within a set were ranked and compared by using AIC corrected for small sample size (AICc). Differences in AICc (ΔAICc) were calculated, as were Akaike weights (w_i). Models with ΔAICc < 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 ΔAICc < 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 & 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 & 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 & Ripley, 2014) packages. R^2 values were calculated with the ‘rsquared.glmm’ function (Lefcheck & Casallas, 2014).
Chapter 4: Effects of the fire regime on native mammal occurrence

4-4 Results

4-4-1 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 4.2; Figure 4.2). 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 4.2). 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 4.2), the long-nosed bandicoot and short-beaked echidna were also included in analyses.
Table 4.2  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.

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

*Species with insufficient detection probability for 80% confidence intervals.
Figure 4.2  Examples of native species detected from camera surveys including a) dusk antechinus, b) agile antechinus, c) bush rat, d) long-nosed bandicoot, e) short-beaked echidna, f) brush-tailed phascogale, g) eastern grey kangaroo, h) common wombat, i) swamp wallaby, j) mountain brushtail possum, k) common brushtail possum, and i) koala.
4-4-2 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 4.3). For the agile antechinus, the only model to have substantial support (ΔAICc < 2) included all five variables at both the site-level and landscape-level (Table 4.3). 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. 4.3). The recording rate of the agile antechinus was lower at sites exposed to an understorey burn compared with unburned sites (Figure 4.4). Recording rates were higher at sites with a short fire history (< 3 years) than a long fire history (> 20 years; Figure 4.4), and lower at sites surrounded by more unburnt forest (Fig. 4.3). 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. 4.3).

For the bush rat, four models had substantial support in explaining the recording rate (Table 4.3). 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. 4.3). 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 history than a long fire history (Figure 4.4), and there was a negative relationship with the length of waterways in the surrounding landscape (Fig. 4.3).
Table 4.3  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 ($\Delta$AIC) and the Akaike weight. Model fit is represented by $R^2_m$ - the variance from fixed predictors, and $R^2_c$ - the variance explained by both fixed and random predictors.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Model structure</th>
<th>df</th>
<th>Log likelihood</th>
<th>AICc</th>
<th>$\Delta$AICc</th>
<th>Akaike weight</th>
<th>$R^2_m$</th>
<th>$R^2_c$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Antechinus agilis</td>
<td>Severity + History + Landscape unburnt area + Heterogeneity + Water</td>
<td>11</td>
<td>-128.66</td>
<td>283.2</td>
<td>0.00</td>
<td>0.60</td>
<td>0.15</td>
<td>0.44</td>
</tr>
<tr>
<td>Rattus fuscipes</td>
<td>Severity + Landscape unburnt area + Heterogeneity + Water</td>
<td>10</td>
<td>-219.63</td>
<td>462.4</td>
<td>0.00</td>
<td>0.35</td>
<td>0.12</td>
<td>0.29</td>
</tr>
<tr>
<td></td>
<td>Severity + History</td>
<td>8</td>
<td>-222.48</td>
<td>463.0</td>
<td>0.55</td>
<td>0.27</td>
<td>0.09</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td>Severity</td>
<td>7</td>
<td>-224.04</td>
<td>463.6</td>
<td>1.20</td>
<td>0.19</td>
<td>0.08</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>Severity + History + Landscape unburnt area + Heterogeneity + Water</td>
<td>11</td>
<td>-219.09</td>
<td>464.1</td>
<td>1.63</td>
<td>0.16</td>
<td>0.12</td>
<td>0.26</td>
</tr>
<tr>
<td>Vombatus ursinus</td>
<td>Null model</td>
<td>4</td>
<td>-164.66</td>
<td>337.9</td>
<td>0.00</td>
<td>0.71</td>
<td>0.00</td>
<td>0.17</td>
</tr>
<tr>
<td>Wallabia bicolor</td>
<td>Severity</td>
<td>7</td>
<td>-218.85</td>
<td>453.3</td>
<td>0.00</td>
<td>0.36</td>
<td>0.03</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>Null model</td>
<td>4</td>
<td>-222.41</td>
<td>453.4</td>
<td>0.10</td>
<td>0.35</td>
<td>0.00</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>Severity + History</td>
<td>8</td>
<td>-218.20</td>
<td>454.4</td>
<td>1.17</td>
<td>0.20</td>
<td>0.03</td>
<td>0.03</td>
</tr>
<tr>
<td>Macropus giganteus</td>
<td>Null model</td>
<td>4</td>
<td>-94.36</td>
<td>197.3</td>
<td>0.00</td>
<td>0.75</td>
<td>0.00</td>
<td>0.11</td>
</tr>
<tr>
<td>Trichosurus cunninghami</td>
<td>Null model</td>
<td>4</td>
<td>-115.25</td>
<td>239.0</td>
<td>0.00</td>
<td>0.55</td>
<td>0.00</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>Severity * History</td>
<td>11</td>
<td>-107.33</td>
<td>240.5</td>
<td>1.51</td>
<td>0.26</td>
<td>0.55</td>
<td>0.57</td>
</tr>
<tr>
<td>Perameles nasuta*</td>
<td>Severity + History</td>
<td>7</td>
<td>-31.68</td>
<td>78.9</td>
<td>0.00</td>
<td>0.94</td>
<td>0.89</td>
<td>0.91</td>
</tr>
<tr>
<td>Tachyglossus aculeatus*</td>
<td>Null model</td>
<td>3</td>
<td>-53.90</td>
<td>114.1</td>
<td>0.00</td>
<td>0.90</td>
<td>0.000</td>
<td>0.29</td>
</tr>
</tbody>
</table>
Fig. 4.3  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).
Figure 4.4 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.
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 4.3). 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. 4.3). 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 (Fig. 4.3 and Figure 4.4). 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 4.3). After model averaging, the recording rate of the swamp wallaby was influenced by the fire severity and history interaction (Fig. 4.3). 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 (Figure 4.4).

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 4.3). 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 4.3). 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 history (< 3 years) than a long fire history (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 4.3).

### 4-5 DISCUSSION

Understanding how fire regimes influence fauna at different scales can improve ecological knowledge for fire management (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 recolonisation of the burnt forest environment from unburnt refuges (see below).

#### 4-5-1 Fire regime effects at the site-level

Different species responded differently to fire severity, consistent with other studies (e.g. Smucker et al., 2005; Roberts et al., 2008; Fontaine & Kennedy, 2012; Buchalski et al., 2013; Doumas & Koprowski, 2013a; Robinson et al., 2014). 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 (Sutherland & Dickman, 1999; Catling et al., 2001). 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.
Chapter 4: Effects of the fire regime on native mammal occurrence

The bush rat is often associated with dense understorey (Holland & Bennett, 2007); whilst the long-nosed bandicoot is linked with dense understorey for nesting and open areas for foraging (Chambers & 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 (*Isoodon 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 similarly negatively affected by wildfire in nearby wet montane forest (Banks et al., 2011b).

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 (Chapter 3). 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 & 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 dead trees, logs and tree hollows (Haslem et al., 2011).

4-5-2 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 (Bradstock et al., 2005; Lunney et al., 2008; Garvey et al.,...
2010; Banks et al., 2011b). 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 (Whelan et al., 2002; Pastro et al., 2011). For such species, rapid regeneration of ground cover provides suitable habitat, and also facilitates dispersal and recolonization across the landscape after fire.

4-5-3 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 unburned 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 environmental 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 protects 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 (Chapter 3) 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.

4-6 Acknowledgements

This study is part of the Faunal Fire Refuges Project, funded by the Department of Environment, Land, Water and Planning, Victoria. We thank Parks Victoria, Victorian State Forests, and associated staff. Natasha Robinson provided valuable contributions to the overall project design and site selection. We appreciate the help of numerous staff and volunteers for field assistance; and Dale Nimmo for advice on statistical models. Comments from anonymous reviewers improved the final version of this manuscript. EKC and MB were supported with Australian postgraduate research awards. Research was conducted under DEPI permit (10005478) and Deakin animal welfare permit (A56-2010).

4-7 Supplementary material

Table S4.1 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.

<table>
<thead>
<tr>
<th>Model set</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null model</td>
</tr>
<tr>
<td>Severity</td>
</tr>
<tr>
<td>Severity + History</td>
</tr>
<tr>
<td>Severity * History</td>
</tr>
<tr>
<td>Severity + Landscape unburnt area + Heterogeneity + Waterways</td>
</tr>
<tr>
<td>Severity + History + Landscape unburnt area + Heterogeneity + Waterways</td>
</tr>
<tr>
<td>(Severity * History) + Landscape unburnt area + Heterogeneity + Waterways</td>
</tr>
<tr>
<td>Landscape unburnt area + Heterogeneity + Waterways</td>
</tr>
</tbody>
</table>
CHAPTER 5 The influence of wildfire and landscape heterogeneity on introduced mammals in a fire-prone forest ecosystem

The red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) detected by camera traps in the study area.
5-1 Abstract

Globally, introduced species can profoundly affect species’ populations, communities and ecosystem function. Disturbance processes, such as wildfire, may create opportunities for invasive species to establish or extend their distribution and interact with native plants and animals. However, the way in which introduced species respond to changes in the post-fire environment, and as influenced by fire regime components (e.g. fire severity, fire frequency) and landscape context, are poorly known. We examined the distribution of introduced mammals in fire-prone eucalypt forests of south-eastern Australia, 2-3 years after a major wildfire. We tested the relative influence of fire severity and fire history, landscape context (i.e. the surrounding landscape pattern) and topography on the occurrence of introduced mammals at forest sites. We undertook systematic camera trap surveys at 80 forest sites, each comprising a paired gully and adjacent slope. Six introduced species were detected, and those with the highest activities were black rat (Rattus rattus), house mouse (Mus musculus), red fox (Vulpes vulpes) and feral cat (Felis catus). Each of these were widespread across all levels of fire severity in the region. Black rats were the only species whose distribution was influenced by the fire regime, landscape context or topography in the early post-fire succession period. We found few associations between the spatial occurrence of introduced and native species: the introduced feral cat was negatively correlated with the native agile antechinus, and the house mouse was negatively associated with the reporting rate of the native bush rat. Understanding the impact of introduced species on ecosystems after fire requires more detailed insights than those available from a ‘snapshot’ survey. This study shows that introduced species are not strongly influenced by fire regime components or landscape context, at 2-3- years after wildfire in these fire-prone forests.
5-2 Introduction

Invasive species have spread and established into most environments globally, with significant economic, ecological and social consequences (Vitousek et al., 1997a; Mack et al., 2000). Invasive species include ‘introduced species’, those that are introduced by humans into an area that is external to their native range (Strauss et al., 2006). Introduced species can modify ecosystem structure and function in a variety of ways (Vitousek et al., 1997a; Ehrenfeld, 2010; Doherty et al., 2015). For example, introduced species may act as ecosystem engineers and alter the physical structure of ecosystems (e.g. Bohlen et al., 2004; Sousa et al., 2009), they may change predator and prey relationships (Salo et al., 2007; Letnic et al., 2008), and alter entire food webs by causing trophic shifts (e.g. Levin et al., 2006).

Introduced species are considered to be one of the most significant threats to communities of native animals globally (Vitousek et al., 1997b; Molnar et al., 2008), because their interactions with native species can result in reduced population sizes, homogenization of the composition of communities (Clavero et al., 2009), and even local extinction of species (Clavero & García-Berthou, 2005; Szabo et al., 2012; Woinarski et al., 2015). Such negative consequences are attributed to many facets of introduced species: for example, they may bring in novel pathogens that cause mortality (Gozlan et al., 2005), they can degrade habitat and cause declines in isolated populations (Koprowski et al., 2005), and they may compete with native species and reduce populations (e.g. black rat (Rattus rattus); Stokes et al., (2009b)). In Australia, predation by introduced vertebrates (e.g. red fox (Vulpes vulpes) and feral cat (Felis catus) have been associated with the marked decline and extinction of numerous species of native mammals (Johnson et al., 2007; McKenzie et al., 2007; Woinarski et al., 2015).

Introduced species often are associated with disturbances to ecosystems (Mack et al., 2000). Fire is one such disturbance process, which influences vegetation structure in many ecosystems across the world (Bond & Keeley, 2005; Bowman et al., 2009). Fire-induced changes to ecosystems create opportunities for introduced species to colonise;
or, if already present, to increase in population size and expand their distribution (Fleming et al., 2009; Doherty et al., 2015). They may then exert new and severe impacts on native species in the altered environment (Sutherland & Dickman, 1999). For example, reduced vegetation cover in the post-fire environment can increase the exposure of small native mammals to introduced predators (Sutherland & Dickman, 1999); as has been described in south-western Australia where the red fox reduced populations of the brush tailed bettong (*Bettongia penicillata*) (Christensen, 1995). Similarly, predation by the red fox and feral cat reduced native rodent populations after wildfire in arid Australia (Letnic & Dickman, 2005).

Different components of a fire regime (Gill, 1975), such as fire intensity and fire history, can influence the distribution and abundance of animal species. The fire regime creates variation in habitat suitability in a landscape at multiple spatial scales. It influences the suitability and quality of habitat at an individual site, and also influences the landscape context of a site (e.g. the surrounding fire heterogeneity) (Bradstock et al., 2005). In addition to the fire regime, the landscape context of a site is also determined by environmental attributes, such as topographic variation, and other disturbance processes such as land clearing. Both the attributes at a site and its landscape context can be expected to influence the distribution of introduced species, as well as native species. The red fox, for example, is thought to favour forest edges and heterogeneous landscapes (Graham et al., 2012).

Interactions with introduced species of mammals and variation in fire regimes, respectively, are both known to independently affect the distribution and abundance of native mammals (e.g. Fontaine & Kennedy, 2012; Kelly et al., 2012; Kovacs et al., 2012; Paull et al., 2012; Anson & Dickman, 2013; Smith & Banks, 2014; VanTassel et al., 2015). They may also act synergistically to bring about change in the native fauna (Brook et al., 2008). A first step in understanding the potential for synergistic impacts on native fauna from wildfire and introduced species is to identify the way in which introduced species respond to wildfire – the focus of this study.
Here, I examine the distribution of introduced species of mammals in relation to variation in fire components and landscape attributes after a major wildfire. Systematic surveys of mammals were undertaken, using a stratified landscape design, ~2-3 years post-fire, thus providing an opportunity for a ‘snapshot’ view of the status of introduced species in the early phase of post-fire recovery. The study was undertaken in the temperate, foothill eucalypt forests of south-eastern Australia, one of the most fire-prone regions in the world (Adams & Attiwill, 2011). This study has three main components, based on the following questions:

1. What is the relative influence of wildfire severity, fire history and landscape context on the distribution and occurrence of introduced terrestrial mammal species?
2. Does topographic location (gully/slope) influence the occurrence of introduced species in the post-fire environment?
3. Are there associations in occurrence (positive or negative) between introduced and native mammal species after wildfire, based on potential interactions (e.g. predation and competition)?

5-3 Methods

The study area, site selection, fauna survey procedures, species identification, and methods for determining detection probability are described in Chapter 4. Site selection and statistical methods specific to this study are outlined below.

5-3-1 What is the relative influence of wildfire severity, fire history and landscape context?

I used generalised linear mixed models to examine the relative effects of fire severity, fire history, and landscape context on the occurrence of introduced mammal species. Four species were examined: house mouse (*Mus musculus*), black rat, red fox, and feral cat. The response variable was the presence or absence of each species at a site (i.e. from the combined records for both gully and slope transects at a site).
Detection/non detection was used, rather than the proportion of camera nights on which a species was detected, because of lower recording rates and fewer number of sites at which species were recorded (typically 10-20 sites).

I chose six predictor variables, representing aspects of the fire regime and landscape context, expected to influence the distribution and abundance of these mammals. Fire severity of the wildfire (i.e. unburnt, understorey burnt, severely burnt), and fire history before the wildfire (i.e. long > 20 years, short < 3 years before 2009 fires) were categorical variables (Table 5.1). Unburnt sites included those within the fire boundary as well as unburnt reference sites located close to the fire boundary. Four continuous variables were chosen to represent the landscape within a 1 km radius surrounding each site: area (ha) of unburnt forest, area (ha) of cleared land, heterogeneity of fire severity classes, and the length (km) of waterways. These landscape variables were extracted from spatial data layers in a GIS (ArcMap v 10) as described in 4.3.4.2. Response and predictor variables. The amount of cleared land was calculated from aerial photography in GIS. Continuous predictor variables were not strongly correlated (Spearman’s rank coefficient for all < 0.30). Variables were made comparable by scaling (subtracting the mean and dividing by the standard deviation for each observation). If there was adequate support for improved linearity by transformation (log10), then the transformed variable was used in the model.

A binomial distribution and a log-link function were applied for the GLMM models. I used an information theoretic approach to compare a set of alternative hypotheses for each species. Six models were built for each species, with the selected combinations of predictor variables based on ecological knowledge (Burnham & Anderson, 2002) (Table 5.2). There was limited evidence for interaction effects between fire severity and history, and so these were excluded from the model set.
Table 5.1 Description of predictor variables and levels used in alternative models for investigating a) the relative influence of the fire regime and landscape context, and b) topography. The first level for each categorical variable was treated as the reference level.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Variable Description</th>
<th>Level</th>
<th>Level Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Severity</td>
<td>Fire severity of forest of 2009 wildfire</td>
<td>Unburnt</td>
<td>Unburnt forest inside and within 3 km from the fire boundary</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Understorey</td>
<td>Understorey and/or ground burnt</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Severe</td>
<td>Canopy scorched or completely burnt</td>
</tr>
<tr>
<td>History</td>
<td>Fire history before 2009</td>
<td>Long</td>
<td>Unburnt ≥20 years before wildfire</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Short</td>
<td>Burnt &lt; 3 years before wildfire</td>
</tr>
<tr>
<td>Landscape unburnt area</td>
<td>Unburnt forest in surrounding landscape</td>
<td>Continuous</td>
<td>Area of unburnt forest within a 1 km radius of site (m²)</td>
</tr>
<tr>
<td>Heterogeneity</td>
<td>Fire heterogeneity of forest in surrounding landscape</td>
<td>Continuous</td>
<td>Heterogeneity of fire severity classes within a 1 km radius of site, calculated by Shannon’s diversity index.</td>
</tr>
<tr>
<td>Water</td>
<td>Waterways in surrounding landscape</td>
<td>Continuous</td>
<td>Total length of waterways within a 1 km radius of site (m).</td>
</tr>
<tr>
<td>Land</td>
<td>Cleared land in the surrounding landscape</td>
<td>Continuous</td>
<td>Area of cleared land within a 1 km radius of a site (m²).</td>
</tr>
<tr>
<td>Reserve</td>
<td>Random effect</td>
<td>NA</td>
<td>Geographic location of sites based on land management</td>
</tr>
<tr>
<td>Season</td>
<td>Random effect</td>
<td>NA</td>
<td>Surveys undertaken in three seasons: summer, autumn, winter</td>
</tr>
<tr>
<td>Site</td>
<td>Random effect</td>
<td>NA</td>
<td>Added into models with topography to minimise spatial correlation</td>
</tr>
<tr>
<td>Topography</td>
<td>Topographic position</td>
<td>Gully</td>
<td>Gully location</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Slope</td>
<td>Slope location</td>
</tr>
</tbody>
</table>

All models included a random effect term to account for 1) potential spatial autocorrelation of sites across the landscape (‘reserve’) and, 2) the time of year of the survey (‘season’), respectively (Table 5.1). Spatial correlation was further checked by visual assessment using bubble plots of model residuals. If models had unexpected variance of model residuals (Pearson’s residuals; overdispersion > 1.5 but less than 2), then an additional observational-level random effect was built in to account for additional variance (Zuur et al., 2009).
Table 5.2  Model set containing a combination of model structures of predictor variables fitted to each response variable (i.e. black rat (*Rattus rattus*), house mouse (*Mus musculus*), red fox (*Vulpes vulpes*), and feral cat (*Felis catus*) testing the relative influence of fire regime and landscape context 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.

<table>
<thead>
<tr>
<th>Model set</th>
</tr>
</thead>
<tbody>
<tr>
<td>Introduced species ~ Null model</td>
</tr>
<tr>
<td>Introduced species ~ Severity</td>
</tr>
<tr>
<td>Introduced species ~ Severity + History</td>
</tr>
<tr>
<td>Introduced species ~ Severity + Landscape context (i.e. Unburnt area + Heterogeneity + Water + Land)</td>
</tr>
<tr>
<td>Introduced species ~ Severity + History + Landscape context (Unburnt area + Heterogeneity + Water + Land)</td>
</tr>
<tr>
<td>Introduced species ~ Landscape context (Unburnt area + Heterogeneity + Water + Land)</td>
</tr>
</tbody>
</table>

I ranked models within a set and compared them with Akaike’s Information Criterion (AIC) corrected for small sample size (AICc). Akaike weights ($w_i$) were also calculated for each alternative model. Models with $\Delta$AICc < 2 were considered to have substantial support. If there was no single best model (i.e. lowest AICc, $w_i > 0.90$), model averaging was performed on all models for which the $\Delta$AICc < 6. Model-averaged coefficients and standard errors were estimated for each parameter; and predictor variables were considered influential if the 95% confidence intervals of the model-averaged coefficient did not cross zero (i.e. if $z < -1.96$ or $z > 1.96$) (Burnham & Anderson 2002). Model predictions for a species were generated for influential variables; and represent the probability of occurrence of a species at a random site.

I checked assumptions of global models by assessment of residuals from the global model, and for each predictor variable. A measure of the variance explained was determined by calculating the marginal $R^2$ (i.e. that associated with the predictor variables) and the conditional $R^2$ (that associated with both the predictor variables and random effects) (Nakagawa & Schielzeth, 2013).
5-3-2 **Does topographic location influence the occurrence of introduced species in the post-fire environment?**

To test the influence of topography on the local occurrence of introduced mammal species, I used a GLMM for each species with the detection/non detection of the species at each gully and slope transect as the response variable, and topography as the predictor variable (Table 5.1). To account for spatial correlation of gully and slope transects, a random effect of ‘Site’ was included, in addition to the random effects of ‘reserve’ and ‘season’ (see above). Model assumptions were checked as described above.

5-3-3 **Are there associations in occurrence between introduced and native mammal species after wildfire?**

I tested whether the occurrence of four introduced species (house mouse, black rat, red fox, and feral cat) was related to the recording rate of several native mammal species (agile antechinus (*A. agilis*), bush rat (*R. fuscipes*)) at sites. I used a GLMM with the detection/non-detection of each introduced species at a site (gullies and slopes combined) as a predictor variable. The response variable was the ‘recording rate’, the proportion of total camera nights (up to 84) for which a native species was recorded at a site, to account for minor variation between sites. A binomial distribution and a log-link function were used for each response variable. Two random variables, ‘reserve’ and ‘season’ were included to account for potential spatial and temporal correlation. An observation- level random effect was added if the global model for each response variable was overdispersed (unexpected variance of model residuals) to account for additional variance (Zuur *et al.*, 2012). Predictor variables were considered important if the 95% confidence intervals did not cross zero (i.e. if $z < -1.96$ or $z > 1.96$). The model of the relationship between detection/non detection of the red fox and the native agile antechinus was not reliable (overdispersion could not be accounted for), and hence was excluded from analysis.
All statistical analyses were conducted in the R statistical package 3.1.1 (R Development Core Team, 2014). GLMMs and model averaging were run using the ‘lme4’ and ‘MuMIn’ packages respectively (Bartoń, 2014; Bates et al., 2014). Model predictions were generated with the ‘AICcmodavg’ and ‘boot’ packages (Canty & Ripley, 2014; Mazerolle, 2014). $R^2$ values were calculated with the ‘rsquared.glmm’ function (Lefcheck & Casallas, 2014).

5-4 Results

5-4-1 Species recorded and detection probability

From a total of for a total of 6084 trap nights, across 80 sites, six introduced mammal species were detected: house mouse, black rat, red fox, feral cat, European rabbit (*Oryctolagus cuniculus*) and sambar deer (*Cervus unicolor*) (Table 5.3; Figure 5.1). The most common species were black rat (20 sites), red fox (17 sites), house mouse (15 sites) and feral cat (*Felis catus*) (10 sites) (Table 5.3). Typically, at sites at which a species was recorded, the number of detections varied over the 14 night survey period. The detections per site were lower for the feral cat (present for 1-2 nights out of 14 nights) and red fox (1-6 nights), whilst higher for house mouse (1-7 nights), and most frequent for the black rat (1-14 nights).

Table 5.3 Introduced species recorded during 14 nights of camera surveys.

Presented are the number of sites at which species were detected, naïve occupancy (number of sites detected/ 80 sites surveyed), detection probability per site, and the number of survey nights (rounded up to nearest whole number) required for 80% confidence that a lack of detection was a true absence.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sites present</th>
<th>Naïve occupancy</th>
<th>Detection probability (P)</th>
<th>SE (P)</th>
<th>Number of survey nights required</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Mus musculus</em></td>
<td>15</td>
<td>0.19</td>
<td>0.15</td>
<td>0.03</td>
<td>11</td>
</tr>
<tr>
<td><em>Rattus rattus</em></td>
<td>20</td>
<td>0.25</td>
<td>0.35</td>
<td>0.03</td>
<td>4</td>
</tr>
<tr>
<td><em>Felis Catus</em></td>
<td>10</td>
<td>0.13</td>
<td>0.03</td>
<td>0.02</td>
<td>56</td>
</tr>
<tr>
<td><em>Vulpes vulpes</em></td>
<td>17</td>
<td>0.21</td>
<td>0.101</td>
<td>0.02</td>
<td>16</td>
</tr>
</tbody>
</table>
Figure 5.1 Introduced species detected during camera surveys at 2-3 years after wildfire including a) house mouse, b) black rat, c) red fox, d) feral cat, e) European rabbit, and f) sambar deer.
Records were insufficient for the sambar deer and European rabbit and hence no further analysis of these were conducted. The sambar deer had infrequent records at few sites (5 sites), which encompassed all fire severity classes. Records of the European rabbit were also sparse (7 sites), and were from burnt sites only (understorey or severely burnt sites), across both fire histories (long and short). Domestic dogs were recorded once in forest close to urban areas, but are not considered further.

Statistical analyses were undertaken for the four most common species. Fourteen survey nights were sufficient for two species, house mouse and black rat, for an 80% detection probability at a site (Table 5.3). The other two species, the red fox and feral cat had lower detection probabilities and required more than 14 nights to be 80% confident that a lack of detection was a true absence (Table 5.3); this is considered in interpretation of results.

5-4-2 What is the relative influence of wildfire severity, fire history and landscape context?

The house mouse, black rat, red fox and feral cat were widespread across the fire-affected landscape and were recorded in each of the fire severity classes – unburnt, understorey burnt and severely burnt sites. For the black rat, two models showed substantial support ($\Delta AIC < 2$; Table 5.4); the fire severity plus fire history model, and the fire severity model. These variables (and random factors) accounted for 27% and 26%, respectively, of the variance in the data ($R^2_c$) (Table 5.4). Akaike weights for both of these models were < 0.9, and so model averaging was conducted. Fire severity was an important influence: there was a higher probability of occurrence of the black rat at burnt sites (i.e. understorey only, and severely burnt) than at unburnt sites (Figs 5.2 and 5.3). The occurrence of the house mouse had support from two models; the null model and fire severity model ($\Delta AIC < 2$; Table 5.4). However, after model averaging, no variables were considered important (Figure 5.2). The null model had the most support for the occurrence of both red fox and feral cat ($\Delta AIC < 2$; Table 5.4). Again, after model averaging was conducted, no variables were an important influence on their distribution (Figure 5.2).
Table 5.4  Models with the most support (ΔAIC<2) in a model set for each introduced species testing the relative influence of fire regime and landscape context. Values presented for each alternative model include the df, Log likelihood, AICc, the difference in AICc from the best model (ΔAIC) and the Akaike weight. Model fit is represented by R²: R²m is the variance from fixed predictors and R²c is the variance explained by both fixed and random predictors.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Model structure</th>
<th>df</th>
<th>Log likelihood</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Akaike weight</th>
<th>R²m</th>
<th>R²c</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Mus musculus</em></td>
<td>Null model</td>
<td>3</td>
<td>-34.11</td>
<td>74.5</td>
<td>0.00</td>
<td>0.52</td>
<td>0.00</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>Severity</td>
<td>5</td>
<td>-32.70</td>
<td>76.2</td>
<td>1.69</td>
<td>0.22</td>
<td>0.04</td>
<td>0.45</td>
</tr>
<tr>
<td><em>Rattus rattus</em></td>
<td>Severity + History</td>
<td>6</td>
<td>-39.05</td>
<td>91.2</td>
<td>0.00</td>
<td>0.48</td>
<td>0.24</td>
<td>0.27</td>
</tr>
<tr>
<td></td>
<td>Severity</td>
<td>5</td>
<td>-40.40</td>
<td>91.6</td>
<td>0.35</td>
<td>0.40</td>
<td>0.18</td>
<td>0.26</td>
</tr>
<tr>
<td><em>Vulpes vulpes</em></td>
<td>Null model</td>
<td>3</td>
<td>-39.14</td>
<td>84.6</td>
<td>0.00</td>
<td>0.81</td>
<td>0.00</td>
<td>0.30</td>
</tr>
<tr>
<td><em>Felis Catus</em></td>
<td>Null model</td>
<td>3</td>
<td>-30.10</td>
<td>66.5</td>
<td>0.00</td>
<td>0.75</td>
<td>0.00</td>
<td>0.05</td>
</tr>
</tbody>
</table>
Figure 5.2 Model-averaged estimates with 95% confidence intervals for reporting rate of introduced species based on generalized linear mixed models that tested the relative influence of fire regime components and landscape context. Parameters are important if confidence intervals do not cross zero (bold). Reference levels for categorical predictor variables include unburnt (fire severity) and long > 20 years (fire history). Model averaging was conducted for models with $\Delta$AICc < 6; these models did not include any landscape variable for the fox and cat.
Chapter 5: The influence of wildfire and landscape heterogeneity on introduced mammals

Figure 5.3  Predicted occurrence (95% CI) for the black rat from generalized linear mixed models testing the relative influence of fire regime components and landscape context. Fire severity was important at 2-3 years after wildfire, with a higher occurrence predicted in severely burnt sites.

5-4-3 Does topographic location influence introduced species in the post-fire environment?

All four species of house mouse, black rat, red fox and feral cat were detected at both topographic locations of gully and slope transects in the post-fire environment. Only one species was influenced by topographic position: there was a higher occurrence of the black rat in gullies compared with slopes (estimate = -5.01, SE = 1.52, Z = -3.30). The other three species were not influenced by gully or slope location: house mouse (estimate = -0.65, SE = 0.59, Z = -1.10), feral cat (estimate = 0.43, SE = 0.67, Z = 0.65), and red fox (estimate = 0.00, SE = 0.48, Z = 0.00).
5-4-4 Are there associations in occurrence between introduced and native mammal species after wildfire?

There were few important relationships between the spatial pattern of occurrence of introduced and native species. One introduced predator was associated with the occurrence of one native prey species. The detection/non detection of the introduced feral cat was negatively correlated with the agile antechinus (est = -0.05, SE = 0.001, Z = -33.5). There appeared to be no significant relationships of the occurrence of the red fox with the bush rat (est = 0.02, SE = 0.48, Z = 0.03), nor of the feral cat with the bush rat (est = 0.17, SE = 0.55, Z = 0.30).

There was support for only one correlation between introduced small mammal species and native species. The detection/non detection of the house mouse was negatively associated with the reporting rate of the bush rat (est = -1.24, SE= 0.58, Z = -2.16). The occurrence of the house mouse appeared not to be associated with the native agile antechinus (est = 0.95, SE= 0.53, Z = 1.80). There was minimal evidence for an association between the detection/non detection of the introduced black rat and the recording rate of the bush rat (est = 0.56, SE = 0.42, Z = 1.34), or the agile antechinus (est = 0.63, SE= 0.41, Z = 1.55).

5-5 Discussion

I investigated the distribution of introduced mammal species in relation to components of the fire regime and the landscape context of sites in the early post-fire environment after a major wildfire. I found three main results. First, the most common introduced species were widespread across the region, and were not greatly affected either by the fire regime at a site-level or at the landscape-level, 2-3 years post-fire. Second, sampling was undertaken systematically in a gully and on adjacent slope at each site but topographic position at the local scale did not influence the detection of most introduced species. Third, there were minimal associations between the occurrence of introduced and native species at the site-level, based on potential interactions (e.g. predation and competition). Together, these findings indicate that at this stage in the
post-fire succession the distribution of introduced species is not strongly affected by fire severity or fire-induced heterogeneity at either the site or landscape level.

5-5-1 Fire regime, landscape context and topography, and the distribution of introduced mammals

In the early post-fire environment, four species (house mouse, black rat, red fox and feral cat) were widespread within each level of fire severity. The introduced rodent, the black rat, was the only species that was influenced by the fire regime, favouring sites burnt in the wildfire at 2-3 years post fire. It was also the only species influenced by topography at the local scale, being positively associated with gullies. The black rat has been recorded to decrease in abundance immediately after a wildfire (Stokes et al., 2009a), as well as favouring simplified forest structure after frequent low-intensity burns (Catling, 1991). The black rat has also been associated with dense understorey, abundant vertical stems and leaf litter (Cox et al., 2000). Although leaf litter was minimal in burnt sites at the time of surveys, dense regeneration of vegetation with vertical stems may have provided adequate habitat in simplified burnt forest sites. Moist gullies may also facilitate survival after fire, and the black rat has previously been correlated with habitats indicative of both moist rainforest and open forests (Stokes et al., 2009a).

I expected that fire regime components and landscape context would have a greater influence on the occurrence of introduced species. Fire severity in particular, was expected to have a strong influence because a) the mortality of mammals could be greater in areas of high severity fire (Newsome et al., 1975; Whelan et al., 2002), and b) fire simplifies vegetation structure and alters the availability of resources, which can have consequences for both introduced and native species alike (Fox, 1982; Torre & Diaz, 2004; Forsyth et al., 2012; Robinson et al., 2013). For example, the abundance of the house mouse is reported to be greater 1-2 years after wildfire (Fox, 1982), as well as favouring recently burnt vegetation with lower structural complexity (Catling, 1991; Recher et al., 2009; Kelly et al., 2010). However, I found limited effects of the
fire regime on house mouse and other introduced species. There are several possible explanations for these results.

First, introduced species can often adapt to a variety of habitats, which assists widespread persistence in the early post-fire environment. Species that have a more generalized diet can use a wider range of resources (Gehring & Swihart, 2003), which is beneficial after fire. For example, the house mouse is particularly adaptable; it is omnivorous, has a high reproductive rate, and is able to disperse to and recolonise burnt areas after wildfire (Fox, 1982). Indeed, the house mouse, black rat, red fox and feral cat are all considered to benefit from a decrease in habitat complexity resulting from fire (Catling, 1991). Similarly, the red fox can generally inhabit diverse environments (Saunders et al., 2010), has a high recruitment rate and can move into empty territories in the absence of other foxes, in areas without fire (Newsome et al., 2014). The cat can also occupy a wide range of habitats (Doherty et al., 2015). These attributes are likely to promote persistence in, or exploitation of, the post-fire environment. For example, the mobility of the red fox would assist animals to escape from fire (Newsome et al., 1975). Cats selected intensely burnt grass habitats that were more open and in tropical savanna woodlands in the central Kimberley, north-west Australia, (McGregor et al., 2014). In mallee vegetation in a semi-arid landscape, Australia, Payne et al., (2014) similarly found the red fox to be widespread in the post-fire environment with limited effects of fire and landscape variables on local occurrence, most likely due to flexibility in diet and adaptability to a wide range of habitats. In the same way, native carnivores in the chaparral habitats of California, USA, showed limited response to wildfire (2-3 years after fire) highlighting their ability to adapt to the post-fire environment, probably due to their generalist foraging and habitat behaviours (Schuette et al., 2014).

Second, I observed dense regeneration of vegetation in severely burnt sites during surveys at 2-3 years post-fire, after drought-breaking rains in 2010-2011. This regeneration would affect introduced species in this study. Here, the black rat and house mouse may benefit from dense understorey and explain their occurrence in burnt forest sites. Dense understorey can provide cover or refuge from predators (Cox et al., 2000). For instance, thick understorey was a habitat component favoured by the black
rat in microhabitats in coastal NSW, Australia (Cox et al., 2000); and the house mouse used dense vegetation when predation risk was high in coastal shrubland, open woodlands, and tall forests in south-west western Australia (Dickman 1992). Although dense regeneration may restrict predator movements, red fox abundance was not influenced by habitat complexity or time since fire after wildfire in forest and heathlands of south-eastern NSW, Australia (Catling et al., 2001). Similarly, an increase in sambar deer abundance in Kinglake National Park (located in our study area) was observed to coincide with the regeneration of understorey vegetation in burnt sites at 16-24 months after wildfire (Forsyth et al., 2012). Rapid regeneration of vegetation in burnt sites following drought-breaking rains at 2-3 years after wildfire, appeared to contribute to limited differences in habitat structure between sites of differing fire severity, with unburnt and burnt sites not being greatly differentiated for introduced species at this time.

5-5-2 Associations in occurrence between introduced and native mammal species

Associations in occurrence may reflect predator-prey interactions after wildfire, as suggested in previous studies. For example, the Florida panther (Puma concolor coryi) selected recently burnt areas (< 1 year) that corresponded with increased prey availability of white-tailed deer (Odocoileus virginianus); which were the consequence of altered vegetation structure by prescribed burns in pine habitats of the sub-tropics of southern Florida, USA (Dees et al., 2001). Similarly, in eucalypt forests of coastal NSW, Australia, the introduced cat was positively associated with the southern brown and long-nosed bandicoots (Isoodon obesulus and Perameles nasuta), whilst the introduced red fox was negatively correlated with the abundance of the native long-nosed potoroo (Potorous tridactylus) 10 years after wildfire (Arthur et al., 2012). Areas burnt at high intensities may also increase exposure of small mammals as prey, and therefore increasing hunting opportunities for cats (McGregor et al., 2014).
In this study, the introduced house mouse was negatively associated with the small native rodent, the bush rat. This is likely to be due to the differing response of each species to structural changes in vegetation at 2-3 years post wildfire and/or a competitive interaction, which could be assessed in a more detailed study. In coastal eucalypt forest of south-eastern Australia, the house mouse colonised burnt forest within 2 years of wildfire where it was previously absent and increased in abundance, this is likely due to an increase in vegetation productivity in the immediate post-fire environment, but also from a decrease in competition and/or predation from bush rat and Antechinus spp. (Recher et al., 2009).

The introduced black rat has the potential to compete with bush rat (Stokes et al. 2009). Here, a relatively higher frequency of occurrence of the black rat in burnt sites, compared with unburnt sites, similar to that of the bush rat (Chapter 4), may provide a food source for predators in the recovering burned forest. Introduced predators could also feed on introduced and native small mammals (Smith & Quin 1996), which could reduce native prey survival (e.g. red fox activity can reduce survival of the bush rat; Kovacs et al., 2012). In some cases native prey may be more vulnerable because they have not evolved to learn avoidance behaviour (Banks & Dickman 2007; Salo et al., 2007).

Although there were few associations between introduced predators and native prey species, the widespread presence of predators after fire could potentially affect native prey populations at different stages in the post-fire succession. Native prey species have been reported to be particularly susceptible to predation immediately after fire (1-2 years) due to open vegetation in burnt areas that allows ease of movement by predators and little shelter or refuge for prey species (Sutherland & Dickman 1999; McGregor et al., 2014). For example, McGregor et al., 2014, suggested that cats can take advantage of small mammal species that have survived the fire but are more exposed after intense fires in savanna woodlands of the central Kimberley region, northern Australia. In the later stages of post-fire secondary succession, predation risk may increase if vegetation cover reduces as regeneration dies off, thus decreasing shelter for small prey species (Torre & Diaz 2004). Here at 2-3 years post fire, dense regeneration in previously burnt sites provided ample cover for prey species.
Our capacity to detect complex interactions between species was limited in this observational study, particularly when understanding the response of species to fire is already challenging for species that are hard to detect (Driscoll et al., 2012). Increasing the number of survey nights may increase the capacity to reliably detect species such as the feral cat and red fox, but any association derived from such distributional data remains correlative. Experimental studies, such as a replicated Before After Control Impact (BACI) design, including manipulation of predators or herbivores conducted at an appropriate scale, are required to evaluate and fully understand potential interactions between introduced and native species after wildfire (Edelman et al., 2009; Arthur et al., 2012; Pedersen et al., 2014).

5-5-3 Implications for conservation and management

The widespread occurrence of introduced species in the post-fire environment (2-3 years), indicates limited effects of fire severity, fire history and fire-induced landscape attributes at this time. The post-fire environment does not have a negative influence on most introduced mammal species at this point in time. This suggests that it is difficult to develop a particular fire management regime to reduce or eliminate these introduced species in the early stages after fire. However, management of introduced species after wildfire in fire-prone forests remains an important issue because their widespread presence could adversely affect native mammal species that are in the early stages of population recovery. For example, native species that are negatively affected by fire severity, such as arboreal mammals (see Chapter 3; Lindenmayer et al., 2013), may be more vulnerable to introduced predators in the early post-fire habitat (e.g. ringtail possum and foxes and cats (Russell et al., 2003). Others potentially at risk include native prey species, such as bush rats, bandicoots and potoroos (Smith & Quin 1996; Arthur et al., 2012), as well as threatened species that are rare or localized.

Interactions between climate, fire and mammal populations are intricate (Recher et al., 2009). Climatic conditions, such as drought or high rainfall, in combination with fire could change predation pressure on native species possibly leading to threats or range declines of native species (Letnic et al., 2005; Smith & Quin 1996). For instance, in
coastal eucalypt forests of NSW, Australia, the abundance of the agile antechinus decreased during drought, and then declined to local extinction within 14 months after a wildfire (Recher et al., 2009). Hence, integrated management for introduced species and fire could be beneficial immediately after extreme wildfire and under particular climatic conditions, such as drought (Letnic et al., 2005; Doherty et al., 2015). Management of introduced species could also be prioritized in refuges of forest blocks or reserves known to support important populations of native species.

I propose three key areas that require better understanding in relation to the status of introduced species after wildfire. First, knowledge of changes in the distribution and abundance of introduced species in different successional stages (e.g. 2, 10, 30 years) after wildfire is necessary to understand the temporal dynamics of such species in forest ecosystems. The early post-fire environment (< 1 year), when the landscape is dramatically transformed with reduced vegetation cover from understorey to canopy layer, is an especially important time. Long term studies that track changes in population sizes in relation to interactions between climatic conditions and disturbance processes can provide important insights for conservation (e.g. Letnic et al., 2005; Recher et al., 2009).

Second, demographic studies would be valuable to better understand how populations change after fire. For example, studies of the relative survival and mortality of males and females, reproductive rates of females that survive/persist in different fire severities, dispersal distances from unburnt to burnt patches or vice versa, are all important to help understand the spatial dynamics of populations and vulnerability of species after fire (Banks et al., 2011b).

Third, manipulative experimental studies would help to pin point the impacts of introduced species on native species, especially after disturbances like fire when there may be synergistic effects on native species from the disturbance and from introduced species (Doherty et al., 2015). This could be achieved by identifying potential interactions between introduced and native species, such as predation or competition. For example, manipulative experiments could be conducted after fire where the
invasive predator/competitor is absent or removed, compared to sites containing introduced species. The abundance or density, reproductive rates, and mortality rates of both species could be measured to test if the presence of invasive species limits the native population in the post-fire environment. Ideally these would be enclosed areas, unless an accurate measure of numbers of individuals that dispersal or influx could be achieved. These suggestions could provide necessary understanding of interactions with disturbances such as fire and introduced species in forest systems (Dale et al., 2001; Doherty et al., 2015).
CHAPTER 6 The effects of wildfire, landscape heterogeneity, and habitat on an ecosystem engineer, the superb lyrebird (*Menura novaehollandiae*)

A male superb lyrebird (*Menura novaehollandiae*). Photo: Alex Maisey
Chapter 6: The effects of wildfire and landscape heterogeneity on an ecosystem engineer

6-1 Abstract

Ecosystem engineers influence environments by altering the structural attributes of habitats in ways that influence the abundance of other species. The superb lyrebird (*Menura novaehollandiae*), a large, ground-dwelling species, is an ecosystem engineer in eucalypt forests of south-eastern Australia. This species forages by turning over forest soils and litter, which alters the forest ground layer and influences the rate of litter decomposition. The fire regime in these fire-prone eucalypt forests potentially affects the distribution and occurrence of this species. Here, I used a unique opportunity to examine the occurrence of the superb lyrebird after a severe wildfire in foothill eucalypt forests, Victoria, Australia. First, I tested the relative influence of fire severity and fire history at sites, together with landscape context, on the occurrence of the superb lyrebird. Second, I determined whether topography moderated the effect of fire severity on the occurrence of the superb lyrebird. Third, I examined the relative influence of vegetation and habitat components on the occurrence of this species in different topographic positions. Remote cameras were used to survey 80 sites across a large forested region, 2-3 years after a severe wildfire. Superb lyrebirds were detected in all fire severity classes (unburnt forest, understorey burnt, severely burnt, reference). Fire severity and its interaction with fire history exerted the greatest influence on the occurrence of this species, with no evidence for the influence of fire-related patterns in the surrounding landscape. There was a higher recording rate at sites that remained unburnt within the 2009 wildfire than at sites that were burnt. For sites burnt in 2009, there was a lower recording rate at those that had experienced recent prior fire (< 3 years) than those with a longer fire history (> 20 years). Topographic position moderated the effect of fire severity, with gullies favoured over slopes. Shrub cover (< 2 m) in gullies was the only habitat component identified as influencing the recording rate of the superb lyrebird. These results indicate that unburnt forest and gullies have an important role in the persistence of the superb lyrebird at 2-3 years after wildfire. Fire management that increases the number of unburnt patches likely to occur after wildfire, particularly in topographic gullies, will be of benefit to the conservation of the superb lyrebird in the fire-prone, foothill eucalypt forests of south-eastern Australia.
Ecosystem engineers are organisms that regulate the availability of resources for other species directly or indirectly, through the physical creation, alteration or maintenance of habitat (Jones et al., 1994). They occur worldwide, with most ecosystems being substantially influenced by at least one species of ecosystem engineer (Jones et al., 1994; Lawton, 1994; Jones et al., 1997; Wright & Jones, 2006). The structural changes to habitats by ecosystem engineers influence the abundance of other taxa and the richness and composition of communities (Jones et al., 1997; Jones et al., 2010). Such changes can also create a feedback effect, whereby the physical changes to habitat have direct positive effects on the ecosystem engineer itself (Jones et al., 1997). For example, the dam-building activities of the beaver (Castor canadensis) provides an essential habitat for this species, while also altering the heterogeneity of riparian landscapes and the species richness of herbaceous plants (Wright et al., 2002), amphibians and wetland bird species. Soil engineers, such as some species of termites and ants, build biogenic structures which can influence soil quality, plants and microorganisms, as well as affect the fitness of the organisms’ themselves (Jouquet et al., 2006). Given the large impacts of ecosystem engineers, and that their impacts may last longer than the life of the engineer itself (Hastings et al., 2007), it is important to understand how such species might be influenced by disturbance processes to the ecosystems in which they live.

The superb lyrebird (Menura novaehollandiae) is an ecosystem engineer in eucalypt forests in south-eastern Australia (Adamson et al., 1983; Ashton & Bassett, 1997; Eldridge & James, 2009; Nugent et al., 2014). This species is large (76-103 cm head to tail), uniquely-plumed, and forages on the ground (Simpson & Day, 2004). Superb lyrebirds scratch and rake large amounts of leaf litter and soil as they forage for invertebrates, including upturning rocks of up to 2 kg (Adamson et al., 1983; Webb & Whiting, 2006). They also build soil mounds for display during the breeding season (Robinson & Frith, 1981). It has been estimated that superb lyrebirds can turn over up to 200 tonnes ha⁻¹ of soil and litter per year (Ashton & Bassett, 1997). Through foraging activity, this species buries leaf litter with soil, which could accelerate...
decomposition and hence expedite nutrient cycling; as well as potentially increasing the abundance of invertebrates (Adamson et al., 1983; Ashton & Bassett, 1997). Over time, turnover of soil by superb lyrebirds leads to gradual down-slope movement of soil and nutrients from slopes toward gullies (Ashton & Bassett, 1997).

The eucalypt forests in which the superb lyrebird occurs in south-eastern Australia are among the most fire-prone forests in the world (Adams & Attiwill, 2011). The effects of fire on forest fauna may be direct (i.e. mortality during the fire event), or indirect via changes in habitat suitability following the fire (Whelan et al., 2002). Fire severity (which describes the consequences of fire intensity on vegetation), and fire history (time between fire events), are known to influence the abundance of bird species, and the species richness and composition of communities (Smucker et al., 2005; Kirkpatrick et al., 2006; Fontaine et al., 2009; Pons & Clavero, 2010; Fontaine & Kennedy, 2012; Watson et al., 2012b). Fire also creates heterogeneity in the landscape at a larger scale, and the resulting spatial patterns may influence biota (Williams et al., 1994). For example, the spatial configuration of burnt and unburnt patches of vegetation can influence the survival and recovery of bird species in the post-fire environment (e.g. Brotons et al., 2005; Fuhlendorf et al., 2006; Watson et al., 2012a). Environmental variation across the landscape can influence the fire regime, and also affect the distribution of biota. For example, moist gullies in topographically diverse landscapes can evade high intensity fire and hence mitigate severe fire effects on animals (Bradstock et al., 2010; Leonard et al., 2014a).

Here, I examine the effect of an extensive wildfire on the distribution and occurrence of the superb lyrebird in foothill eucalypt forests of central Victoria, Australia. Surveys were undertaken ~ 2-3 years post-fire, at sites carefully chosen to represent different combinations of fire severity and fire history classes, stratified across the landscape. I posed three main questions:

1. What is the relative influence of fire severity, fire history and landscape context on the occurrence of the superb lyrebird?
2. Does topographic variation modify the influence of fire severity on the superb lyrebird?

3. Are there particular habitat components in different topographic locations that influence the occurrence of this species?

I predicted that fire severity would have the greatest influence on the distribution and occurrence of the superb lyrebird, and that unburnt forest sites would support higher activity than burnt sites.

6-3 Methods

The study area and selection of study sites are described in Study area.

6-3-1 Surveys

Surveys were conducted by using passive infra-red cameras at 80 sites, for a total 6084 camera nights, from January-August 2011. Each site comprised a gully and adjacent slope, with a 200 m transect in each, situated ~100 m apart. Six cameras were set at each site to survey terrestrial animals, with three cameras placed on each transect (see Fauna surveys and species identification). On each transect, two cameras targeted small native mammals and were set facing vertically downwards on steel posts from a height of 1.3 m (De Bondi et al., 2010). The third camera targeted larger native and exotic mammals, faced horizontally outwards, and was set on an aluminium post at 0.5 m height (Fauna surveys and species identification). These surveys were effective in detecting the ground-dwelling superb lyrebird. Further details of the camera survey technique, and methods for determining the detection probability of species, are described in Chapter 4.
6-3-2 Relative influence of fire regime components and landscape context

6.3.2.1 Response and predictor variables

I examined the relative effects of fire severity, fire history and fire-induced landscape context on the occurrence of the superb lyrebird, by using generalised linear mixed models (GLMM). The response variable was the proportion of camera days on which the superb lyrebird was detected; that is, the number of camera-days with records of the species divided by the total number of camera days surveyed per site (max = 84 days; i.e. 6 cameras per site x 14 days). Records from gully and slope transects were pooled for each site. I refer to this measure as the ‘recording rate’. Due to the response variable being a proportion, a binomial distribution was specified and a log-link function was applied to all models (including those in the following sections) (Zuur et al., 2009).

Five predictor variables were selected to represent components of the fire regime at the site-level and the landscape-level. The fire regime components at the site scale were categorical variables: fire severity (unburnt, understorey burnt, severely burnt, reference) and fire history (long > 20 years, short < 3 years since last fire) (Table 6.1). Three continuous variables were chosen to represent the landscape context within a 1 km radius surrounding each site: the area of unburnt forest (ha), the heterogeneity of fire severity classes (Shannon-Wiener index), and the length of waterways (km). These landscape context variables were extracted from aerial photography and spatial data layers in GIS (ArcMap v 10) as described in Chapter 4. There was little evidence for correlations among continuous predictor variables (Spearman’s rank correlation coefficients < 0.22). These continuous variables were centred and scaled (i.e. for each observation, subtracting the mean and dividing by the standard deviation) to allow direct comparison of their influence. Linear relationships between the recording rate of the superb lyrebird and continuous predictor variables were assumed after initial assessments of scatter plots. There was minimal support (i.e. if delta AIC < 2) for transformed (log_{10}) continuous predictor variables to improve relationships, hence all remained untransformed.
Table 6.1  Description of predictor variables used in generalised linear mixed models to test the influence of fire regime components on the occurrence of the superb lyrebird in fire-prone eucalypt forests, Victoria. The first level for each categorical variable was treated as the reference level.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Variable Description</th>
<th>Level</th>
<th>Level Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Severity</td>
<td>Fire severity at survey sites</td>
<td>Unburnt</td>
<td>Unburnt forest</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Understorey</td>
<td>Understorey and/or ground burnt</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Severe</td>
<td>Canopy scorched or completely burnt</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Reference</td>
<td>Unburnt and located outside but close to the wildfire boundary</td>
</tr>
<tr>
<td>History</td>
<td>Fire interval at a site prior to 2009</td>
<td>Long</td>
<td>Unburnt for &gt; 20 years before 2009</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Short</td>
<td>Burnt &lt; 3 years before 2009</td>
</tr>
<tr>
<td>Landscape unburnt area</td>
<td>Unburnt forest in surrounding landscape</td>
<td>Continuous</td>
<td>Area (ha) of unburnt forest within a 1 km radius of site</td>
</tr>
<tr>
<td>Heterogeneity</td>
<td>Heterogeneity of fire severity in surrounding landscape</td>
<td>Continuous</td>
<td>Heterogeneity of fire severity classes within 1 km radius of site, calculated by Shannon’s diversity index.</td>
</tr>
<tr>
<td>Waterways</td>
<td>Waterways in surrounding landscape</td>
<td>Continuous</td>
<td>Total length (m) of waterways within a 1 km radius of site.</td>
</tr>
<tr>
<td>Topography</td>
<td>Topographic location at a site</td>
<td>Gully</td>
<td>Gully location</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Slope</td>
<td>Slope location</td>
</tr>
<tr>
<td>Canopy</td>
<td>Canopy cover</td>
<td>Continuous</td>
<td>Percentage canopy cover (visual estimate)</td>
</tr>
<tr>
<td>Shrub</td>
<td>Shrub cover</td>
<td>Continuous</td>
<td>Percentage shrub cover in height class 1-2 m</td>
</tr>
<tr>
<td>Regeneration</td>
<td>Eucalypt regeneration</td>
<td>Continuous</td>
<td>Percentage cover of eucalypts &lt; 3 cm stem diameter at breast height in height class 0-0.5 m</td>
</tr>
<tr>
<td>Log</td>
<td>Log cover</td>
<td>Continuous</td>
<td>Percentage cover of logs (woody debris &gt; 50 cm long and &gt; 5 cm diameter).</td>
</tr>
<tr>
<td>Litter</td>
<td>Litter cover</td>
<td>Continuous</td>
<td>Percentage cover of leaf litter (leaves and twigs &lt; 1 cm diameter)</td>
</tr>
<tr>
<td>Reserve</td>
<td>Geographic location of sites based on land management</td>
<td>NA</td>
<td>Random effect</td>
</tr>
<tr>
<td>Season</td>
<td>Surveys undertaken in three seasons: summer, autumn, winter</td>
<td>NA</td>
<td>Random effect</td>
</tr>
</tbody>
</table>
6.3.2.2 Model selection

An information theoretic approach was used to compare a set of alternative hypotheses concerning the relative effect of predictor variables on the recording rate of the superb lyrebird. These eight models (Table 6.2) contained different combinations of site and landscape predictor variables expected to influence the occurrence of this species. Fire history was only included in models together with fire severity, because it did not make ‘ecological sense’ for fire history alone to influence superb lyrebirds after a wildfire. Two random effects, ‘reserve’ and ‘season’, were included to account for spatial and temporal correlation due to the large geographic area surveyed and the timeframe of sampling (over three seasons, summer, autumn, winter), respectively (Table 6.1). Residuals of the global model were mapped in a bubble plot in relation to location to further assess any spatial correlation in superb lyrebird occurrence. During the first stage of modelling, the global model was overdispersed (Pearson’s residual = 1.69). Hence, an observation-level random effect was included in all models in the set to account for unexplained variance, and these were re-run (Zuur et al., 2009). Model fit was estimated for each model by calculating the marginal R² (i.e. that due to predictor variables) and conditional R² (predictor variables plus random effects) (Nakagawa & Schielzeth, 2013).
Table 6.2  Model structures of GLMMs chosen to test the relative influence of fire regime components and landscape context on the recording rate of the superb lyrebird at each site (gully and slope combined). All models included ‘reserve’ and ‘season’ as random effects to account for spatial and temporal correlation. An additional observation-level effect was included to account for unexplained variance.

<table>
<thead>
<tr>
<th>Fire regime and landscape context model set</th>
</tr>
</thead>
<tbody>
<tr>
<td>Superb lyrebird ~ Null model</td>
</tr>
<tr>
<td>Superb lyrebird ~ Severity</td>
</tr>
<tr>
<td>Superb lyrebird ~ Severity + History</td>
</tr>
<tr>
<td>Superb lyrebird ~ Severity * History</td>
</tr>
<tr>
<td>Superb lyrebird ~ Severity + Landscape unburnt area + Heterogeneity + Water</td>
</tr>
<tr>
<td>Superb lyrebird ~ Severity + History + Landscape unburnt area + Heterogeneity + Water</td>
</tr>
<tr>
<td>Superb lyrebird ~ (Severity * History) + Landscape unburnt area + Heterogeneity + Water</td>
</tr>
<tr>
<td>Superb lyrebird ~ Landscape unburnt area + Heterogeneity + Water</td>
</tr>
</tbody>
</table>

Next, models were ranked by using Akaike’s Information Criterion (AIC) corrected for small sample size (AICc) and Akaike weights (wi). Models with the lowest AICc and those with a ΔAICc < 2 were considered to have substantial support, whilst models with ΔAICc > 6 were deemed to have minimal support. There was no single ‘best’ model (i.e. lowest AICc, wi > 0.90) in the set to explain superb lyrebird occurrence, and therefore model averaging was conducted on all models for which ΔAICc < 6. Model-averaged coefficients and standard errors were estimated for each parameter. Predictor variables were considered influential if the 95% confidence intervals of the model-averaged coefficient did not cross zero (i.e. if $z < -1.96$ or $z > 1.96$) (Burnham & Anderson, 2002). Influential variables were then used to generate model predictions, representing the probability of occurrence of the superb lyrebird at a random site with set attributes. Model validation included an assessment of plots of Pearson’s residuals of the global model against fitted residuals, as well as against each predictor variable.
Chapter 6: The effects of the wildfire and landscape heterogeneity on an ecosystem engineer

6-3-3 Influence of topography and fire severity

I used a GLMM to test the influence of topography in moderating the effect of fire severity on the occurrence of the superb lyrebird. The response variable was the proportion of camera nights on which the superb lyrebird was detected at each gully and slope transect, respectively. Two categorical predictor variables were used: topographic position (gully or slope) and fire severity (unburnt, understorey burnt, severely burnt, reference) (Table 6.1). Random effects in each model included ‘reserve’ and ‘season’ (see above), and also an extra random effect of ‘Site’ to account for the spatial correlation of gully and slope transects.

Three models were built: a) topography plus fire severity (additive influences i.e. topography + severity), b) an interaction between topography and fire severity (topography x severity), and c) fire severity alone (severity). Models were ranked and compared, and assumptions checked, as described above.

6-3-4 Influence of habitat and topographic location

I used GLMMs to test the relative influence of vegetation and habitat components on the occurrence of the superb lyrebird in different topographic positions. The response variable was the proportion of camera nights on which the species was detected. Separate analyses were conducted for gullies and slopes. I chose five predictor variables based on habitat features likely to influence the superb lyrebird (Ashton & Bassett, 1997): canopy cover, shrub cover 1-2 m height, eucalypt regeneration < 0.5 m, log cover, and litter cover (Table 6.1). Habitat variables were measured at gully and slope transects at each site during the spring-summer of 2010-2011, ~2 years after the 2009 wildfire. Transects of 50 m were established in each gully and slope, in the middle of the 200 m camera trap transect. Habitat variables were measured on the transect, based on contacts with a 4 m ranging pole at 1 m intervals.

Predictor variables had a low level of inter-correlation (Spearman’s rank correlation coefficients < 0.51). For canopy cover and eucalypt regeneration, there was improved
linearity ($\Delta$AICc < 2) by using a log_{10} transformation (constant of 0.01 added due to presence of zeros), for both topographic positions; while shrub cover and density of logs were transformed for the gully data set. Predictor variables were made comparable by scaling (subtracting the mean and dividing by the standard deviation for each observation), and model assumptions were checked as described above.

All statistical analyses were conducted in the R statistical package (v 3.1.1; R Development Core Team, 2014). GLMMs were run with packages ‘lme4’ (Bates et al., 2014), and model selection and averaging with ‘MuMIn’ (Bartoń, 2014). Model predictions were generated with the packages ‘AICcmodavg’ (Mazerolle, 2014) and ‘boot’ (Canty & Ripley, 2014). R^2 values were calculated with the ‘rsquared.glmm’ function (Lefcheck & Casallas, 2014).

### 6-4 Results

The superb lyrebird was widespread across the wildfire-affected area, being detected at 38% of sites (30/80). It was detected at sites of all levels of fire severity and fire history, with the exception of reference sites which had been unburnt for > 20 years at the time of the wildfire (i.e. ‘long’ fire history; Figure 6.1). Superb lyrebirds were present in both gullies and on slopes in all fire severity classes, except for severely burnt slopes; but, overall there were more records in gullies than on slopes (Figure 6.1).

If present at a site, the superb lyrebird was recorded from between 1 to 16 camera-days out of a maximum of 84 camera-days (entire survey period of 14 days). Individuals known to be females were detected at 20 sites whilst males were recorded slightly less, at 18 sites. However, the sex of individuals could not be identified for all photo records due to low visibility or only partial photos of an individual, and hence data from both sexes were pooled for further analyses. All but two photos of superb lyrebirds (n = 259) were recorded during daylight hours, from approximately 6 am – 9 pm.
Figure 6.1   Proportion of sites at which the superb lyrebird was detected in relation to categorical predictor variables (total number of sites sampled in each category represented above each column): a) fire severity (unburnt, understorey burnt, severe, reference) and fire history (long unburnt > 20 years, short < 3 years), and b) topographic location in different fire severity classes.
The naïve occupancy (proportion of sites at which recorded) for the superb lyrebird was 0.38. The daily detection probability (P) for this species was 0.25 (95% CI = 0.20 - 0.29). Therefore, 14 survey days was sufficient to have 95% confidence that lack of detection at a site represented a true absence for this species.

6-4-1 Relative influence of fire regime components and landscape context

Four out of eight models testing the relative influence of fire severity, fire history and landscape context had substantial support (ΔAICc < 2) (Table 6.3). The model with the lowest AICc value was that with the interaction between fire severity and fire history, which accounted for some 72% of the variance in the data (Table 6.3).
Table 6.3 Results for models of: a) the relative influence of fire regime components and landscape context variables and b) topography and fire severity on the recording rate of the superb lyrebird. Models with the most support (ΔAIC < 2) from each model set are presented with the df, log likelihood, AICc, the difference in AICc from the best model (ΔAIC) and the Akaike weight. Model fit is represented by $R^2$: $R^2_m$ is the variance explained by fixed predictors and $R^2_c$ is the variance explained by both fixed and random predictors.

<table>
<thead>
<tr>
<th>Model structure</th>
<th>df</th>
<th>Log likelihood</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Akaike weight</th>
<th>$R^2_m$</th>
<th>$R^2_c$</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Fire regime and landscape study</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Severity x History</td>
<td>11</td>
<td>-108.70</td>
<td>243.3</td>
<td>0.00</td>
<td>0.25</td>
<td>0.72</td>
<td>0.76</td>
</tr>
<tr>
<td>Severity + Landscape unburnt area + Heterogeneity + Waterways</td>
<td>10</td>
<td>-110.17</td>
<td>243.5</td>
<td>0.24</td>
<td>0.22</td>
<td>0.20</td>
<td>0.31</td>
</tr>
<tr>
<td>Severity x History + Landscape unburnt area + Heterogeneity + Waterways</td>
<td>14</td>
<td>-104.56</td>
<td>243.6</td>
<td>0.30</td>
<td>0.21</td>
<td>0.50</td>
<td>0.59</td>
</tr>
<tr>
<td>Severity</td>
<td>7</td>
<td>-114.44</td>
<td>244.4</td>
<td>1.15</td>
<td>0.14</td>
<td>0.14</td>
<td>0.22</td>
</tr>
<tr>
<td>B. Topography and fire severity</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Topography x Severity</td>
<td>11</td>
<td>-159.24</td>
<td>342.3</td>
<td>0.00</td>
<td>0.98</td>
<td>0.87</td>
<td>0.93</td>
</tr>
<tr>
<td>Topography + Severity</td>
<td>8</td>
<td>-166.65</td>
<td>350.2</td>
<td>7.99</td>
<td>0.02</td>
<td>0.15</td>
<td>0.56</td>
</tr>
<tr>
<td>Severity</td>
<td>7</td>
<td>-171.08</td>
<td>356.9</td>
<td>14.64</td>
<td>0.00</td>
<td>0.14</td>
<td>0.56</td>
</tr>
</tbody>
</table>
As there was no single best model (lowest AICc, $w_i > 0.90$), I conducted model averaging. Several predictor variables were important (i.e. 95% confidence intervals of estimates did not overlap zero) (Table 6.4). Fire severity at sites was an important driver of the distribution of the superb lyrebird at 2-3 years after wildfire. There was a lower recording rate at both types of burnt sites (understorey-only, severely burnt) compared with sites that remained unburnt (Figure 6.2). The interaction between fire severity and history was important for burnt sites (understorey and severely burnt) (Table 6.4). For a given level of fire severity, the recording rate was lower for sites burnt < 3 years prior to the 2009 wildfire than those burnt > 20 years prior to 2009, and this effect was greater at severely burnt sites. Finally, there was no evidence that the occurrence of the superb lyrebird was influenced by effects of fire at the landscape-level, but the total length of waterways was important: the recording rate was lower at sites surrounded by a greater length of waterways (Table 6.4).
Table 6.4   Results from model-averaging for models of the relationship between the recording rate of the superb lyrebird and fire regime and landscape context. Values presented are the model-averaged coefficient estimates and their standard errors. Variables are considered important if the 95% confidence limits of the coefficient do not overlap with zero (i.e. $z < -1.96$ or $z > 1.96$ (*). Reference levels of predictor variables are Severity (unburnt), and History (long > 20 years).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>SE</th>
<th>Z-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-3.56</td>
<td>0.79</td>
<td>4.43</td>
</tr>
<tr>
<td>Severity understorey</td>
<td>-1.65</td>
<td>0.75</td>
<td>2.18*</td>
</tr>
<tr>
<td>Severity severe</td>
<td>-2.87</td>
<td>0.82</td>
<td>3.44*</td>
</tr>
<tr>
<td>Severity reference</td>
<td>-0.14</td>
<td>2.23</td>
<td>0.06</td>
</tr>
<tr>
<td>History short</td>
<td>-0.43</td>
<td>0.49</td>
<td>0.86</td>
</tr>
<tr>
<td>Severity unburnt x History short</td>
<td>-0.92</td>
<td>0.70</td>
<td>1.30</td>
</tr>
<tr>
<td>Severity understorey x History long</td>
<td>-1.73</td>
<td>0.72</td>
<td>2.36*</td>
</tr>
<tr>
<td>Severity understorey x History short</td>
<td>-2.16</td>
<td>0.77</td>
<td>2.77*</td>
</tr>
<tr>
<td>Severity severe x History long</td>
<td>-2.45</td>
<td>0.82</td>
<td>2.91*</td>
</tr>
<tr>
<td>Severity severe x History short</td>
<td>-4.12</td>
<td>1.21</td>
<td>3.35*</td>
</tr>
<tr>
<td>Severity reference x History long</td>
<td>-11.97</td>
<td>306.94</td>
<td>0.04</td>
</tr>
<tr>
<td>Severity reference x History short</td>
<td>0.65</td>
<td>2.06</td>
<td>0.31</td>
</tr>
<tr>
<td>Landscape unburnt area</td>
<td>-0.67</td>
<td>0.59</td>
<td>1.10</td>
</tr>
<tr>
<td>Heterogeneity</td>
<td>0.35</td>
<td>0.42</td>
<td>0.82</td>
</tr>
<tr>
<td>Water</td>
<td>-0.62</td>
<td>0.23</td>
<td>2.60*</td>
</tr>
</tbody>
</table>
6-4-2 Does topography modify the influence of fire severity on the superb lyrebird?

Given that fire severity influenced the occurrence of the superb lyrebird, it was of interest to test whether this effect may be modified by topographic position (gully or slope). Of three models in the model set, there was overwhelming support for that which included the interaction between fire severity and topography (Akaike weight $> 0.90$) (Table 6.5). This model accounted for 87% of the variation in recording rate of the superb lyrebird (Table 6.3). In general, compared with gullies that remained unburnt during the wildfire (i.e. the reference level) (Table 6.5), the recording rate was notably lower in gullies which experienced high severity fire (severe), on slopes which experienced an understorey burn, and on slopes at reference sites (unburnt areas located outside the fire boundary).
Table 6.5  Results from the ‘best’ model of the relationship between the recording rate of the superb lyrebird, topographic position and fire severity. Estimates of coefficients and associated standard error are presented for the interaction between topography and fire severity. Coefficients are important if $z < -1.96$ or $z > 1.96$ (*). Reference levels of predictor variables are gully (topography) and unburnt (fire severity).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate of coefficient</th>
<th>SE</th>
<th>Z value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-3.69</td>
<td>0.60</td>
<td>-6.10</td>
</tr>
<tr>
<td>Slope / Unburnt</td>
<td>-0.16</td>
<td>0.25</td>
<td>-0.67</td>
</tr>
<tr>
<td>Gully / Understorey burnt</td>
<td>-1.06</td>
<td>0.62</td>
<td>-1.71</td>
</tr>
<tr>
<td>Slope / Understorey burnt</td>
<td>-1.81</td>
<td>0.67</td>
<td>-2.72*</td>
</tr>
<tr>
<td>Gully / Severe</td>
<td>-2.00</td>
<td>0.76</td>
<td>-2.63*</td>
</tr>
<tr>
<td>Slope / Severe</td>
<td>-19.78</td>
<td>2021.24</td>
<td>-0.01</td>
</tr>
<tr>
<td>Gully / Reference</td>
<td>-1.52</td>
<td>0.91</td>
<td>-1.68</td>
</tr>
<tr>
<td>Slope / Reference</td>
<td>-2.40</td>
<td>0.99</td>
<td>-2.43*</td>
</tr>
</tbody>
</table>

6-4-3 How do habitat components influence the superb lyrebird in different topographic positions?

Given that the occurrence of the superb lyrebird was influenced both by fire severity and topography, I examined the relative influence of habitat variables on its occurrence in the different topographic positions. In gullies, only one habitat variable (shrub cover 1-2 m) influenced the recording rate of superb lyrebirds ($r^2_m = 0.19$, $r^2_c = 0.30$ for the global model): the recording rate increased with increasing shrub cover (Figure 6.3). On slopes, none of the measured habitat variables was an important influence on recording rate at the 95% confidence level (Figure 6.3).
Figure 6.3  Model estimates and associated 95% confidence intervals for habitat components for the recording rate of the superb lyrebird in the topographic locations of gully and slope, respectively. Habitat variables are important if the 95% confidence interval does not cross zero.
6-5 Discussion

The superb lyrebird is an ecosystem engineer that, by its foraging activity on the forest floor, exerts an influence on ecological processes and on habitats used by other species in eucalypt forests of south-eastern Australia (Adamson et al., 1983; Ashton & Bassett, 1997; Eldridge & James, 2009; Nugent et al., 2014). Here, I assessed the impact of fire regime components and environmental attributes on this species in one of the most fire-prone regions in the world. Surveys of the distribution and occurrence of the superb lyrebird undertaken 2-3 years after a major wildfire showed three main points: 1) fire severity and fire history at the site level both have an important influence on this species; 2) topographic position can moderate the effect of fire severity; and 3) habitat components in different topographic locations did not have a large impact on the occurrence of this species. These results suggest that unburnt patches of forest, especially associated with gullies, provide important habitat for the superb lyrebird at this early stage of the post-fire environment.

6-5-1 Importance of fire severity and fire history at the site level

Fire severity at survey sites was the most influential driver of the distribution of superb lyrebirds at 2-3 years after wildfire, with severe fire negatively influencing the recording rate of this species. Similarly, Nugent et al., (2014) found, from foraging activity, that superb lyrebirds favoured unburnt sites for foraging in the early post-fire succession, compared with severely burnt sites; and Robinson et al., (2014) reported from diurnal bird surveys that this species occurred more frequently in unburnt sites than at burnt forest sites of varying fire severity. Elsewhere, in NSW, Australia, a lower number of superb lyrebirds was reported in temperate eucalypt forest, at 1-2 years after wildfire (mostly understorey burn) (Smith, 1989); and likewise in forests in East Gippsland, Victoria this species dropped to minimum numbers one year after wildfire (Loyn, 1997).

Several factors could explain the negative response of the superb lyrebird to fire severity. First, wildfire could cause direct mortality and reduce population density in
burnt forest, although the rate of mortality during fire events for fauna has rarely been documented (Whelan et al., 2002). Second, fire alters the vegetation and thereby the suitability of habitat for species (Catling et al., 2001). The loss of structural complexity of vegetation by fire is known to influence the abundance of ground-dwelling mammals (Catling et al., 2001); and is likely to also alter the suitability of habitat for the ground-dwelling superb lyrebird. This species requires habitat with a relatively open understorey, as they forage on bare ground and often build mounds in areas without dense vegetation (Robinson & Frith, 1981; Ashton & Bassett, 1997). They nest most often at the base of trees or treeferns, but rarely in thick ground layer vegetation such as clumps of forest wiregrass (*Tetrarrhena juncea*) (Reilly, 1970; Lill, 1980). In this study, forest vegetation was stimulated by two years of above-average rainfall (2010, 2011) after wildfire (2009), and at the time of the survey many severely burnt sites were covered with dense regeneration of eucalypts and wiregrass. Forest wiregrass re-growth a few years after fire could decrease numbers of this species (Woinarski & Recher, 1997), as the dense regrowth could be a physical barrier that restricts foraging and building of display mounds (Ashton & Bassett, 1997). Hence, thick regeneration in this study could also be a barrier and explain a lower recording rate at severely burnt sites. This situation contrasts with the immediate post-fire environment reported after a low intensity prescribed burn in NSW (Doty et al., 2014), which opened up the understorey and provided easier foraging and movement for the superb lyrebird, 5-20 days post-fire.

A third factor that may result in a negative response to fire severity is that fire may influence availability of food, such as litter invertebrates (Certini, 2005; New et al., 2010). For example, the abundance of soil invertebrates decreased two months after fire in boreal forest (Wikars & Schimmel, 2001), soil macroinvertebrates decreased in savanna woodlands within the first year of fire (Doamba et al., 2014), and terrestrial invertebrate abundance was reduced after frequent low-intensity fire in dry eucalypt forests in Australia (York, 1999).

Finally, the superb lyrebird may be more vulnerable to predators in the early post-fire environment. Introduced species such as the red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) are known to prey on superb lyrebird nests (Lill, 1980). Hence, fire severity
significantly influences superb lyrebird occurrence, most likely through a combination of direct impacts on individuals, and indirect changes to habitat quality in these fire-prone forests.

Fire history was also an important influence on the recording rate of the superb lyrebird in the post-wildfire landscape: it was more likely to occur at sites with a longer fire history (no fire > 20yrs before 2009 wildfire), rather than those with a shorter fire history (i.e. burned within the previous 3 years before 2009). Frequent fires could alter habitat and food resources for this species compared with forests with fewer fires over longer periods. For example, invertebrate abundance in dry eucalypt forests, south-eastern Australia, can be reduced by frequent low intensity fire due to decreases in the amount of leaf litter and related topsoil and litter moisture, and simplified habitat structure (York, 1999). Frequent fire can reduce habitat for the superb lyrebird, by decreasing the amount of shrub and ground cover vegetation on ridges in temperate eucalypt forests (Collins et al., 2012). The nesting habits of birds can be disturbed by frequent fires, possibly reducing opportunities for reproduction and reproductive success (Woinarski & Recher, 1997). These results support those of Nugent et al., (2014), which suggests that recently burnt forest habitat is not favourable for the superb lyrebird.

It is notable that fire effects at the landscape scale did not appear to influence the occurrence of this species at sites 2-3 years after fire. Superb lyrebirds were widespread and present in all levels of fire severity, including severely burnt sites; which suggests either survival in situ, and/or recolonisation of burnt sites after the fire event. In situ survival is possible; Loyn, (1997) observed superb lyrebirds with scorched tails that had survived the initial wildfire event in forests in south-eastern Australia. Robinson et al., (2014) also proposed in situ survival of superb lyrebirds after wildfire. Recolonisation of burnt sites is also plausible, with the rate of recovery likely depending on the rate of regeneration of vegetation, and corresponding food resources such as litter and soil invertebrates (Reilly, 1991; Woinarski & Recher, 1997).
6-5-2 Topography modifies the effect of low severity fire

Topographic position moderated the effect of fire severity for sites less severely burnt in the wildfire. Superb lyrebirds use both gullies and slopes regardless of fire; for example, they often nest within 50 m of creeklines (Robinson & Frith, 1981), and forage on steep slopes (Adamson et al., 1983). Males also use elevated ridges from where they sing to male competitors for territorial defence during the breeding season (Robinson & Frith, 1981). Here, as expected, superb lyrebirds were detected both in gullies and on slopes; but generally they were more frequently recorded in gullies. Gullies are less likely to burn in wildfire, probably due to higher moisture levels (Leonard et al., 2014a). Higher moisture levels are likely to result in greater productivity and provide a more abundant source of litter and soil invertebrates as food for superb lyrebirds, than occurs on drier slopes (Robinson & Frith, 1981).

Patches of vegetation that allow the survival of fauna during or after a fire event, or enable persistence or recolonisation of organisms or populations within the fire boundary, can be defined as fire refuges (Robinson et al., 2013). Here, unburnt gullies contained a higher recording rate of the superb lyrebird than severely burnt gullies and understorey burnt slopes, suggesting that unburnt gullies contributed to persistence in the early post-fire landscape. Superb lyrebirds have been recorded to use creeks during hot weather conditions (Robinson & Frith, 1981), and may migrate to gullies during wildfires, potentially enhancing survival of individuals during the fire event (Garvey et al., 2010). After the fire, higher levels of moisture in gullies may facilitate a faster rate of vegetation recovery than on slopes, and provide more invertebrates for food.

Severely burnt sites had a lower recording rate of the superb lyrebird, possibly from reduced habitat and food resources. The volume of small logs in gullies were reduced in sites exposed to severe fire and a short fire history (< 3 years), and there were more dead trees in severely burnt gullies within the study area (Bassett et al., 2015), which results in less canopy cover, and reduced leaf litter that may also affect invertebrate communities (Andrew et al., 2000). Reduced canopy cover and food resources could influence the superb lyrebird.
This study shows that unburnt forest patches, especially unburnt gullies, are valuable for the superb lyrebird at 2-3 years after fire. Unburnt forest stands and gullies may have been more important immediately after the fire, possibly enabling in situ survival, when the majority of the remaining landscape was burnt and bare of vegetation and habitat. It is likely that the superb lyrebird expanded across the landscape, and into burnt areas, in the several years after the fire.

6-5-3 Importance of habitat components for the superb lyrebird after fire

Habitat components including canopy cover, shrub cover, eucalypt regeneration, and canopy, log, litter and shrub covers were predicted to influence the recording rate of the superb lyrebird in the post fire environment. Unexpectedly, the only habitat component found to influence the superb lyrebird after fire was shrub cover in gullies. No habitat components were influential on slopes. In wet and mixed sclerophyll eucalypt forest in Victoria, nests that had shown signs of predation by large terrestrial mammals were less than 1 m above the ground (Lill, 1980). It is possible that more shrub cover (1-2 m) in gullies may provide greater cover and protection from predators.

6-5-4 Implications for conservation and management

Ecosystem engineers can influence large-scale processes (Jones et al., 1994), and animals that disturb soil can help maintain the health of an ecosystem (Eldridge & James, 2009). The superb lyrebird is an important ecosystem engineer in these foothill forests, and may also contribute to a feedback loop in relation to both vegetation and fire. Nugent et al., (2014) proposed that the turnover of soil and leaf litter by superb lyrebirds increases the rate of litter decomposition, suppresses vegetation growth and promotes bare ground, thereby contributing to a reduction in forest fuels and reduced fire hazard (Nugent et al., 2014). Hence, the depletion of the superb lyrebird in burnt areas could increase leaf litter accumulation, which may lead to a higher probability of wildfire due to more forest fuel (Nugent et al., 2014). This study has highlighted the importance of the effects of fire severity and fire history on the superb lyrebird,
and inclusion of these components at the site-level in future fire regime studies on ecosystem engineers would be valuable.

Unplanned wildfires and altered fire regimes are likely to affect the distribution and abundance of the superb lyrebird. This study shows that unburnt patches of forest and gullies are valuable for the superb lyrebird in the immediate post-fire environment. Hence, when considering fire management of these forests, preservation of long unburnt stands of forest, including moist gullies, will be of value for conserving populations of the superb lyrebird. It has previously been suggested that the superb lyrebird may benefit either from frequent prescribed burns to prevent the development of thick understorey cover, or alternatively to leave the area unburnt and allow the understorey to open up over a long fire interval (Woinarski & Recher, 1997). Results from this study suggest it is preferable to maintain longer fire intervals rather than frequent burning < 3yrs. It is difficult to prevent wildfire under extreme weather conditions; however, protection of forested gullies could be considered during active forest management and planned burns, as they are less likely to burn than slopes due to higher moisture levels (Leonard et al., 2014a). Planned burning on drier slopes surrounding gullies can create a firebreak around gullies to give greater protection during wildfire. The preservation of unburnt forest and moist gully refuges in a fire-prone landscape has an additional benefit of protecting other species sensitive to severe fire (e.g. arboreal mammals).
CHAPTER 7 The influence of wildfire severity and fire history on small mammal populations

Bush rat (*Rattus fuscipes*)
7-1 Introduction

Fire modifies the structure and quality of habitats, and creates heterogeneity in the landscape, which has indirect consequences for populations of many faunal species in fire-prone ecosystems (Fox, 1982; Catling et al., 2001; Whelan et al., 2002; Bradstock et al., 2005; Zwolak, 2009). The quality and heterogeneity of habitat in the landscape can influence the demography of mammal species, including population size, age structure, sex ratio and reproductive rates (Dias, 1996; Diffendorfer, 1998; Lin & Batzli, 2001; Banks et al., 2005; Holland & Bennett, 2010). Changes in habitat quality or the degradation of habitat can lead to demographic changes by influencing \textit{in situ} survival, dispersal and recolonisation of individuals (Koprowski et al., 2005; Holland & Bennett, 2010; Selwood et al., 2015). For example, wildfire reduced food trees in tropical rainforest in Sumatra, Indonesia, which increased the mortality of young primates (\textit{Symphalangus syndactylus}) (O'Brien et al., 2003); while in dry eucalypt forests in south-eastern Australia fire changes vegetation which influences the dispersal and recolonisation of small mammal populations (Recher et al., 2009).

Large fires and the components of the fire regime are known to influence the suitability of habitat for animal species in fire-prone landscapes (Gill & Catling, 2002; Whelan et al., 2002; Gill & Allan, 2008); but knowledge of changes to the demography of small mammal species after wildfire and effects of fire severity is relatively scarce (Banks et al., 2011b). The aim of this study was to determine how fire severity, fire history and topographic variation influence the demography of native small mammal populations in a post-fire landscape. This study was initiated at the start of my PhD research, with the intention of undertaking repeated visits to a set of sites to compare demographic parameters of small mammals between sites. It quickly became apparent that with low trapping success at many sites (see below) it was unlikely that sufficient data would be obtained for meaningful analysis. Consequently, a decision was made to invest effort in intensive camera surveys (see Chapters 4,5,6). However, a brief account and summary of distributional data from the initial trapping results are provided here. Other demographic data (e.g. reproductive status, age classes, body weight) are not presented.
7-2 Methods

The study area is located in the foothill eucalypt forests of the Central Highlands, Victoria, within the boundary of the Kilmore-Murrindindi wildfire, as described in Study area.

7-2-1 Study design

In this study, 36 sites were selected within or adjacent to the Kilmore-Murrindindi fire complex, stratified in relation to two main attributes: a) fire severity and b) fire history (Table 7.1). Fire severity was classified into four categories relevant for small mammal species: unburnt patches (within the fire boundary), understorey-only burnt, severely burnt (crown scorch or crown burn), and unburnt reference sites. Unburnt reference sites were located outside, but within 2 km of, the fire boundary. Fire history describes whether a site was burnt prior to the 2009 wildfire, and was grouped into two categories: burnt < 3 years (‘short’) or > 20 years (‘long’) before the wildfire. All sites were approximately 5 ha in size, had a consistent fire history and severity, and included a separate gully and slope (~100 m apart).

Table 7.1 Number of sites surveyed for small mammal species, stratified by fire severity and fire history.

<table>
<thead>
<tr>
<th>Fire Severity</th>
<th>Fire History</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Long unburnt &gt; 20 years</td>
<td>Short &lt; 3 years</td>
</tr>
<tr>
<td>Unburnt</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Understorey burnt</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Severely burnt</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Reference</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td>19</td>
<td>17</td>
</tr>
</tbody>
</table>
7-2-2 Sampling method

Live-trapping was conducted once per site during the spring-summer (October-January) of 2010-2011. Two x 200 m transects were established along a gully and slope (approximately 100 m apart), respectively, at each site. Twenty aluminium box traps (Elliot type A trap 33 x 10 x 10 cm) were placed along each transect, spaced at ~ 10 m intervals. A standard bait of peanut butter, honey and oats was placed inside each trap, along with cotton wadding for insulation; and a plastic bag (open at one end) covered the trap for weather proofing. Traps were set before dusk, checked the next morning, and reset at dusk on the same day. Trapping was conducted over three consecutive nights at each site.

Mammals that were captured were identified to species, and their weight, sex, and reproductive status were recorded. A small mark (of nail polish) was placed on the tail to distinguish re-captures, and all animals were released at the site of capture.

7-3 Results

7-3-1 Summary of captures

Small mammals were surveyed over a total of 4320 trap nights in 2010-2011, at 1.5-2 years after wildfire. A total of 110 individuals from four species was captured across the 36 sites (combining both gully and slope transects), resulting in a relatively low capture rate of 2.6% (2.6 captures per 100 trap nights) (Table 7.2). The four species detected included three native species: agile antechinus (Antechinus agilis), dusky antechinus (A. swainsonii), bush rat (Rattus fuscipes), and one introduced species, the house mouse (Mus musculus).

The proportion of sites at which each species was present varied (Table 7.2). The bush rat and agile antechinus were present at a higher proportion of sites in the post-fire landscape (> 40%) than the dusky antechinus and house mouse (< 10%) (Table 7.2). The largest number of individuals captured was for the bush rat, followed by the agile...
antechinus. Only three individuals of the house mouse were recorded, all at burnt sites with a long fire history: two of these were on understorey burnt slopes, while the third individual was detected in a crown-burnt gully site. The single dusky antechinus, a female, was caught in an unburnt gully site with a long fire history (burnt > 20 years before 2009) (Table 7.2). Overall, more females were captured than males for all species except for the bush rat (Table 7.2).

Table 7.2  Proportion of sites, and total numbers of females, males, and individuals captured for all species at 1.5-2 years after wildfire.

<table>
<thead>
<tr>
<th>Species</th>
<th>Proportion of sites at which captured (%)</th>
<th>Females</th>
<th>Males</th>
<th>Total number of individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Antechinus agilis</td>
<td>44</td>
<td>33</td>
<td>2</td>
<td>35</td>
</tr>
<tr>
<td>Rattus fuscipes</td>
<td>42</td>
<td>20</td>
<td>51</td>
<td>71</td>
</tr>
<tr>
<td>Antechinus swainsonii</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Mus musculus</td>
<td>8</td>
<td>2</td>
<td>1</td>
<td>3</td>
</tr>
</tbody>
</table>

7-3-2  Topography, fire severity and fire history

The numbers of captures were too few for detailed analyses, but the following provides a brief summary of the data.

The number of captures varied in relation to topographic location for the agile antechinus and bush rat: a higher number of individuals were captured in gullies than on slopes for both species (Figure 7.1). Gullies contained higher numbers of individuals than slopes for both species across all severity classes, with the exception of unburnt gullies and slopes where equal numbers of agile antechinus were captured (Table 7.3).
Figure 7.1  Total number of individuals captured in different topographic locations for the agile antechinus (*A. agilis*) and bush rat (*R. fuscipes*). Data are pooled across all sites.

Table 7.3  Total number of individuals of the agile antechinus and bush rat captured in different topographic locations and in different levels of fire severity.

<table>
<thead>
<tr>
<th>Topography</th>
<th><em>Antechinus agilis</em></th>
<th>Gully</th>
<th>Unburnt</th>
<th>Understorey burnt</th>
<th>Severely burnt</th>
<th>Reference</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>7</td>
<td>8</td>
<td>4</td>
<td>2</td>
<td></td>
<td>21</td>
</tr>
<tr>
<td></td>
<td></td>
<td>7</td>
<td>4</td>
<td>3</td>
<td>0</td>
<td></td>
<td>14</td>
</tr>
<tr>
<td><em>Rattus fuscipes</em></td>
<td></td>
<td>23</td>
<td>5</td>
<td>24</td>
<td>12</td>
<td></td>
<td>64</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0</td>
<td>0</td>
<td>7</td>
<td>0</td>
<td></td>
<td>7</td>
</tr>
</tbody>
</table>
The agile antechinus was present in all fire severity classes, with the lowest capture rate (individuals per site) in reference sites outside of the fire boundary and in severely burnt sites. Capture success in understorey burnt sites was similar to that in unburnt sites (Figure 7.2). Interestingly, the two male antechinus were captured only in sites with an understorey burn severity (Figure 7.2).

![Figure 7.2](chart.png)

**Figure 7.2** Mean number of individuals of the agile antechinus (*A. agilis*) captured across fire severity classes for gullies and slopes pooled: a) mean number of individuals (males and females combined) per site (SE), and b) raw numbers of males and females.
The bush rat was also captured in every level of fire severity. Severely burnt sites appeared to have the highest capture rates of bush rats, whilst sites with an understorey-burn contained less captures (Figure 7.3). This trend appeared to be similar for both males and females (Figure 7.3).

![Figure 7.3](image)

**Figure 7.3**  Mean number of individual bush rats (*R. fuscipes*) captured per site (gully and slopes pooled, (SE) in different fire severity classes for a) combined males and females, b) males, and c) females.
The agile antechinus and bush rat were present at sites in both classes of fire history, across all classes of fire severity within the fire boundary (except for reference sites where no agile antechinus were captured; Table 7.4).

### Table 7.4 Total number of individual agile antechinus and bush rats captured at sites with different fire severities (unburnt, understorey-burnt, severely burnt, reference) and fire histories (long > 20 years, short < 3 years).

<table>
<thead>
<tr>
<th>Fire severity and history</th>
<th>Antechinus agilis</th>
<th>Rattus fuscipes</th>
<th>Total number of sites surveyed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unburnt Long</td>
<td>9</td>
<td>23</td>
<td>5</td>
</tr>
<tr>
<td>Unburnt Short</td>
<td>5</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Understorey Long</td>
<td>3</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Understorey Short</td>
<td>9</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Severe Long</td>
<td>11</td>
<td>19</td>
<td>5</td>
</tr>
<tr>
<td>Severe Short</td>
<td>6</td>
<td>12</td>
<td>5</td>
</tr>
<tr>
<td>Reference Long</td>
<td>0</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Reference Short</td>
<td>0</td>
<td>9</td>
<td>2</td>
</tr>
</tbody>
</table>

### 7.4 Discussion

The relatively low number of captures of individuals at each site in this first trapping round suggested that it would be difficult and excessively time consuming to collect sufficient data to be able to undertake meaningful analyses of demographic parameters between treatments (e.g. reproductive condition, sex ratio, age classes, population density, body weights). Consequently, a decision was made to conduct a broad-scale study examining the effects of fire severity and fire history on distributional patterns, by using remote camera traps across the fire-affected landscape. This study and subsequent findings can be found in Chapter 4.

The results from this collation of initial trapping data indicate that topographic location, fire severity, and possibly fire history may be influencing population size of the bush rat at 1.5-2 years after wildfire. The trends from the raw data suggest that
moist gullies and severely burnt sites may contain higher density of the bush rat than slopes and unburnt sites in the early post-fire environment. This may be due to gullies being less likely to burn in severe fire (Leonard et al., 2014a), and rodents can recover quickly in moist areas after fire, possibly from greater shelter and cover (Newsome et al., 1975; Banks et al., 2011b). Interestingly, understorey sites and those with a recent fire history appeared to contain less numbers of the bush rat than unburnt sites, possibly because there was less rapid regeneration of vegetation as habitat at these sites.

Agile antechinus could be susceptible to fire because they have an unusual life history, where mating is synchronised during two-three weeks of the year from mid-August to late September, followed by the death of all males in the population (Strahan, 1995; Menkhorst & Knight, 2001). Young males disperse after they are weaned and only live for one year, whilst females remain within natal areas and survive for 1-2 years (Cockburn et al., 1985). Only two male agile antechinus were captured in this study; these are likely to have dispersed away from natal sites as the offspring after the fire. The captured females were likely to be ~1-2 years old, that have stayed within their natal range, and those present on burnt sites could indicate in situ survival, similar to the survival at sites of agile antechinus and bush rats in the nearby wet montane forests after the same wildfire (Banks et al., 2011b).
CHAPTER 8 Synthesis

Sunset at Mount Robertson State Forest
8-1 Introduction

Large fires and fire regime components have substantial impacts on ecosystems and on the distribution and abundance of biota globally (Bond & Keeley, 2005; Bowman et al., 2013). Fire regimes are projected to change in fire-prone regions due to climate change, which could threatens biodiversity in ecosystems around the world (Shlisky et al., 2007; Moritz et al., 2012). Despite this threat, few studies have examined the effects of large fires, fire regime components and landscape heterogeneity on the distribution of native and introduced fauna in fire-prone landscapes. In this thesis, I endeavoured to gain an understanding of how large fires, fire regime components and landscape heterogeneity influence the occurrence of forest fauna in the foothill eucalypt forests of south-eastern Australia, one of the most fire-prone regions in the world (Adams & Attiwill, 2011). The study had two key objectives:

i) To determine the effects of fire severity and fire history on forest fauna at the site-level, and

ii) To investigate the influence of fire-created heterogeneity on forest fauna at the landscape-level.

These objectives were examined in relation to the distribution and abundance of four groups of forest fauna: arboreal mammals, terrestrial native mammals, terrestrial introduced mammals, and an ecosystem engineer, the superb lyrebird. The key objectives and main findings from each component of the study are summarised in Table 8.1 and discussed below.
Table 8.1 Outline of the key objectives and main findings of each component of this study.

<table>
<thead>
<tr>
<th>Chapter/Faunal group</th>
<th>Spatial scale</th>
<th>Objectives</th>
<th>Main findings</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chapter 3: Arboreal mammals</td>
<td>Site-level</td>
<td>1. Determine the effects of topography on arboreal mammals, and, 2. Test the relative influence of wildfire severity and fire history.</td>
<td>1. Topography influenced the abundance of arboreal mammals: higher numbers of mammals (all six species combined) were recorded in moist gullies than on slopes. 2. Fire severity influenced the abundance of arboreal mammals (all species combined), and the number of greater gliders: unburnt patches of forest contained higher numbers of mammals than severely burnt sites. 3. Mesic forested gullies and patches of unburnt or less severely burnt patches of vegetation are facilitating persistence of arboreal mammals at 2-3 years after wildfire.</td>
</tr>
<tr>
<td>Landscape-level</td>
<td>1. Investigate the influence of landscape context for sites in severely-burnt forest with different levels of spatial isolation from unburnt forest.</td>
<td>1. Spatial isolation influenced the overall abundance of arboreal mammals in severely burnt sites: higher numbers of arboreal mammals (all four species combined), and greater gliders were detected in sites surrounded by more unburnt and less-severely burnt forest. 2. Unburnt or less-severely burnt areas are contributing as source areas in the severely burnt landscape, assisting recolonization and recovery of arboreal mammals in the post-fire environment.</td>
<td></td>
</tr>
<tr>
<td>Chapter 4: Terrestrial native mammals</td>
<td>Site-level vs landscape-level</td>
<td>1. Test the relative influence on the distribution of species in the post-fire landscape of: a) wildfire severity and fire history at the site level, and b) the amount of unburnt forest and heterogeneity of fire severity within the surrounding landscape.</td>
<td>1. Fire severity was the most influential variable. 2. Different species responded to fire severity in different ways. 3. Fire history had minimal influence on species. 4. Fire-related heterogeneity at the landscape-level did not influence the occurrence of species. 5. Mammal species were widespread across the landscape and appear to be recovering in response to rapid regeneration of vegetation after drought-breaking rains.</td>
</tr>
<tr>
<td>Chapter/Faunal group</td>
<td>Spatial scale</td>
<td>Objectives</td>
<td>Main findings</td>
</tr>
<tr>
<td>----------------------</td>
<td>--------------</td>
<td>------------</td>
<td>---------------</td>
</tr>
</tbody>
</table>
| Chapter 5: Terrestrial introduced mammals | Site-level vs landscape-level | 1. Determine the relative influence of:  
   a) wildfire severity and fire history at the site level, and  
   b) the area of unburnt forest and heterogeneity of fire severity in the surrounding landscape at the landscape level. | 1. Four species of introduced species (black rat, house mouse, red fox, feral cat) had a widespread occurrence at 2-3 years after fire.  
2. The black rat was the only species to be positively influenced by fire severity: higher recording rates at severely burnt sites.  
3. There was limited effects of wildfire severity, fire history and landscape variables at both the site-level and landscape-level on the occurrence of the remaining three introduced species. |
|                      | Site level   | 2. Examine the influence of topographic location (gully/slope).  
3. Identify any associations in occurrence between introduced and native mammal species based on potential ecological interactions (e.g. predation, competition). | 1. The black rat was the only species to be influenced by topographic location, favouring gullies.  
2. There was limited evidence for the occurrence of the house mouse, red fox and feral cat to differ between topographic positions.  
3. There were few correlations between the spatial distribution of introduced and native mammal species:  
   a. The introduced feral cat was negatively correlated with the native agile antechinus,  
   b. The introduced house mouse was negatively associated with the reporting rate of the native bush rat. |
<table>
<thead>
<tr>
<th>Chapter/Faunal group</th>
<th>Spatial scale</th>
<th>Objectives</th>
<th>Main findings</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Chapter 6: Superb lyrebird, an ecosystem engineer</strong></td>
<td>Site level vs landscape level</td>
<td>1. Determine the relative effects of: a. wildfire severity and fire history at the site-level, and b. the amount of surrounding unburnt forest and fire heterogeneity at the landscape-level.</td>
<td>1. Wildfire severity and fire history influenced the occurrence of the superb lyrebird at the site-level. a. Unburnt forest sites had higher recording rates than either understorey-burnt or severely burnt sites. b. Within burnt sites, the recording rate was lower at sites with a short fire history (&lt; 3 years before 2009) than those with a longer fire history (&gt; 20 years), and this effect was larger at severely burnt sites.</td>
</tr>
<tr>
<td>Site level</td>
<td>2. Test whether topographic variation (gully/slope) modifies the influence of fire severity. 3. Examine the effect of habitat components in different topographic locations.</td>
<td>2. Topography moderated the effect of fire severity: unburnt gullies contained higher recording rates than both understorey-burnt slopes and severely burnt gullies, and slopes at reference sites (unburnt outside the fire boundary). 2. Shrub cover (1-2 m) was the only measured habitat component to influence the superb lyrebird: the recording rate increased with increasing shrub cover. 3. Unburnt forest and mesic gullies provide valuable habitat for the superb lyrebird at 2-3 years after wildfire.</td>
<td></td>
</tr>
</tbody>
</table>
8-2 Main findings

8-2-1 Effects of fire regime components and landscape heterogeneity on arboreal mammals

The effects of fire on faunal species and communities have not been studied as extensively as for plant communities (Bradstock et al., 2002; Clarke, 2008; Driscoll et al., 2010). In particular, the response of arboreal mammal species to fire have received less attention than other species of mammal, most likely due to their cryptic and arboreal nature. Based on previous studies in the wet montane forests of the Central Highlands, Victoria and the dry forests of coastal NSW (Newsome et al., 1975; Lunney, 1987; Catling et al., 2001; Banks et al., 2011a; Collins, 2012; Lindenmayer et al., 2013; Berry et al., 2015a), arboreal mammals in this study were expected to be detrimentally influenced by fire. However, no previous studies have examined the effects of fire severity, fire history, and spatial heterogeneity on arboreal mammals in foothill forests.

Both fire regime components and landscape heterogeneity influenced the occurrence of arboreal mammals (Chapter 3; see Table 8.1 above). At the site level, arboreal mammal species were influenced by both topography and wildfire severity. First, mesic gullies contained a higher abundance of arboreal mammals (total number of all species combined) than slopes. Moist gullies are less likely to burn in severe fire (Leonard et al., 2014a), and hence can maintain structural complexity (e.g. hollow bearing trees) that are suitable habitat for arboreal mammals. Second, wildfire severity influenced the abundance of arboreal mammals at 2.5 years after fire: fewer individuals (all species combined and the greater glider) were recorded in severely burnt sites compared with unburnt sites. Consistent with predictions, the number of greater glider also increased at sites with more large trees; large trees are an important habitat resource for arboreal mammals (Gibbons & Lindenmayer, 1997). Third, the landscape context influenced the abundance of both arboreal mammals (all species combined) and the number of greater glider at 3.5 years after fire. Higher numbers
were found at severely burnt sites surrounded by more unburnt and less-severely burnt (understorey-only burnt) forest.

The few unburnt areas of forest (< 1 % of total region; Leonard et al., 2014a) and forest gullies likely were important contributors to in situ survival during or immediately after the fire event. In contrast, areas burnt with high intensity fire is likely to have caused mortality of arboreal mammals (e.g. Koprowski et al., 2006; Lunney et al., 2007). Later, at the time of these surveys, unburnt areas appear to be enhancing the persistence of arboreal mammal populations within the burnt landscape, possibly due to greater availability of habitat components that provide food (e.g. canopy foliage), protection from predators, and shelter (such as tree hollows) (Catling et al., 2001; van der Ree & Loyn, 2002; Lindenmayer et al., 2013). For example, the number of dead trees was higher in severely burnt gullies within the study area (Bassett et al., 2015), suggesting that high intensity fire reduces habitat resources (e.g. live trees) for arboreal mammals. Unburnt areas together with less-severely burnt areas also appear to be sources for the recolonisation of severely burnt forest by arboreal mammals. However, post-fire recovery of arboreal mammals is not complete: few mammals were recorded in severely burnt sites, even with re-sprouting canopies at 2.5 years after fire. The rate of recolonisation is likely to depend on the rate of forest regeneration and the ability of species to use the burnt habitat (Fox, 1982).

Collectively, these findings show that mesic gullies and patches of unburnt forest are assisting in both the persistence and recolonisation of arboreal mammal populations at 2-3 years after severe wildfire. Fire refuges are those habitats that enable the survival and persistence of individuals and populations, and can contribute to the re-establishment of populations in post-fire landscapes (Robinson et al., 2013). Hence, unburnt areas and gullies are acting as refuge habitat for arboreal mammals in the post-fire environment.

Overall, the number of observations of arboreal mammals at many sites was relatively low, despite an intensive survey effort. This meant that it was not possible to analyse the response of each species individually. Additional survey effort, or the use of a
combination of survey techniques, could result in a larger data set with more power to detect patterns of occurrence. For example, thermal imaging cameras that detect heat signatures can be used in conjunction with spotlighting because they can detect fast moving animals that may otherwise be hidden by dense vegetation (Lumsden et al., 2013), resulting in higher detection rates than spotlighting alone (Focardi et al., 2001). Detection rates can also increase when thermal cameras are used together with call playback techniques for suitable species e.g. yellow bellied glider (Lumsden et al., 2013). However, thermal cameras are expensive and were not available for this work.

8-2-2 Influence of fire severity, fire history and landscape context on terrestrial native mammals

Terrestrial or ground-dwelling native mammals are some of the better understood faunal species in relation to fire in Australia (e.g. Lunney et al., 1987; Sutherland & Dickman, 1999; Catling et al., 2001; Fox et al., 2003; Woinarski et al., 2004; Recher et al., 2009; Letnic & Dickman, 2010; Di Stefano et al., 2011; Arthur et al., 2012; Griffiths & Brook, 2014). Most such studies conducted in forests have investigated the response of mammals at the site-level in dry sclerophyll forests of south-eastern Australia, with the majority focused on the response of species to time since fire or successional changes in post-fire habitat (Fox, 1982; Lunney et al., 1987; Catling et al., 2001; Recher et al., 2009; Arthur et al., 2012). Less attention has been given to the relative influence of different fire regime components or the landscape heterogeneity surrounding a site.

I investigated the effects of wildfire on terrestrial native mammal species at both the site and landscape level (Chapter 4; Table 8.1). Thirteen mammal species were detected, and eight of these were examined further (with sufficient data to analyse). Seven out of eight species were widespread and present in every level of fire severity (unburnt, understorey-burnt, severely burnt, reference) in the post-fire landscape. Fire severity was the most influential variable on mammal species at the site-level, although these effects were not strong at 2-3 years after fire. Terrestrial species are influenced
by the changes in habitat caused by fire, and how this influences the resources they need for food and shelter (Fox, 1982; Whelan et al., 2002).

Species responded to fire severity in different ways, likely due to different habitat requirements or preferences after fire (Fox, 1982; Keith et al., 2002; Diffendorfer et al., 2012). For example, the bush rat responded positively to fire severity, probably in response to complex vegetation structure provided by dense re-generation at severely burnt sites. The varying response of individual species to burn severity is consistent with the findings of studies on different taxa, such as on forest birds within the same study area (Robinson et al., 2014), arboreal mammals in the wet montane forests of Victoria (Lindenmayer et al., 2013), and research on birds, small mammals, and bats in the forests of north America (Kotliar et al., 2007; Fontaine & Kennedy, 2012; Buchalski et al., 2013). Hence the ecological requirements of individual species need to be considered in developing fire management plans for biodiversity conservation.

The apparent tolerance of terrestrial mammals to fire severity and a short fire history at the time of survey appears to be strongly influenced by the response to rapid and dense regeneration of vegetation at the ground level (see below), and is in contrast with the initial post-fire environment. High mortality of native mammals is likely during or immediately after the wildfire (Recher et al., 1975a; Whelan et al., 2002) in areas of high severely burnt areas where the forest vegetation was burnt, open and bare, but this study was not designed to detect this. In fact, very low numbers of small mammal species were recorded at 1.5-2 years fire in burnt sites (Chapter 7), which suggests that populations were severely reduced. Terrestrial native mammals that survived the fire front could use alternative refuges that avoid burning (e.g. wombat burrows, moist streams) (Recher et al., 1975b; Whelan et al., 2002; Bradstock et al., 2005) allowing in situ survival, or they may be able to better escape the fire event due to mobility (e.g. swamp wallabies; Keith et al., 2002; Garvey et al., 2010). In the immediate post-fire environment, herbivores such as the common wombat, swamp wallaby and eastern grey kangaroo, prefer to graze on re-sprouting grasses and shrubs in burnt areas (Gill & Catling, 2002; Murphy & Bowman, 2007). At 2-3 years after fire, the vegetation changed to a dense understorey of eucalypts and shrubs, and
resprouting of the canopy, which has appeared to reduce the effects of fire on native mammals.

In contrast with the response of arboreal mammals, the occurrence of native terrestrial species was not dependent on the proximity or extent of unburned forest. Thus, there was no evidence that, at 2-3 years post-fire, unburned forest was serving as a refuge to enhance the colonization or persistence of species in areas burned in the wildfire. The lack of effects from fire patterns at the landscape level indicates either in situ survival of sufficient individuals to recolonise internally, or rapid response and recolonisation associated with rapid recovery of vegetation across the landscape. Terrestrial mammals may be less influenced by isolation of unburnt sites than arboreal mammals because they can use a broader range of habitats, such as they are not restricted to the canopy which is substantially depleted by crown fires, or are more mobile which enables easier recolonisation (e.g. eastern grey kangaroo) (Keith et al., 2002). Likewise, bird species richness and abundance were not influenced by landscape effects of fire in the same study area (Robinson, 2014), possibly because they are more mobile than arboreal mammal species.

The results from this study indicate that native mammal species are recovering at 2-3 years after a major wildfire, most likely in response to rapid regeneration of vegetation at ground and shrub layers after drought-breaking rains (Figs 8.1 and 8.2). These results are consistent with the habitat accommodation model proposed by Fox, (1982), in which mammal species undergo secondary succession after fire, and respond to changes in vegetation as part of plant succession after fire. Species enter the succession when their habitat requirements are met, depending upon the regeneration time of vegetation (Fox, 1982). The rapid recovery of structurally complex vegetation in less than three years provides food resources, physical shelter, and cover to facilitate dispersal and recolonisation through what was a bare, charred landscape immediately post-fire (Figs 8.1 and 8.2). Understanding changes in the interactions between native species after fire at different stages in the post-fire succession would be valuable, but we were not able to assess this here. If the drought had continued well beyond the time of the wildfire, I would expect fire severity, fire history, and landscape context to have had a much stronger influence on species.
Photos: Immediately after wildfire - Department of Environment, Land, Water and Planning. 2.5 years after fire - Natasha Robinson.

Figure 8.1  Examples of understorey burnt forest slopes and gullies (different sites) showing a) burnt vegetation and bare ground immediately after the 2009 wildfires, and b) regenerating vegetation 2.5 years after wildfire at the time of surveys.
Photos: Immediately after wildfire - Department of Environment, Land, Water and Planning. 2.5 years after fire - Natasha Robinson.

**Figure 8.2** Examples of severely burnt forest slopes and gullies (different sites) showing a) burnt vegetation and bare ground immediately after the 2009 wildfires, and b) dense regenerating vegetation 2.5 years after wildfire at the time of surveys.
Camera trapping was an appropriate method to gain an understanding of the broad scale effects of fire on the distributional patterns of a wide range of mammal species. If time or economic factors were not a constraint, camera traps could be set for a longer period of time (e.g. 21 days) to increase detections of less common species (e.g. dusky antechinus) and rare species (e.g. smoky mouse). In addition, I attempted to understand how demographic processes of small mammal populations were influenced by fire regime components by live capture (Chapter 7). However, trap success of small mammals was low at 2.6% (2.6 captures per 100 trap nights), over 4320 trap nights. Hence, a decision was made to invest in conducting broad-scale camera traps surveys. If live capture surveys were attempted in the future, ideally it would be conducted over multiple sessions over 1-2 years, as well as at further points in the post-fire succession to uncover demographic change.

8-2-3 Impact of fire and spatial variability on introduced mammals

Introduced species are considered to be one of the largest threats to biodiversity in the world, because they can lead to native species declines or extinctions (Vitousek et al., 1997b; Woinarski et al., 2015). Fire changes ecosystems, which gives introduced species a chance to colonise the disturbed environment, or allows existing populations to increase in population size and expand their distribution (Mack et al., 2000; Doherty et al., 2015). However, the impacts of fire on the distribution and abundance of introduced mammal species across large spatial regions is largely unknown.

I investigated the occurrence of introduced mammal species in foothill forests in relation to fire regime components and landscape context and found limited influence of these variables on the distribution of these species (Chapter 5; Table 8.1). Six species of introduced mammal were detected via camera surveys. Four species, the black rat, house mouse, red fox and feral cat, were detected with sufficient records to analyse further. These four species were present in all fire severity classes (unburnt, understorey-burnt, and severely burnt forest sites) in the landscape at 2-3 years post fire. With the exception of the black rat, that was positively influenced by fire severity and topographic location, the occurrence of the remaining three species was not
influenced by fire regime components at either the site or landscape-level, nor by topographic position of gully or slope.

The widespread occurrence of introduced species after fire can be attributed to their ability to adapt to a wide range of habitats, such as by having generalised diets (e.g. house mouse); and their mobility (e.g. red fox) (Newsome et al., 1975; Fox, 1982). Predators, although native, in the chaparral habitats of California, USA, also were not influenced by fire most likely because they are foraging and habitat generalists (Schuette et al., 2014). Similarly, other studies have recorded the house mouse to occupy the post-fire landscape, being a short-term early colonizer of burnt vegetation, and reaching high abundances at 1-2 years after fire (Fox & McKay, 1981; Fox, 1982; Catling, 1991; Recher et al., 2009; Kelly et al., 2010). Other studies have shown introduced foxes and cats to be similarly persistent in the early post-fire environment (e.g. Newsome et al., 1975; Catling et al., 2001; Arthur et al., 2012; Payne et al., 2014). For instance, in dry sclerophyll forest, NSW, fox abundances were associated with habitat cover after fire, whilst cat abundance increased after fire, possibly from an increase in densities prey species of bandicoot which increased with shrub cover (Arthur et al., 2012).

The occurrence of introduced species across the landscape at 2-3 years post fire, is likely to have a range of impacts on native species. For example, introduced predators are known to be advantaged in burnt areas where movement is less impeded and where there is less cover and refuge for native prey species: such predation pressure can result in a high level of mortality for individuals that survive fire (e.g. brush-tailed bettong in eucalypt forests, Australia (Christensen, 1995), and cotton mice in pine forests, Georgia, USA (Conner et al., 2011). Predation pressure can also prevent population growth of native prey species and reduce species richness (e.g. small mammals in Mediterranean forests, Spain (Torre & Diaz, 2004), as well as restrict native species to localized areas (Sutherland & Dickman, 1999; Robinson et al., 2013; McGregor et al., 2014).
Competition from introduced species may also impact on native species after fire by causing native species to shift habitat or reduce population size (Sutherland & Dickman, 1999). For example, the black rat is a competitive threat to the native bush rat because it can cause spatial avoidance of the bush rat, and reduce the population size by negatively affecting survival, breeding success, and recruitment of young (Stokes et al., 2009b); these effects may be amplified after fire.

Introduced species can also negatively affect plant species in the post-fire environment. For example, the sambar deer increased in abundance in the study area after the 2009 fires (Forsyth et al., 2012), which has implications for the threatened plant species (*Nematolepis wilsonii*) that suffers reduced health and foliage cover from damage caused by deer rubbing against the side of trunks and by the thrashing of saplings (Bennett & Coulson, 2010). These types of negative effects of introduced species on native populations can be exacerbated by fire, potentially posing a threat to native species and loss of biodiversity in ecosystems (Arthur et al., 2012; Doherty et al., 2015).

There were few significant correlative relationships between the spatial pattern of occurrence of introduced and native species. The negative correlation between the house mouse and bush rat is consistent with other studies (Catling & Newsome, 1981; Fox, 1982) indicating that introduced rodents are scarce or absent where populations of native rodents are present. However, correlative associations do not provide a strong basis for identifying causal mechanisms. A stronger approach would be to carry out experimental manipulations of species (e.g. Dexter & Murray, 2009; Moseby et al., 2009; Claridge et al., 2010; Salo et al., 2010; Kovacs et al., 2012), in combination with the effects of fire, to better understand ecological interactions, such as predation and competition, between introduced and native species, and fire e.g. (Morris et al., 2011). The scale at which the interaction may occur between species (e.g. resource use) is also an important consideration (Edelman et al., 2009).

Even though camera trap surveys are effective at detecting mammal species (both native and introduced species of different sizes (Vine et al., 2009; De Bondi et al.,
2010; Paull et al., 2012; Swan et al., 2015), the effects of fire on the distribution of several introduced species could not be modelled due to few records or low detection rates (e.g. sambar deer). Greater duration of camera surveys or repeated surveys would increase records and detection rates of cryptic species. If sufficient data is available, it is possible to test for species interactions in time between introduced and native mammal species by examining the times when different species were active (Ridout & Linkie, 2009; Fancourt et al., 2015; Farris et al., 2015). Studies that examine temporal variation in the activity of introduced species can help to understand their distribution in the landscape (Moseby et al., 2009; Carter et al., 2012).

8-2-4 Impacts of the fire regime on an ecosystem engineer, the superb lyrebird

Ecosystem engineers alter the structure of habitats in ways that influence the distribution and abundance of other organisms (Jones et al., 1994; Lawton, 1994). The superb lyrebird is considered an important ecosystem engineer in the forests of south-eastern Australia, because its foraging activity on the forest floor substantially influences habitats for other species, it manipulates forest fuel for fires, and influences ecological processes such as nutrient cycling (Adamson et al., 1983; Ashton & Bassett, 1997; Eldridge & James, 2009; Nugent et al., 2014).

There were three main findings from this study of the influence of the fire regime and landscape heterogeneity on the superb lyrebird (Chapter 6; Table 8.1). First, both fire severity and fire history influenced the occurrence of the superb lyrebird in foothill forests after wildfire. It was recorded less frequently in burnt forest (including both understorey burnt and severely burnt fire severity classes) at 2-3 years after wildfire; and for sites burnt in 2009, it was less frequent at those with a short fire history (< 3 years) compared to a long history (> 20 years). Second, topographic location influenced the effect of fire severity on the superb lyrebird, with gullies generally having a higher recording rate than slopes. Third, contrary to expectations, the measured habitat components at gully and slope sites were not significantly associated
with the occurrence of the superb lyrebird after wildfire, with the exception of shrub cover (< 2 m).

The relationship of the superb lyrebird with fire severity and fire intervals could be caused by three mechanisms. First, a higher level of mortality may have occurred in areas of forest exposed to high intensity fire (Recher et al., 1975a; Whelan et al., 2002). Second, the dense regeneration of vegetation in the post-fire environment likely creates an unsuitable environment for this species. The superb lyrebird requires forest habitat with a relatively open understorey for foraging, building mounds and nesting (Reilly, 1970; Lill, 1980; Robinson & Frith, 1981; Ashton & Bassett, 1997), and the dense regeneration of vegetation after the drought-breaking rains could act as a barrier for this species and restrict foraging and nesting (Woinarski & Recher, 1997; Nugent et al., 2014).

Third, repeated fires within short fire intervals has consequences for food resources. Frequent fires reduces leaf litter and depletes food resources for the lyrebird, such as leaf litter invertebrates, due to decreased moisture levels and simplified structure (York, 1999; New et al., 2010). In foothill forests, at 0-2 years after fire, there is normally little leaf litter, and it can take 10-40 years after fire for a deep leaf litter layer to accumulate and re-establish (Cheal, 2010). Therefore, short fire intervals reduce leaf litter, and in turn cause a reduction in food resources for this species. Robinson et al., (2014) also suggested that unburnt patches with long time since fire are valuable for the superb lyrebird, because they contain greater food sources of leaf litter invertebrates than burnt patches, in the same region.

As for arboreal mammals, unburnt forest areas and gullies may have enabled in situ survival of the superb lyrebird, and persistence after the fire by providing more suitable habitat and greater abundance of food resources than burnt areas (e.g. more open understorey than severely burnt sites). In addition, the foraging activity of the superb lyrebird can reduce the amount of forest fuel and connectivity, which reduces the possibility of fire in these forests (Nugent et al., 2014). These patches of unburnt vegetation are likely to assist in the recovery of the superb lyrebird if they remain
unburnt for longer fire intervals, and the activity of this species may also be able to reduce the flammability of forest patches (Nugent et al., 2014).

8-3 Implications for management and conservation of fauna in foothill forests

Large wildfires are inevitable in the forests of south-eastern Australia (Bradstock, 2008; Adams & Attiwill, 2011), and the inherent variation in fire severity associated with such fires creates spatial patterns in the forest vegetation and heterogeneity in the landscape (Schoennagel et al., 2008; Roman-Cuesta et al., 2009; Leonard et al., 2014a). Fire regime components and landscape heterogeneity arising from fire influence the biota in this and in other fire-prone regions (Whelan et al., 2002; Bradstock et al., 2005; Gill & Allan, 2008). Ecological knowledge of the effects of fire on faunal species can be used for biodiversity conservation, and for management of fire in such fire-prone regions. I outline some key suggestions to be considered during the development of fire management plans for biodiversity conservation in foothill forests, Victoria, south-eastern Australia.

Fire severity was the most influential driver of mammal species occurrence in the early post-wildfire in foothill forests, but species responses varied. This implies that there is not a single ‘ideal’ burn severity that is suitable for all species. Hence, when using fire for ecological purposes, a spatial mosaic of differing levels of fire severity – including unburned patches – is most likely to provide for the diverse requirements of species. Hence, these results support the ecological theory that pyrodiversity, planned burning that results in a variety of habitats in space and time, will help the persistence of multiple species in the landscape (Bradstock et al., 2005; Parr & Andersen, 2006). The spatial pattern of fire mosaics that are more, or less, suitable for biota is a current area of research (Pastro et al., 2011; Kelly et al., 2012; Taylor et al., 2012; Di Stefano et al., 2013; Nimmo et al., 2013; Sitters et al., 2014). Where there are individual species that are known to be rare or threatened, or fire-sensitive, these need to be given priority during the development of fire management plans for large regions.
Fire management that aims to reduce severe fires often involves fire suppression and fuel treatment. Reduction of fuel loads can include thinning, clearing and planned burning (Penman et al., 2015). In Australia, planned burning is one management tool that is commonly used to reduce fuel loads and hence ameliorate the likely effects of wildfire on biodiversity (Pasch & Koprowski, 2011; McCaw, 2013; Murphy et al., 2015; Penman et al., 2011). Planned burning can be used strategically to protect habitat for species that are negatively affected by wildfire, such as for arboreal mammals and the superb lyrebird in foothill forests. Here, unburnt patches of forest and mesic gullies assisted the persistence and recolonisation of arboreal mammals. Planning burning could be used to protect or create such refuge habitat against future wildfires by strategically reducing fuel loads adjacent to areas known to be valuable for faunal groups (Robinson et al., 2013). Such areas include mesic gullies and drainage lines that are less likely to burn (Bradstock et al., 2010; Leonard et al., 2014a), and mature forest stands with a high density of large or hollow-bearing trees (Gibbons & Lindenmayer, 1997; Koch et al., 2008; Koch et al., 2009; Goldingay, 2012; Lindenmayer et al., 2013).

Planned burns, by reducing fuel loads, can reduce the intensity of wildfire in foothill forests for up to 5-10 years (Price & Bradstock, 2012), and reducing the amount of area that is severely burnt is likely to be of benefit for mammal species which are negatively affected by high fire severity. Decreasing fire severity and protection of habitat may not always be possible because wildfires are difficult to control, especially under extreme weather conditions (Fernandes & Botelho, 2003; Price & Bradstock, 2012; McCaw, 2013). After the 2009 Black Saturday fire, unburnt patches of forest within the fire boundary were rare, and were influenced by topography, type of vegetation, and previous burns (Leonard et al., 2014a). Hence, low intensity planned burning could be applied in some areas that have a lower probability of burning (e.g. moist gullies) so that they retain vegetation structure, and reducing fuel loads around the area means it will be less likely to burn in a future wildfire (Leonard et al., 2014a).

However, repeated burns at short fire intervals can reduce habitat and structural complexity for fauna, such as decrease the volume of logs (Bassett et al., 2015), cause the collapse of large trees (more likely to have hollows) on ridges (Collins et al., 2012),
and can lead to animal species extinctions (Bradstock et al., 2005). In this study, the effect of the previous fire largely was overshadowed by the effects of the 2009 wildfire; nevertheless, for several species such as the superb lyrebird, forest sites that had been burnt < 3 years before the wildfire were less suitable than those with longer (> 20 years) fire history. Hence, some areas should also remain unburnt from planned burning to reduce impacts on fire-sensitive species, including those which avoid burnt areas and remain within their home ranges (Leonard & Koprowski, 2010). The recommended minimum fire interval for foothill forests of 10 years for low severity fire, and 25 years for high severity fire (Cheal, 2010) is an appropriate minimum value for these species.

The widespread occurrence of introduced mammal species in the early post-fire environment and the limited effects of fire regime components or landscape heterogeneity on their distribution, suggests there is no ideal pattern of planned burning to reduce their occurrence. Introduced predators, particularly the red fox and cat, are major threats to native fauna in Australian ecosystems, and can lead to the decline or local extinction of populations (Sutherland & Dickman, 1999; Johnson et al., 2007; McKenzie et al., 2007; Woinarski et al., 2015). To minimize the detrimental effects of predation on local populations of native species, management to control introduced predators (e.g. baiting, culling, shooting) is likely to be most effective immediately after wildfire, with continuation of control programs into the future (Robley et al., 2012; Newsome et al., 2014).

At this time, introduced species are likely to add an additional threat to native mammal populations that have already experienced both direct mortality from fire and indirect effects via loss of vegetative cover and shelter (Doherty et al., 2015). Where fire has limited native mammals to isolated habitat patches (Catling, 1991), they can be exposed to increased predation and small populations are at risk (Sutherland & Dickman, 1999; Robley et al., 2013); the level of predation may exceed a threshold that prevents populations from recovering to pre-fire levels (Russell et al., 2003). For instance, arboreal mammals were in low abundance in refuge habitat at 2-3 years after fire, possibly from the lasting effects drought, and could be further depleted by introduced predators in these habitats. Such loss in source habitats could reduce
recolonisation into the burnt landscape, and limit the overall recovery of populations across the region. Hence, such refuge habitat, where identified for species vulnerable to introduced predators, could also be targeted as a priority for introduced predator management after fire.

This study considered the potential effects of fire at both the site scale and considering the surrounding landscape. Investigation of fire effects at a single scale may fail to capture the full effects of fire and responses of different species (including rare or vulnerable species) that may respond at a larger or smaller scales (Driscoll et al., 2010). Here, for example, arboreal mammals were influenced by fire effects at both the site-level and landscape-level. Although landscape-level effects, surprisingly, were not influential for most other terrestrial mammals at 2-3 years after fire, the surrounding landscape may exert greater influence at other points in time such as immediately post-fire, or during drought. Studies conducted at appropriate spatial scales are likely to capture a greater understanding of the effects of fire on fauna, particularly those which capture the home ranges of species, can be used for more effective fire management (Driscoll et al., 2010; Lawes et al., 2015).

8-4 Future directions for research and conservation in fire-prone ecosystems

This study together with other work from the collaborative Faunal Refuge Project undertaken by Deakin and La Trobe universities (Robinson et al., 2013; Leonard et al., 2014a; Leonard et al., 2014b; Nugent et al., 2014; Robinson, 2014; Robinson et al., 2014; Bassett et al., 2015; Buckingham et al., 2015) has gained unique insights into of the effects of fire severity, fire history and landscape heterogeneity on multiple groups of taxa (i.e. mammals, birds, invertebrates, plants), in a fire-prone region. Further research, in this ecosystem and in others, could build on the results from this study in a number of ways.

1. Fire severity is an important component of the fire regime to include in future studies.
2. Further work is needed on the identification and attributes of habitat refuges for different species, and their role through time in the post-fire succession (Robinson et al., 2013). Knowledge of the characteristics and locations of habitat that act as fire refuges can be used to guide the location and timing (e.g. season) of planned burns, to enhance the conservation of species, including threatened species (Garvey et al., 2010; Pereoglou et al., 2011; Blount & Koprowski, 2012).

3. Long-term studies are needed to complement ‘snap shot’ studies at a particular point in time (such as this, at 2-3 years after wildfire). Fauna at the present sites could be re-surveyed in a long-term study, at different times through the post-fire succession (e.g. 2, 5, 10, 20, 30 years) to gain further understanding of species’ distributions, relative abundance and recovery after fire (e.g. Recher et al., 2009; Woinarski et al., 2010). Longitudinal studies also are vital to understand interactions between fire and climate (e.g. during extended drought), and the synergistic effects of fire with introduced species and other disturbances, such as logging and grazing (Gill & Catling, 2002; Clarke, 2008; Driscoll et al., 2010; Doherty et al., 2015).

4. Manipulative experiments are an important tool for understanding faunal responses and species interactions after fire, including both native and introduced species (Clarke, 2008; Driscoll et al., 2010). For example, new insights could be gained from experimental approaches that involve a before and after study design with planned burns (Driscoll et al., 2010; Tuft et al., 2012). An experimental approach would be valuable to understand the interactions between introduced predators and native mammal species (Doherty et al., 2015; Mowat et al., 2015), potentially by manipulating the abundance of red fox and feral cat (e.g. control programs, fenced exclosures) and measuring changes in native species abundance or activity (e.g. Dexter & Murray, 2009; Moseby et al., 2009; Claridge et al., 2010) after fire. Studies that control the impact of introduced herbivores (e.g. deer) on vegetation and native mammal species after fire are also valuable (e.g. Pedersen et al., 2014). Experimental manipulation of vegetation after fire could also help identify habitat attributes that are important for the recovery of native species (Sutherland & Dickman, 1999; Mowat et al., 2015).
5. A key issue is to better understand the mechanisms behind the response of faunal species to fire (Driscoll et al., 2010). For instance, the immediate effects of wildfire on faunal mortality and survival are not well understood (Whelan et al., 2002). Similarly, knowledge of the processes associated with in-situ survival and recolonisation of the burnt environment, and changes in species demography during the recovery of faunal populations after fire, is scarce (Banks et al., 2011b).

6. Understanding of the effects of fire on less common species and less-studied faunal groups would also be beneficial. This includes species that are functionally important, such as pollinators (e.g. bats, bees), predators (e.g. in this ecosystem, owl species including the threatened powerful owl (*Ninox strenua*) and sooty owl (*Tyto tenebricosa*), and other rare or threatened species (e.g. in this system, smoky mouse, broad-toothed rat).

7. It would be valuable to conduct similar parallel studies of the effects of fire regime components and landscape heterogeneity that span different vegetation types and regions, to better understand responses that are common among ecosystems versus those that may be idiosyncratic to a particular situation.

8. Fire, as a disturbance process, does not occur in isolation, but occurs in forests subject to other impacts. Thus, a challenging frontier in fire ecology is to understand the synergistic impacts of other processes that may interact with fire; such as climate change, introduced plant and animal species, expanding human settlements, land clearing, grazing, logging, hydrological and other natural disturbance processes (e.g. drought) (Bennett et al., 2009; Driscoll et al., 2012). These all place considerable pressure on the resilience of native fauna and biodiversity in fire-prone forests (Brook et al., 2008; Spies et al., 2012; Doherty et al., 2015).
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References


Myself and a bush rat (*Rattus fuscipes*)

Working in a severely burnt gully and camping at Black Range State Forest
Appendix 1. Refuges for fauna in fire-prone landscapes: their ecological functions and importance.

Refuges for fauna in fire-prone landscapes: their ecological function and importance

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Summary

1. Rapid environmental change is placing increasing pressure on the survival of many species globally. Ecological refuges can mitigate the impacts of change by facilitating the survival or persistence of organisms in the face of disturbance events that would otherwise lead to their mortality, displacement or extinction. Refuges may have a critical influence on the successional trajectory and resilience of ecosystems, yet their function remains poorly understood.

2. We review and describe the role of refuges in faunal conservation in the context of fire, a globally important disturbance process.

3. Refuges have three main functions in relation to fire: they enhance immediate survival during a fire event, facilitate the persistence of individuals and populations after fire and assist in the re-establishment of populations in the longer term. Refuges may be of natural or anthropogenic origin, and in each case, their creation can arise from deterministic or stochastic processes. The specific attributes of refuges that determine their value are poorly known, but include within-patch attributes relating to vegetation composition and structure; patch-scale attributes associated with their size and shape; and the landscape context and spatial arrangement of the refuge in relation to fire patterns and land uses.

4. Synthesis and applications. Refuges are potentially of great importance in buffering the effects of wildfire on fauna. There is an urgent need for empirical data from a range of ecosystems to better understand what constitutes a refuge for different taxa, the spatial and temporal dynamics of species’ use of refuges and the attributes that most influence their value to fauna. Complementary research is also required to evaluate threats to naturally occurring refuges and the potential for management actions to protect, create and enhance refuges. Knowledge of the spatial arrangement of refuges that enhance the persistence of fire-sensitive species will aid in making decisions concerning land and fire management in conservation reserves and large natural areas. Global change in the magnitude and extent of fire regimes means that refuges are likely to be increasingly important for the conservation of biodiversity in fire-prone environments.

Key-words: biodiversity, biological legacies, disturbance, prescribed fire, residual habitat, unburnt patch, wildfire

Introduction

Globally, the survival of many species is under mounting pressure from environmental change, including the impacts of habitat loss and modification, invasive species, overexploitation of resources and climate change (Lindemayer & Fischer 2006; Brook, Sodhi & Bradshaw 2008). Such anthropogenic pressures can modify the temporal and spatial dynamics of natural disturbance regimes, placing the inherent resilience of ecosystems under greater stress (McKenzie et al. 2004; Brook, Sodhi & Bradshaw 2008). The ability of species to cope with change arising from disturbance will depend on their ecological and
life-history attributes (Sousa 1984). Species with low dispersal capabilities are less able to directly avoid rapid shocks and will be at increased risk of mortality unless they possess other adaptations (e.g. behaviours or physiologies) that allow them to survive in situ (Whelan 1995). Specific components of a landscape that endure (or escape) change caused by a disturbance can lessen the impacts of environmental shocks on organisms and increase their likelihood of surviving: these components are commonly referred to as refuges (e.g. Lindenmayer et al. 2009; Brennan, Moir & Wittkuhn 2011). Refuges may have a critical influence on the successional trajectory and resilience of ecosystems to disturbance events. Consequently, if the specific properties of high-quality refuges can be successfully identified, then these areas can be located and managed to ameliorate against major environmental pressures.

Refuges are defined here as habitat features within a landscape that facilitate the survival or persistence of organisms (or species) in the face of a disturbance event that would otherwise result in their mortality, displacement or extinction (see also Mackey et al. 2002). We review the concept and role of refuges in faunal conservation in the context of fire. Fire profoundly influences the structure and composition of ecosystems, and the distribution and abundance of organisms globally (Bond, Woodward & Midgley 2005). The impact of fire is inherently heterogeneous (Burton et al. 2008). This reflects variation in fire regimes (i.e. fire intensity, time since fire, interfire interval, season of burning; Gill 1975) and in the spatial pattern of fires (e.g. their size, shape and context of unburnt vegetation). The occurrence of refuges is an element of this heterogeneity. Thus, the relationship between refuges, disturbance regimes and the environment involves complex interactions that are both spatially and temporally dynamic.

In the context of fire, refuges typically occur at relatively small spatial scales (e.g. forest patches, logs, burrows) within the fire boundary. They may occur as isolated patches or as peninsulas surrounded by the burnt matrix (Perera, Buse & Routledge 2007), but are distinct from large tracts of unburnt vegetation adjacent to the fire boundary. Conceptually, refuges partially overlap with the idea of ‘biological legacies’ (Franklin et al. 2000). However, the latter concept is broader and refers to all biological or biologically derived features that persist following disturbance (including organisms themselves) and the range of functions these may fulfil. Whilst some biological legacies can act as refuges (e.g. hollow trees, undisturbed patches of vegetation), others have extremely limited capacity to fulfil this role (e.g. plant propagules, faeces). In addition, there are features that function as refuges that are not biological in origin (e.g. rock outcrops).

In many fire-prone environments, synergies with anthropogenic threats, such as habitat fragmentation and invasive species, suggest that present-day impacts of fire potentially are greater than those experienced by species during their evolutionary history (Brook, Sodhi & Bradshaw 2008). In these circumstances, refuges may have an even greater role in sustaining species and communities. Further, with global climate change, fire-prone regions are predicted to differentially experience changes in the length of fire seasons and the frequency and/or intensity of wildfires (Flannigan et al. 2009). This may increase the importance of refuges for the persistence of fire-sensitive fauna, whilst potentially also decreasing the likelihood of refuges existing (McKenzie et al. 2004). The limited understanding of the role of refuges and the factors that determine their value for the persistence of biota in fire-prone landscapes means that land managers have little guidance for incorporating the maintenance or creation of refuges into fire planning.

We outline a conceptual model of the functions of refuges in relation to fire, describe the origins of refuges, review current understanding of the factors that influence the value of refuges for fauna and identify knowledge gaps. We acknowledge that some species are dependent on fire, being either pyrophilic or associated with early postfire successional stages (e.g. Hutto 2008), but focus here on species that are likely to do less well in a world experiencing more frequent and severe fires.

Refuges and their role in survival and postfire recovery of fauna

Refuges have three primary roles in relation to fire: (i) they enable survival of organisms during and immediately after a fire event; (ii) they facilitate in situ persistence of organisms and populations within the fire boundary; and (iii) they assist the re-establishment of populations within the burnt area as it recovers. The length of time that a specific habitat component may fulfil a refuge role for an organism will vary, and through time, organisms and populations may use different habitat components for different roles.

SURVIVAL DURING A FIRE

The likelihood of immediate survival of an individual during a fire will be influenced by the severity of the fire, the individual’s location in relation to potential refuges in the landscape and the physical or behavioural mechanisms the organism may use to avoid direct flames and radiant heat (Friend 1993; Whelan 1995).

Numerous studies have linked postfire population sizes with fire severity (e.g. Smucker, Hutto & Steele 2005). Individual survival may be relatively high after low intensity or patchy fires in which vegetative components remain unburnt or only partially burnt (Ford et al. 1999; Brennan, Moir & Wittkuhn 2011). In contrast, severe fires can result in large declines in population sizes (Newsome, McLroy & Catling 1975; Banks et al. 2011; Couturier et al. 2011).

Species that live permanently within less flammable habitats (e.g. rock outcrops, rain forest gullies) may rarely
have direct contact with fire (Whelan 1995). For other species, individuals may either seek out or fortuitously be present within a refuge when the fire passes (Grafe, Döbler & Linsenmair 2002; Garvey et al. 2010). Individual or social behaviour can also influence access to refuges and affect survival rates (Whelan et al. 2002). For example, swamp wallabies *Wallabia bicolor* moved to moist creekline vegetation during a fire, and then, individuals doubled back through the fire front to safety in burned areas (Garvey et al. 2010). Savanna chimpanzees *Pan troglodytes verus* exhibit a complex suite of behaviours in avoiding fire, including individuals apparently warning other group members of approaching fire and monitoring the progress of fires at close range (Pruetz & LaDuke 2010).

**PERSISTENCE OF INDIVIDUALS AND POPULATIONS POSTFIRE**

Whilst all animals must avoid the immediate passage of fire, by using either a refuge or fleeing, refuges can also facilitate the postfire persistence of individuals and populations within the burned landscape. The importance of refuges for the species’ persistence depends on the degree to which they provide resources that, otherwise, are unavailable in the burnt matrix. Species exhibit a continuum of levels of reliance on refuges for postfire persistence (e.g. Legge et al. 2008), and at least five patterns of refuge use can be recognized.

First, individuals may use a refuge temporarily to survive the fire front, but then live within the burned area with no further dependence on the refuge (e.g. Garvey et al. 2010). Second, individuals may persist within the burned area, albeit at a reduced density, assisted by the presence of postfire legacies (e.g. partly burned logs, stumps) that provide physical refuge or shelter (Banks et al. 2011). Third, individuals of some species may survive postfire by using both unburnt refuge habitat and adjacent burned areas (Fraser et al. 2003). Such species are likely to be favoured by fine-grained fire mosaics. Fourth, persistence of a species may depend primarily on unburned patches of vegetation to meet all their resource requirements in the short term (up to several years) (Watson et al. 2012a), before they gradually recolonize the surrounding environment. Lastly, species that are late-successional specialists may depend on unburned refuges for many years. For example, the Malalee Emu-wren *Stipiturus malleus* is essentially absent from burned vegetation until at least 17 years postfire (Brown, Clarke & Clarke 2009). In the absence of suitable refuges, such specialists will be at high risk of local extinction (Silveira et al. 1999; Peres, Barlow & Haugaasen 2003).

**RE-ESTABLISHMENT OF POPULATIONS**

In the longer term, refuges may contribute to re-establishment of populations in extensively burned landscapes in two ways: as a source for population expansion from within the fire boundary and by facilitating the colonization of individuals from outside the fire boundary (Banks et al. 2011; Watson et al. 2012a).

If a species survives and persists within refuges, this offers the potential for population expansion into the surrounding landscape from multiple dispersed nuclei when conditions in the burnt environment become suitable (Watson et al. 2012a). Little is known, however, of the spatial dynamics of species in such situations, despite the potential importance in recolonization processes (Banks et al. 2011). Depending on the spatial isolation of refuges relative to the mobility of the organism, spatial population structure within the burned landscape may vary through time along a gradient from a series of disjunct isolated populations, to a metapopulation and to a patchy population linked by frequent movements (Templeton, Brazeal & Neuwald 2011; Driscoll, Whitehead & Lazzari 2012).

Alternatively, refuges may facilitate colonization by individuals from outside the fire boundary, by providing resources in the short term (food, shelter) or longer term (resident habitat). The distance from the fire boundary and the spatial arrangement of refuges within the burned area will influence the rate and capacity for colonization by different species (Turner et al. 1998). Refuges close to the boundary are more likely to be occupied (Watson et al. 2012a).

**Origins of refuges**

Refuges can be created by natural processes, or by human manipulation of the environment, often with the intent of conserving organisms and communities. In both cases, the processes giving rise to refuges may be deterministic or stochastic.

**NATURAL REFUGES**

Patches of unburnt vegetation and features such as logs and rock outcrops that provide refuge occur naturally in burned landscapes (Burton et al. 2008). Few studies have quantified the proportion of vegetation remaining unburnt during wildfires. Reported values range from as little as approximately 1–22%, of the fire-affected landscape, with this value largely depending on weather conditions during the fire and landscape characteristics (Román-Cuesta, Gracia & Retana 2009; Madoui et al. 2010; S.W.J. Leonard, A.F. Clarke & M.F. Bennett, in review).

Due to the influence of topographic position and environmental features, unburnt patches often occur in a non-random (deterministic) manner (Mackey et al. 2002; Bradstock et al. 2005). Typically, the vegetation differs in composition or moisture content from that in the surrounding fire-prone landscape, such as moist gullies within temperate eucalypt forests (Penman et al. 2007), rain forest patches within savanna woodlands (Bowman 2000) or deciduous forest within mixedwood boreal

forests (Burton et al. 2008). In some instances, negative feedback between vegetation succession and flammability reduces the probability of fire over time (e.g. succession from eucalypt forest to rain forest, Jackson 1968). Sites that exhibit reduced flammability due to topography, microclimate or vegetation type may remain unburnt over several fire cycles in the surrounding landscape and therefore escape fire for extended periods (Camp et al. 1997). In extreme fire weather conditions, however, even these sites can burn (Gill & Allan 2008). In addition, deterministic refuges may be compromised or lost if they are subject to anthropogenic disturbances such as logging or land clearing (Lindenmayer et al. 2011).

Natural refuges also arise due to stochastic processes (Mackey et al. 2002). The interaction of weather and fire is complex and can be unpredictable, particularly at the local scale. Sudden variation in wind speed or direction results in localized changes in fire intensity or direction of travel, which in turn has the potential to result in patches remaining unburnt. Such unburnt patches can be considered ‘transient’ refuges, as they ‘escape’ one fire event, but not necessarily the next (Bradstock et al. 2005).

Animals may modify fuel characteristics within a site, such that the likelihood of burning is reduced. Intense herbivory may reduce fuel loads to the extent that fire is excluded (Leonard, Kirkpatrick & Marsden-Smedley 2010). Burrowing animals can create bare or sparsely vegetated areas around warrens that inhibit fire spread (Kotliar et al. 1999). Other soil-disturbing activities such as wallowing (Knapp et al. 1999) may have similar effects. Animals may also reduce fuel loads and hence flammability through removing leaf litter (Mikami et al. 2010). The duration of fire suppression from these actions varies from weeks to months (e.g. migratory herbivores, McNaughton 1992) to decades (e.g. Cynomys spp. colonies, Kotliar et al. 1999).

REFUGES OF ANTHROPOGENIC ORIGIN

Land management practices can reduce fuel loads so that areas adjacent to a treated area function as refuges or to create potential refuges within a large treated area.

Prescribed burning may be used in a deterministic fashion (i.e. in a particular place and time) to maintain designated refuges by manipulating the location, size and frequency of burns such that they prevent future wildfire from spreading into adjacent designated areas (Burrows 2008). Other means of reducing fuel loads, such as mechanical removal of fuel (Waldrop, Phillips & Simon 2010) or manipulation of grazing or browsing animals (Valderrabano & Torrano 2000), may also be used to protect areas from fire. However, fuel reduction by such means needs to be carefully considered as there are examples of both mechanical fuel removal (e.g. salvage logging, Donato et al. 2006) and herbivory (Leonard, Kirkpatrick & Marsden-Smedley 2010) that increased vegetation flammability.

Prescribed burning can also be used to create potential refuges within a large treated area. Conservation managers often adopt some form of patch mosaic burning with the aim of introducing or maintaining landscape heterogeneity by creating patches that vary in fire history and severity of the most recent fire, including patches that remain unburnt (Parr & Andersen 2006). The exact location and size of unburnt patches is usually not predetermined, but the general pattern of the mosaic (e.g. overall burn cover, patch grain) may be managed by selecting the timing and pattern of ignition (Yibarbuk et al. 2001). For example, to maintain populations of relatively sedentary, refuge-dependent fauna in northern Australian savanna, a fine-grained fire mosaic is required in which fire patch size is less than the home range of the species concerned (in some cases <1 ha; Fraser et al. 2003; Yates, Edwards & Russell-Smith 2008). The resultant mosaic may limit the spread and intensity of subsequent wildfire, such that a higher proportion of the landscape remains unburnt and natural refuge patches are protected from fire incursion.

Alternatively, patches recently burnt by prescribed fire may escape burning during a subsequent wildfire and thus act as a refuge. However, their ability to function as a long-term refuge may be limited by their simplified (fuel reduced) structure (Catling 1991). The fate of prescribed burns during subsequent wildfire depends on numerous factors, including severity of the prescribed burn, time since burn, rates of fuel re-accumulation, weather (both between and during fires) and intensity of the wildfire (Cary et al. 2009).

The likelihood of areas burning, or not burning, can also be an unintentional effect of human activities. Vegetation fragmentation, for instance, can inhibit fire spread and result in unburnt patches (Duncan & Schmalzer 2004). Other anthropogenic changes, such as invasion of exotic plant species, can reduce or increase vegetation flammability (Brooks et al. 2004). A widely observed example of the latter effect is a positive feedback between exotic grass invasion and fire intensity (the ‘grass–fire cycle’; D’Antonio & Vitousek 1992), which may result in an increased extent and decreased patchiness of fires (Miller et al. 2010).

What attributes of refuges contribute to their value?

The attributes of faunal refuges can be considered in relation to temporal requirements of fauna associated with a fire event (see Fig. 1).

SHORT-TERM SURVIVAL

The immediate survival of organisms during fire will be greatest in patches or components that provide shelter and physical protection from flames and radiant heat (Fig. 1). Several types of refuges enhance the immediate survival of organisms. These include habitat components
that are not flammable (e.g. burrows, termite mounds, Yarnell et al. 2008), components that are less flammable (e.g. topographic locations such as gullies, or specific vegetation types, Pennan et al. 2007), through to vegetation components or habitat features that are intrinsically flammable, but due to fire behaviour do not burn or burn at lower intensity (e.g. hollows in large trees, Xanthorrhoea preissii, Brennan, Moir & Wittkuhn 2011). Each of these functions at a range of scales: for example, intrinsically flammable refuge habitats range from microhabitats associated with logs (Andrew, Rodgerson & York 2000) and unburned litter (Kiss & Magnin 2006) to larger patches of unburned vegetation (Swengel & Swengel 2007; Watson et al. 2012a). Biotic interactions also influence immediate survival, including competition for refuges just prior to and during the fire event, and predation during or shortly after the event (Whelan et al. 2002).

LONGER TERM PERSISTENCE AND RECOLONIZATION
In the longer term, refuge attributes that allow species to persist or recolonize are complex and species specific. There are few empirical studies on the relative value of different attributes of refuges. However, the body of literature on the occurrence of species in habitat patches in fragmented landscapes (Mazerolle & Villard 1999; Lindenmayer & Fischer 2006; Thornton, Branch & Sunquist 2011) suggests that three kinds of attributes will influence the longer term value of refuges: within-patch structural and biotic attributes, size and shape of the patch and landscape context of the patch (Fig. 1). The temporal context of the fire, with respect to other disturbances, biotic interactions and climatic events (e.g. drought or rain), may further influence refuge quality.

Patch quality
For an individual to persist in a refuge, suitable resources need to be available (Fig. 1). Within-patch attributes that influence longer term survival include vegetation composition and habitat structural features (e.g. Pereoglou et al. 2011). Attributes of patches are likely to be most important in the short- to medium-term postfire, when the contrast between patches and the surrounding environment may be stark. However, as the burned environment recovers, resources become available more widely (Lindenmayer et al. 2009) and the distinctiveness of within-patch attributes declines (Fig 1). Patch characteristics partly depend on the mechanism through which a refuge is created. Environmental conditions that contribute to the creation of natural deterministic refuges typically lead to different habitat qualities than those found within refuges created by chance. Natural deterministic refuges such as riparian zones and gallery forests (Palmer & Bennett 2006) or rock outcrops (Clarke 2002) have intrinsically different vegetation and harbour different assemblages than those in the broader, more flammable landscape. Deterministic refuges, including those of both natural and anthropogenic origin, are likely to have older, more mature vegetation than those arising stochastically, due to the lower probability of burning in the former (DeLong & Kessler 2000; Gandhi et al. 2001).

Stochastic refuges, on the other hand, may reflect the broader vegetation composition and structure of the landscape prior to disturbance. The fire history, or fire regime, influences these habitat attributes. Long fire intervals result in older vegetation of greater structural complexity within patches created stochastically. Patches burnt recently, or at high frequency, are likely to have a simplified vegetation structure and provide less suitable refuge for species requiring resources associated with long-undisturbed vegetation (Catling 1991). However, they may provide other services to the fauna, such as protection during fire, foraging areas and habitat for early-seral species (Brotons, Pons & Herrando 2005).

Patch size and shape
The size of a refuge patch influences its detectability and availability to different organisms and the number of individuals it can support, whilst patch shape determines the availability of core habitat uncompromised by edge effects (Forman 1995). In general, the probability of species occurring within a patch increases with increasing patch area and decreasing isolation (Lindenmayer & Fischer 2006). However, the relationship between patch metrics and occurrence of species in large fire mosaics is more
complex than, for example, forest fragments in agricultural landscapes. First, the postfire environment is a complex array of different fire severities, compounded by environmental gradients (e.g. topography, vegetation) and spatial variation in the number and type of biological legacies after fire (Burton et al. 2008). Consequently, patch boundaries are often indistinct and represent gradients in quality rather than marked contrasts. Second, what constitutes a refuge patch differs amongst species. In some instances, such as unburnt vegetation surrounded by severely burnt vegetation, patches are visibly distinct. In other situations, such as the persistence of small mammals (Banks et al. 2011) or ants (Andrew, Rodgerson & York 2000) amongst logs and rocks in burnt vegetation, the difference between refuge and matrix may be subtle. Third, the postfire mosaic is temporally dynamic, changing in quality and contrast as vegetation recovery proceeds (e.g. Ashton 1981). To the degree that patches become less distinct from their surroundings over time, it is likely that the importance of patch size and shape will also diminish (Fig. 1).

**Landscape context**

The spatial arrangement of refuge patches and their context in the broader fire mosaic is important for re-establishing and maintaining populations over time (Watson et al. 2012a) (Fig. 1). For species that depend on refuge patches, the ability of individuals to either disperse through the burned landscape or use refuge patches as ‘stepping stones’ is an important determinant of re-colonization of unoccupied habitat (Brotons, Pons & Herran 2005; Pereoglou et al. 2013). A greater potential for individuals to (re)establish local populations in unoccupied habitat increases the chances of species surviving in patchy habitats (Templeton, Brazeal & Neuwald 2011). The dispersal ability of a species is determined by the mobility of individuals and the extent to which they perceive the burned landscape as hostile or benign.

The optimal spatial arrangement of refuge patches within the postfire environment will vary amongst species (Bradstock et al. 2005; Clarke 2008), and the value of different configurations may also differ between ecosystems. For example, in fire-prone savanna woodlands of northern Australia, a fine-grained mosaic of burned and unburned vegetation is considered desirable for many species, such as the partridge pigeon *Geophaps smithii* (Fraser et al. 2003). A trend towards coarse-grained fire mosaics in this system has been linked to declines of small mammal species (Andersen, Woinarski & Parr 2012). In contrast, in other ecosystems, a fine-scale patch arrangement may be detrimental to taxa if perceived as fragmentation (Taylor et al. 2012).

**Biotic interactions**

The value of a refuge is also influenced by interactions with other species. Although few examples are available from fire ecology, changes in interactions including predation, competition, parasitism and mutualisms have been documented after landscape change and isolation of habitats in other situations (Lindenmayer & Fischer 2006; Ritchie et al. 2009). For example, loss of predators in isolated fragments can lead to cascading effects on ecosystems, with resultant outbreaks of herbivores significantly altering habitat structure (Ritchie & Johnson 2009). Many generalist predators are not restricted to unburned refuges and may be favoured by fire (Dees, Clark & Manen 2001). In the immediate postfire environment, predator abundance can increase due to greater availability of food from burnt carcasses and increased hunting efficiency due to reduced vegetative cover for prey (Conner, Castleberry & Derrick 2011).

**Knowledge gaps and further steps in understanding refuges**

The commonly assumed importance of refuges for survival, persistence and recovery of fauna from fire contrasts with the paucity of published evidence. Studies relating to the value of faunal refuges, often undertaken opportunistically after wildfire, have frequently been limited by issues such as inadequate documentation of fire severity, history and spatial properties; monitoring on limited spatial and temporal scales; inadequate replication; inability to separate mortality from emigration; and interactions with other disturbances (e.g. Newsome, McLroy & Catling 1975; Murphy et al. 2010; Zozaya, Brotons & Vallecillo 2011). The limited understanding of fire refuges contrasts with that for refuges in freshwater systems where knowledge is more advanced and functions and attributes have been outlined (Sedell et al. 1990). To give direction to future research, we highlight knowledge gaps in three broad areas.

**POSTFIRE PATTERNS AND DYNAMICS OF POTENTIAL REFUGE HABITATS**

An important step is to develop a stronger, predictive understanding of the relationship between fire characteristics (e.g. severity, size, seasonality) and the spatial pattern of potential refuge areas that occurs postfire. Systematic mapping of areas remaining unburnt in relation to vegetation type and topography (e.g. Madoui et al. 2010) provides a valuable opportunity to determine the spatial patterns of potential refuges, including natural deterministic refuges (moist drainage lines, less flammable vegetation), natural stochastic refuges (e.g. patches that escape burning) and anthropogenic refuges arising from prior prescribed burns. The occurrence and dynamics of other types of refuges, such as burrows, rock outcrops and unburnt habitat components (e.g. logs, tree hollows, litter patches), are less readily mapped remotely, but can be assessed by systematic survey of the postfire environment. Of particular value are quantitative studies that examine
spatial attributes of potential refuges – including number, size, location and configuration – in relation to aspects of fire regime and land management (e.g. Collins et al. 2012). Such studies are required in relation to both wildfires and prescribed burns in different ecosystems.

FAUNAL USE OF REFUGES

A comprehensive understanding of how refuges mitigate the effects of fire requires more empirical data on refuge use by a wide range of taxa from different types of fire-prone ecosystems. This includes greater insight into what constitutes a refuge for particular taxa, specific attributes of the refuge and when it is used (e.g. during fire, immediate postfire, longer term). A key challenge is to identify potential relationships between life-history attributes of species and their need for, and use of, different types of refuges. Opportunistic studies after wildfire will continue to be an important source of information, as will planned studies of responses of individuals and populations to prescribed burns of different severity, size and season (e.g. Fraser et al. 2003). Longitudinal studies of responses of fire-sensitive species that extend beyond a few years are scarce (Driscoll et al. 2010). Consequently, there is little knowledge of the time period over which species may depend on refuges or how refuge use changes over time. Such insights are particularly important for species known to favour late-successional vegetation or that rely on habitat components that take many years to recover (Haslem et al. 2011; Watson et al. 2012b).

A major knowledge gap relates to the spatial patterns and dynamics of populations within postfire mosaics. Such knowledge would assist in conservation planning for fire-sensitive species by determining whether there is a need for management intervention to protect or create refuge habitats, and if so, their spatial arrangement. Empirical data on species’ dependence on refuges, refuge spatial isolation and patterns of movement by individuals between them will give important insight into the spatial structure (or continuity) of the population within the fire boundary.

ANTHROPOGENIC CREATION AND MANAGEMENT OF REFUGES

As natural fire regimes are increasingly altered by land-use change, wildfire suppression, anthropogenic burning and effects of climate change (Flannigan et al. 2009), active management of refuges to safeguard sensitive species from displacement or local extinction will become more important. Knowledge of the location of natural refuges should be used to highlight areas for protection, either from natural or from anthropogenic disturbances (Mackey et al. 2002). Management actions that improve connectivity between such refuges may also be beneficial (e.g. Brown, Clarke & Clarke 2009). However, planning in this regard will need to consider potential risks such as increased wildfire propagation and spread of pests and disease (Camp et al. 1997). Planned burns can be used to protect or create refuge habitats, either in specific locations or as part of a landscape mosaic (Parr & Andersen 2006; Andersen, Woinarski & Parr 2012), but this requires a sound understanding of what constitutes a suitable landscape pattern, as well as technical skills to deliver the required burn pattern under a range of fire conditions.

There is a great need for further evaluation of the outcomes of fire management practices designed to mitigate the effects of fire on biodiversity, including their effectiveness in creating or maintaining refuges. It is also essential to evaluate the effects of fire management for purposes such as hazard reduction and other land management practices that may result in the loss or degradation of refuges. Much progress could be made by the integration of experimental management with systematic monitoring and research (Driscoll et al. 2010). This includes experimentally testing different management options for creating or protecting refuge habitats, together with long-term monitoring of faunal abundance and habitat use at the landscape scale.

Faunal fire refuges are likely to become increasingly important under expected changes in the occurrence, intensity and extent of wildfires (McKenzie et al. 2004). Managing for the refuge needs of fauna will help mitigate the detrimental impacts of fire and facilitate biodiversity conservation in fire-prone landscapes.

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Appendix 2. The effects of topographic variation and the fire regime on coarse woody debris: insights from a large wildfire.

The effects of topographic variation and the fire regime on coarse woody debris: Insights from a large wildfire

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Abstract

Coarse woody debris (CWD) is a common structural component of terrestrial ecosystems, and provides important habitat for biota. Fires modify the distribution of CWD, both spatially and temporally. Changes in fire regimes, such as those arising from prescribed burning and changing climatic conditions, make it critical to understand the response of this resource to fire. We created a conceptual model of the effects of fire on logs and dead trees in topographically diverse forests in which trees often survive severe fire. We then surveyed paired sites, in a damp gully and adjacent drier slope, ~3 years after a large wildfire in south-eastern Australia. Sites were stratified by fire severity (unburnt, understorey burnt and severely burnt), and fire history (burnt ≤3 years or >20 years prior to the wildfire). Both components of the fire regime influenced CWD availability in gullies. Severe wildfire and fire history ≤3 years reduced the volume of small logs (10–30 cm diameter) in gullies, while severe wildfire increased the number of large dead trees in gullies. CWD on slopes was not affected by fire severity or history at ~3.5 years post-fire. Log volumes on slopes may recover more quickly after wildfire through rapid collapse of branches and trees. Gullies generally supported more logs than slopes, but longer inter-fire intervals in gullies may allow fuel loads to accumulate and lead to comparatively larger fire impacts. Given that fire severity and fire interval are predicted to change in many fire-prone ecosystems in coming decades, this study highlights the importance of understanding the interacting effects of multiple components of the fire regime with landscape structure. In particular, variation in fire interval and fire severity in relation to topographic position will influence the pattern of accumulation of coarse woody debris across the landscape, and therefore the structure and quality of habitats for biota.

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1. Introduction

Fire shapes the composition of ecosystems through its effects on vegetation structure (Bond et al., 2005; Bowman et al., 2009), which in-turn affects the distribution of fauna (Fox, 1982; Friend, 1993). The immediate and longer-term effects of fire on faunal habitat depend on the fire regime: fire severity, fire frequency, time-since-fire, fire interval and the season of fire (Gill and McCarthy, 1998; Smucker et al., 2005; Haslem et al., 2012). Fire regimes can vary within relatively small areas, because even large, intense fires create a mosaic of severities at multiple scales (Turner et al., 1994; Román-Cuesta et al., 2009; Leonard et al., 2014).

Coarse woody debris (CWD: here defined as logs and dead trees) is a common component of many terrestrial ecosystems (Harmon et al., 1986; Jonsson and Kruys, 2001; Lohr et al., 2002). It has an important role in nutrient cycling and carbon storage, and provides habitat for plants and animals (Harmon et al., 1986; Lindenmayer and Franklin, 2002). The dynamics of CWD are driven by the interaction of long-term processes, such as senescence and decay, with shorter-term disturbance processes, such as timber harvesting and fire (Harmon et al., 1986; Haslem et al., 2011).

Fire is integral to the dynamics of CWD, as it both consumes existing debris and generates new material through its influence on tree death and collapse (Harmon et al., 1986; Tinker and Knight, 2000). Diverse responses to aspects of the fire regime have been observed. For example, the effects of time-since-fire on the abundance of logs ranges from a post-fire increase (Monsanto
and Agee, 2008), to a peak at intermediate fire ages (Roccalforte et al., 2012), or no detectable effect (Pedlar et al., 2002; Eyre et al., 2010). Such diverse relationships suggest that responses to fire vary between, and potentially within, ecosystems. However, such variable effects of time-since fire could also be influenced by failing to account for other aspects of the fire regime, both spatial and temporal. Fire severity (e.g. Smucker et al., 2005) and fire interval (e.g. Haslem et al., 2012) are known to strongly influence habitat structure, but are rarely accounted for in fire ecology studies, including those on CWD (but see Collins et al., 2012b).

Topographic variation influences fire behaviour, as moist gullies often repeatedly escape fire, or burn less severely than the surrounding landscape (Pettit and Naiman, 2007; Bradstock et al., 2010; Leonard et al., 2014). When gully vegetation does burn at high intensity, for example during extreme fire conditions (Leonard et al., 2014), the vegetation may recover more quickly due to the protected aspect and high soil moisture (Romme and Knight, 1981; Segura and Snook, 1992). Thus, topographic variation may interact with fire regimes to determine the dynamics of CWD.

Research on the post-fire dynamics of CWD has been conducted largely in forests that experience stand-replacing fires, such as the boreal forests of North America and Europe (Harmon et al., 1986; Tinker and Knight, 2000; Pedlar et al., 2002; Monsanto and Agee, 2008), and tall wet eucalypt forests of south-eastern Australia (Lindenmayer et al., 1999). In other forests, such as the mixed Eucalyptus species foothill forests that cover some 7.9 million ha of south-eastern Australia, trees often survive severe fires through epicormic sprouting. Despite the complex role of fire in structuring these ecosystems (Gill, 2012), and the key role that CWD plays within them (Lindenmayer et al., 2006), understanding of the drivers of CWD is limited, particularly in relation to fire regimes.

Here, we explore the role of multiple components of the fire regime and topographic variation on the dynamics of CWD in a foothill forest ecosystem following the 2009 ‘Black Saturday’ wildfire in central Victoria, Australia, which burnt 228,000 ha of forest. We had four primary objectives: (1) to develop a conceptual model of the effects of wildfire on CWD over time; (2) to determine the effects of fire severity and fire history on the relative abundance of CWD (logs and dead standing trees); (3) to examine whether the effects of the fire regime are modified by topographic position (i.e. damp gullies vs. drier slopes); and (4) to determine whether the size of logs and dead trees influences how they are affected by the fire regime.

1.1. Conceptual model and predictions

We developed a conceptual model of the post-fire dynamics of logs in forest ecosystems in which trees often survive severe fire (Fig. 1). There are four main sources of logs following fire. First, at least part of the existing log resource is likely to remain post-fire. Second, trees not killed by fire may drop branches, resulting in a pulse of smaller logs. Third, some trees are damaged at the stem base and are killed by fire, and either fall shortly after the fire or remain as standing dead trees for many years before collapsing. Finally, trees that regenerate in gaps created by fire will contribute to the log resource in the longer term.

The magnitude and rate of log consumption, tree death, tree collapse and tree regeneration will depend on several aspects of the fire regime, including fire severity and fire history. More severe fires will result in the consumption of more logs and kill more trees, but may obscure the effects of previous fire on CWD. Characteristics of logs, including their size, moisture content and level of decay, will affect their flammability; while the death and collapse of trees will be influenced by the composition of tree species, tree health and the (non-fire) disturbance history of the forest. Moisture differentials associated with topographic position will influence the abundance of logs and dead trees, as well as their decay rate. Gullies, with their moister and more sheltered microclimate, experience longer fire intervals than drier slopes, allowing more time for logs to accumulate. These conditions allow growth

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**Fig. 1.** Conceptual model of log volume over time following a wildfire in a forest in which trees often survive severe fire. The side panels show the trajectories of logs from four sources: (1) existing logs at the time of the fire (some of which are consumed by fire and those not consumed continue to decay); (2) input from live trees following fire (branches are lost immediately following the fire, and after time these trees continue to drop branches, die and collapse); (3) trees killed by fire (a number of trees die and collapse immediately following the fire, while some trees are killed but remain standing, and collapse as a cohort many years later); and (4) input from the next generation of trees (seedlings that grow following the fire, reach maturity and begin to drop branches). The main plot shows the cumulative volume of logs from these sources. The specific pattern of each log source will depend on the severity of the fire and topographic location (i.e. damp gullies or dry slopes). Trajectories may be affected by fire interval, with a likely overall decline in log volume over time if short fire intervals do not allow regenerating trees to mature.
of larger trees and, therefore, the potential production of larger logs, but also promote more rapid decay. The moist conditions and higher topographic relief may also mitigate the effects of fire on CWD.

We used our conceptual model as a base to predict how topography, fire severity, and fire history will interact to affect the availability of CWD ~3.5 years after wildfire. We predict that:

1. Gullies will support a greater volume of large logs and greater abundance of large dead trees than slopes.
2. Sites burnt in the 2009 wildfire will experience a reduction in the volume of logs, especially small logs, and an increase in the abundance of dead standing trees compared to sites not burnt in the wildfire. The magnitude of change will be greater at severely burnt than understorey burnt sites, and on slopes compared to gullies.
3. Unburnt sites with a short fire history (time-since fire <3 years) will have fewer logs, and more dead trees, compared to unburnt sites with a long fire history (time-since-fire >20 years).
4. Sites in which only the understorey was burnt by wildfire will have fewer logs, and more dead trees, when the fire history was short (interval <3 years) compared to long (interval ≥20 years), however differences will be small.
5. Severe wildfire will obscure the effects of previous fires, and there will be no detectable effect of fire history.

2. Methods

2.1. Study area

On ‘Black Saturday’, 7 February 2009, two wildfires in central Victoria, Australia, joined to form the Kilmore–Murrindindi fire complex. The study area includes private land, townships, and several State Forest and National Park reserves. Approximately half of the 228,000 ha area burnt was foothill forest, a topographically diverse forest system consisting of damp gullies and drier slopes. Our study was undertaken in these foothill forests, which range in elevation from 153 to 937 m and have a temperate climate with mean annual rainfall of ~1300 mm (Australian Government Bureau of Meteorology). The drier slopes support eucalypt forests dominated by messmate Eucalyptus obliqua and broad- or narrow-leaf peppermint E. dives or E. radiata. The understorey is characterised by a high cover and diversity of grasses and herbs, with a variable shrub layer (Oates and Taranto, 2001). Damp gullies are dominated by a mixture of Eucalyptus species, including messmate, broad and narrow-leaf peppermint and blue gum E. globulus. Gullies have a dense shrub layer, and a ground layer of herbs, grasses, and moisture-dependent ferns (Oates and Taranto, 2001).

2.2. Study design and selection of study sites

Study sites were located within or adjacent to the perimeter of the Kilmore–Murrindindi fire complex (Fig. 2). They were stratified by (1) 2009 wildfire severity; and (2) fire history (time-since-fire prior to the 2009 wildfire). Fire severity was categorised as either (1) unburnt, (2) understorey burnt (canopy intact), or (3) severely burnt (understorey burnt and canopy fully scorched or burnt). Fire history was defined as ‘short’ when a site had been burnt <3 years before 2009, or ‘long’ when a site had not burnt for ≥20 years prior to 2009. These time-since-fire/fire interval periods were selected to represent a strong contrast in fire history. Prescribed burning in foothill forests can reduce fuels for 4–5 years, with negligible effects after 10 years (Price and Bradstock, 2012; Leonard et al., 2014). By 20 years after wildfire, these forests have reached vigorous maturity (Cheal, 2010).

Fig. 2. Location of the study area. The 2009 ‘Black Saturday’ wildfire boundary is shown in black outline. Sites were stratified by the severity of the 2009 wildfire (unburnt, understorey burnt and severely burnt) and fire history prior to wildfire (time-since-fire of ≤3 years or ≥20 years prior to 2009).
We selected 24 sites that represented replicated combinations of each level of fire severity and history (Fig. A.1 in Supplementary material). Each site included a damp gully and drier slope which had similar fire severities. We interrogated post-fire aerial images and spatial layers using a geographic information system (GIS; ArcMap v 9.0) and spatial data layers of previous fire boundaries, timber harvesting history, and vegetation type (provided by the Victorian Government). On-ground assessments were undertaken to verify the accuracy of spatial layers. In severely burnt areas, where evidence of previous burns was not visible, we relied on the maps to determine fire history. While it is likely that all sites had been selectively harvested within the previous 100 years, sites were selected within areas that had no record of timber harvesting within the last 50 years, and no evidence of previous clearcut harvesting.

2.3. Sampling protocol

Surveys were undertaken ~3.5 years after the 2009 wildfire. At each site we surveyed logs and dead standing trees along two 200 m transects: one in a gully and one on a parallel slope, ~100–150 m from the gully edge.

2.3.1. Logs

The diameter of each log (\( \geq 10 \text{ cm diameter, } \geq 100 \text{ cm length} \)) that intersected a transect was measured at the point of intersection, and its angle to the transect recorded. The volume of logs was estimated using a modified version of the line intersect method (Warren and Olsen, 1964; Van Wagner, 1968). This method assumes that the angles of logs along a transect are random, giving a probability factor of encountering each log as \( \frac{2}{\pi} \). In this study, logs were consistently more likely to lie across the slope or gully than parallel to it. To correct this non-random distribution, we calculated the probability factor of encountering a log on our transects using the angles of all surveyed logs. Incorporating this factor, log volume \( (V) \left( \text{m}^3 \text{ ha}^{-1} \right) \) was estimated using the equation:

\[
V = 1.229276 \times \frac{\pi \sum d^2}{4L} \times 100
\]

where \( d \) = diameter (m) at right angles to the length of the log and \( L \) = length (m) of the transect.

2.3.2. Trees and stumps

The diameter (at breast height, DBH) of each live and dead tree stem \( \geq 1.5 \text{ m tall} \) was measured within a 100 \( \times \) 10 m belt transect in the gully and slope, respectively. The mean DBH of all stems was calculated for each transect. Cut tree stumps (<1.5 m tall) were surveyed and the basal area \( (\text{m}^2 \ 0.1 \text{ ha}^{-1}) \) was calculated to approximate the prior timber harvesting intensity at each site.

2.4. Statistical analysis

2.4.1. Response variables

Statistical modelling proceeded in two stages. First, to test initial predictions about the interacting effects of topography and fire severity, we modelled the volume of small and large logs, and the abundance of small and large dead trees, by the interaction of topography with fire severity. Second, we investigated the effects of fire regimes and timber harvesting on small logs, large logs, small dead trees and large dead trees separately for gully and slope transects. Two-stage modelling avoided the inclusion of the three-way interaction term between fire severity, fire history and topography. High order interaction terms are difficult to model successfully and difficult to interpret in an ecologically meaningful way, particularly when predictor variables are categorical.

Response variables were modelled using generalised linear mixed-effects models, which allow the inclusion of random grouping factors (Zuur et al., 2009). The volume of logs was modelled assuming a Gaussian distribution of errors, with values being \( \log_{10} \) transformed to improve normality (with a constant of 0.01 added to all data points if zero values were present). The abundance of dead trees was modelled assuming a Poisson distribution.

2.4.2. Fire regime predictor variables and model building

Predictor variables were chosen to represent components of the fire regime (i.e. fire severity and fire history) and to account for stem size of standing trees and past timber harvesting. The variables ‘fire severity’ (unburnt, understorey burnt, or severely burnt), ‘fire history’ (short or long), ‘tree DBH’ (mean DBH of live and dead stems; cm), and ‘cut stumps’ (basal area \( \text{m}^2 \ 0.1 \text{ ha}^{-1} \)) were considered ecologically plausible predictors for all response variables, with the exception of ‘tree DBH’ in models of dead trees.

In the first stage of modelling, we used the model ‘topography \( \times \) fire severity’ to determine whether the interaction term was important. In the second stage, the model set comprised three combinations of fire regime components: ‘fire severity’, ‘fire severity \( \times \) fire history’, and ‘fire severity \( \times \) fire history’. Each model of log volume also included ‘tree DBH’ and ‘cut stumps’, while each model of dead tree abundance included ‘cut stumps’. ‘Fire history’ was only modelled in combination with ‘fire severity’, as it is ecologically implausible that fire history would affect the response variables independently of fire severity following a large wildfire.

We included random effects to account for potential spatial autocorrelation of model residuals due to sites being clustered within reserves, and gully and slope transects being paired. Thus, ‘reserve’ was included in all models; and ‘site’ was included in models that included the predictor variable ‘topography’. Where necessary, an observation-level random effect was included in Poisson family models to account for overdispersion in model residuals (Nakagawa and Schielzeth, 2010). Model fit was quantified using the marginal (fixed terms only) and conditional (full model) \( R^2 \) values of the global model (Nakagawa and Schielzeth, 2013).

Scatter plots of each response variable by each continuous predictor were created to check linearity of response, and no evidence for non-linear relationships was found. There was no evidence of excessive correlation of predictor variables (Pearson pair-wise correlation coefficients <0.6).

2.4.3. Model selection

When modelling CWD on gullies and slopes separately, we employed an information theoretic approach to identify the model(s) with most support. Akaikie’s information criterion for small sample sizes (AICc) was used to rank models. If there were multiple models with substantial support (i.e. multiple models with an AICc difference <2 of the top ranked model), we inferred from all such models. We did not model average, as we were interested in the importance of the interaction term, for which model averaging is problematic (Dochtermann and Jenkins, 2011). Predictor variables were regarded as important if the 90% confidence interval did not include zero. We chose to use the 90% confidence interval due to the relatively small sample size (24 sites) and the possible management implications of understimating the importance of fire on CWD (Smith et al., 2013).

Statistical analyses were undertaken using the R statistical package version 2.15.2 (R Development Core Team, 2010). We used the ‘lmee’ package for regression modelling (Bates and Maechler, 2011), the ‘MuMln’ package for model selection (Bartoń, 2009),
and the AICcmodavg package for creating model predictions (Mazerolle, 2012).

3. Results

Following initial modelling to determine whether topography and fire severity interacted to influence CWD availability (see Table A.1 for parameter coefficients and model fits), we developed separate model sets for gullies and slopes to test the relative influence of fire regime components and timber harvesting on the volume of small and large logs and the abundance of small and large dead trees in gullies and on slopes. A single ‘best model’ was evident for all CWD components except small logs in gullies, for which we based our inferences on the two models with support (Table 1).

3.1. Effects of topography, fire, timber harvesting and tree size on logs

Modelling gullies and slopes together revealed an important interaction between fire severity and topography for small logs. There was a higher volume of small logs in gullies than on slopes in unburnt and understorey burnt sites, but in severely burnt sites there were more small logs on slopes (Fig. 3a). The volume of large logs was greater in gullies than on slopes, regardless of fire severity (Fig. 3b).

When gully sites were modelled alone, the models ‘fire severity’ and ‘fire severity + fire history’ had support for the volume of small and large logs on slopes (Table 1). Model estimates and confidence intervals indicated that fire severity and fire history had important influences on the volume of small and large logs (Table A.2). The volume of small logs was lower in severely burnt than unburnt gullies, and fire history had an additive effect to fire severity, such that in each severity category (including unburnt), gullies with a short fire history (<3 years) had lower volumes of small logs than those with a long fire history (>20 years) (Fig. 4).

The fire severity model was the best model explaining the volume of large logs in gullies and both small and large logs on slopes (Table 1); however, no predictor variables were important in explaining these response variables (Tables A.2 and A.3).

3.2. Effects of topography, fire and timber harvesting on dead standing trees

Modelling gullies and slopes together showed that small dead trees were more abundant in severely burnt sites than unburnt sites (Fig. 3c). They were also generally more abundant on slopes than in gullies, with this difference most pronounced in understorey burnt sites (i.e. an important topography × fire severity interaction; Fig. 3c). Large dead trees were more abundant in severely burnt sites than unburnt (Fig. 3d).

When gullies were modelled alone, dead tree abundance was best explained by the fire severity model (Table 1). There was an increased abundance of large dead trees in severely burnt gullies compared to unburnt gullies (Fig. 5), but fire severity did not have an important influence on small dead trees (Table A.3).

On slopes, fire severity was the preferred model explaining the abundance of small and large dead trees (Table 1), but no variables were important (Table A.3).

4. Discussion

Despite the important role of coarse woody debris in ecosystem function (Harmon et al., 1986; Tinker and Knight, 2000), the effects of multiple fire regime components on CWD have rarely been studied concurrently. Here, we have demonstrated that the availability of CWD is influenced by two components of the fire regime – fire severity and fire history – and that the response of structural components to fire depends both on their size and topographic location.

4.1. Fire severity

Log volume and abundance of dead trees in gullies were influenced by fire severity—3.5 years after wildfire, but there was less evidence of an effect of fire severity on CWD on slopes. While initial models of topography and fire severity indicated that the abundance of small and large dead trees on both slopes and gullies increased after severe wildfire, when CWD was modelled separately for slopes and gullies, only small logs in gullies and large dead trees in gullies were affected by fire severity. The apparent stronger effects of severe wildfire in gullies than slopes may have occurred as a result of either replacement of logs on slopes but not in gullies, and/or higher loss of logs in gullies compared to slopes. Moisture stress before fire has been associated with increased tree death after fire (van Mantgem et al., 2013), and it is likely that the decade-long drought prior to 2009 negatively affected the health and resilience of trees, particularly on dry slopes (Bennett et al., 2013). Fire-related tree death may therefore have been higher on slopes than in gullies, with rapid fall of branches and collapse of trees on slopes replacing logs consumed by fire. The dip in log volume following wildfire that we expected (conceptual model; Fig. 1) may, therefore, have occurred prior to our surveys. If this is the case, the availability of logs on slopes will decrease in the coming decades, as the trees that were most likely to collapse have already done so. Additionally, although gullies more often escape fire (Leonard et al., 2014), when gullies burn following long dry periods, the accumulation of dry fuels can result...
in severe fire effects (Pettit and Naiman, 2007), sometimes more severe than surrounding slopes (Segura and Snook, 1992).

There was some indication of loss of large logs in severely burnt gullies and slopes, but the confidence intervals were large relative to effect sizes. Large logs and dead trees are rare in the landscape, and the study may not have had sufficient power to detect small changes in their availability. Loss of large logs and dead trees is important, because they have disproportionate habitat value for flora and fauna (Harmon et al., 1986; Lindenmayer et al., 2000).

4.2. Fire history

A short time-since-fire or fire interval can reduce the availability of logs (Catling, 1991; Spencer and Baxter, 2006) but increase the abundance of dead trees (Harmon et al., 1986). We predicted that this would be the case in our study, but that any effects would be obscured by severe wildfire. We found no effects of fire history on logs or dead trees on slopes, regardless of wildfire severity, indicating that prior fires, which were predominantly low severity prescribed fires, did not substantially affect CWD on slopes.

In gullies, severe wildfire did not obscure the effects of fire history on small logs; a short fire history reduced volumes of small logs in all fire severity categories. While prescribed fires can consume logs (Fahnestock and Agee, 1983; Knapp et al., 2005), the effects of prescribed fire on habitat structure in moist gullies are often negligible (Bêche et al., 2005). We found that dead tree abundance in gullies was not largely affected by fire history, consistent

Fig. 3. Predicted volume (±SE) of (a) small (10–30 cm diameter) and (b) large (>30 cm diameter) logs (log_{10}), and predicted abundance (±SE) of (c) small and (d) large dead trees from generalised linear mixed models that included the fixed predictor variables topography, fire severity, and their interaction.
with evidence that dead trees collapse predominantly following severe wildfire (Collins et al., 2012a). Drought conditions prior to fires, however, may result in log combustion and even low severity fires should not be considered benign.

4.3. Topography and timber harvesting

Consistent with our predictions, gullies had higher volumes of logs than slopes, with the exception of small logs in severely burnt sites. Large logs, which provide the most important ecosystem functions (Harmon et al., 1986), showed a particularly strong association with gullies. Logs are more abundant in gullies in various forest types (Webster and Jenkins, 2005; Collins et al., 2012a), as moist gullies are highly productive. We expected to find more large dead trees in gullies than on slopes, but abundances did not differ. The higher volume of large logs, but not large dead trees, in gullies compared to slopes may be the result of a higher rate of collapse of dead trees in gullies during wet periods (Franklin et al., 1987), as well as past timber harvesting of large trees across the study area. Timber harvesting removes potential CWD, but can also cause an influx of logs if cut stems are left onsite. Felled rotten stems were historically left onsite (Grove, 2001) which, in our study area, may have contributed to the higher volume of large logs in gullies than on slopes. Our estimation of the basal area of cut stumps, and therefore the role of timber harvesting in shaping CWD dynamics, is most likely an underestimate, as it was difficult to determine whether burnt out stumps were the result of timber harvesting or natural tree fall.

4.4. Foothill forests and effects on fauna

Foothill forests in south-eastern Australia are composed of trees which predominantly survive even severe fire, resprouting from the stem and canopy. The impacts of wildfire on CWD appear to be smaller in these forests compared with systems where whole stands of trees are killed by fire (Harmon et al., 1986). Forests that experience only patchy tree death are unlikely to experience extreme shifts in forest type, which can occur when stand replacing fire intervals are insufficient for trees to reach maturity (Lindenmayer, 2009). The exception in our system may be some damp gullies, as frequent fire will encourage drying, and therefore fire, resulting in changes in species composition (Pettit and Naiman, 2007).

Many animal species use CWD for shelter, nesting and foraging (Harmon et al., 1986; Lindenmayer and Franklin, 2002), and fire-mediated changes to their habitat have long-term impacts on persistence (Smith et al., 2013). For example, decreased fecundity was observed in a population of hollow-dependent mountain brushtail possums Trichosurus cunninghamii after loss of den trees following wildfire (Banks et al., 2011); while saproxylic invertebrates are threatened by fire regimes that reduce the abundance of dead wood (Davies et al., 2008). Large logs, which provide important habitat for fauna (Harmon et al., 1986), were resistant to fire in our system, potentially providing habitat legacies (Foster et al., 1998). Small logs, which were reduced by fire in gullies, provide relatively fewer ecosystem services (Harmon et al., 1986), but do provide important habitat for some species (Nordén et al., 2004; Brin et al., 2011). Severe wildfire resulted in more large dead trees...
in gullies: this may increase the availability of hollows and other resources while these standing trees decay (Inions et al., 1989), but depletes the availability of large living trees. Thus, wildfire both removes and creates CWD from ecosystems. The persistence of native fauna species in many ecosystems is threatened by habitat loss (Millennium Ecosystem Assessment, 2005), and the influence of wildfire, prescribed fire and timber harvesting should be managed to ensure that CWD is not depleted over time.

5. Implications and conclusions

Our results suggest that, while coarse woody debris in foothill forests is relatively resilient to fire, both wildfire severity and fire history are important determinants of CWD dynamics. Damp gullies, which support the greatest abundance of CWD in this system and many others (e.g. Webster and Jenkins, 2005; Collins et al., 2012a), may be particularly vulnerable to changed fire regimes (Bradstock et al., 2010). Frequent fires in gullies, particularly severe wildfires, will reduce the existing CWD resource, and will slow the accumulation of CWD that occurs when gullies remain unburnt for many years. Reduced CWD could, in turn, lead to diminishing fauna populations, particularly as animals may use gullies as both drought and fire refuges (Mackey et al., 2012; Robinson et al., 2013).

Use of low-severity prescribed fire for ecological management of forests should be carefully planned to ensure that some areas remain unburnt for many years. Long unburnt ‘fire refuges’ provide distinct habitats in many ecosystems (Robinson et al., 2013). Foothill forests reach vigorous maturity within 20 years, but large reserves of CWD, as well as habitat components such as tree hollows, may take many more years to develop (Cheal, 2010). During times of drought, prescribed fire may not be an appropriate ecological management tool, and measures will be required to exclude fuel reduction fires from damp gullies. This study has revealed important effects of fire regime components on CWD at a ‘snap shot’ in time, but was not able to examine changes in CWD over time. Our conceptual model provides a useful framework for designing longer-term studies to investigate and test the complex interactions between fire regimes and landscape processes.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.12.028.

References


Appendix 3. Refuges for flora and fauna in fire-prone landscapes.

Refuges for Flora and Fauna in Fire-Prone Landscapes

Large bushfires, such as those that occurred on Black Saturday 2009, are a reality in Australian forests. As well as threatening human life and property, they have profound impacts on native animals and plants.

Yet even within these large fires, unburnt or less severely burnt patches remain. Do these function as refuges allowing animals and plants to remain in the post-fire landscape? Can planned burning be used to create more of these refuges?
The Kilmore – Murrindindi bushfire

The Kilmore-Murrindindi fire complex began as two separate ignitions on 7th February 2008 ('Black Saturday'). Weather conditions were extremely hot (>40°C), dry (RH < 10%) and windy (gusts > 100 km/h). The fires initially moved in a south-western direction. A wind change late in the day caused the fires to break out to the northeast on wide fronts. The Kilmore-Murrindindi fires ultimately affected 250,000 ha, destroyed over 1700 houses and resulted in the deaths of 158 people.

Variation in fire intensity created a mosaic of patches burnt to varying degrees. In most of the area burnt during extreme conditions on 7th February, the fire canopy was incinerated or scorched. As conditions ameliorated later that day, the fire mainly burnt the forest understory (ground burn).

Movement and severity of the Kilmore-Murrindindi fire complex. Stars indicate ignition points. Strong north-westerly winds on 7th February caused the fires to move in a south-westerly direction (solid arrows), until a wind change in the evening caused the fires to break out to the north-east on wide fronts (hollow arrows). Fire severity mapping courtesy of Department of Environment and Primary Industries.

Fire severity

Fire severity refers to the degree of damage to vegetation caused by fire. Fire severity had a strong effect on the vegetation structure present 2-3 years post-fire, when this study was undertaken. Crown-burn and crown-scorch sites had a denser layer of eucalypt seedlings and saplings that had germinated post-fire. Ground-burn sites tended to have lower shrubs than sites that remained unburnt. The response of the fauna to fire severity reflects a response to vegetation structure, rather than to fire severity per se.

Refuges in fire-prone environments

Refuges can serve three main functions:

a) assist organisms to survive during and immediately after a fire;

b) facilitate the persistence of organisms and populations within the fire boundary;

c) assist the re-establishment of populations within the burnt area as it recovers.

Refuges arise from natural processes, or by human manipulation of the fire environment. Natural refuges include patches of unburnt vegetation that missed being burnt by chance, or because they are less flammable (e.g. moist gullies). Other features, such as rock outcrops or unburnt logged areas, may also serve as natural refuges for some species of plants and animals. Refuges may also be created by reducing fire fuel loads. Planned burning can reduce fuel loads that a particular site is less likely to burn in a subsequent bushfire, or it can be used strategically to prevent a bushfire spreading into adjacent unburnt habitat.

Refuge function: Patches may allow plants and animals to escape incineration. However, longer-term persistence and recolonisation depend on patch attributes, i.e. the degree to which a patch provides the resources needed by organisms. The relative importance of attributes (represented here by the thickness of bars) varies over time after fire.

Unburnt forest patches within the Kilmore-Murrindindi fire boundary

Unburnt forest patches within the fire boundary were rare (note that much of the area mapped as unburnt canopy in the map on the previous page was ground burnt). Examination of aerial photographs taken after the fire revealed only 85 unburnt patches, greater than 1 ha in size (range from 1 – 336 ha), together making up less than 1% of the overall fire area. These mostly consisted of rainforest or wet eucalypt forest along gullies. Unburnt patches were most likely to arise due to moister fuels in sheltered locations.

However, a small number of unburnt patches occurred in dry eucalypt forest. These patches were more common where burning had occurred less than three years prior to the 2009 bushfires.

A typical unburnt patch - rainforest vegetation along gully lines.
Our study involved a ‘natural experiment’. We selected 56 sites to represent combinations of two main attributes:

a) different fire severities after the 2009 fire (i.e. not burnt, ground burn, canopy scorch, canopy burn);
b) different fire histories before the bushfire (i.e. burnt a 3 years prior, or not burnt for >20 years prior to the bushfire).

Sites were within, or close to, the perimeter of the 2009 fire (plus reference sites > 2 km outside the fire boundary), in tall-eucalypt forests (i.e. not including wet mountain forests). Each site was 5 ha, and encompassed a guilty and adjacent slope. The forest vegetation comprised two main Ecological Vegetation Classes. Damp Forest (gullies) and Heath-rich Foot-hill Forest (tops).

Research questions

How common are unburnt patches of forest after a major bushfire and what determines their distribution?

To what extent do recent burnt patches moderate the impact of a larger-scale bushfire on fauna and flora through the creation of unburnt, or less severely burnt, refuge areas?

How important is the extent of natural and transient (fuel reduced) refuge areas in maintaining the diversity of organisms in the landscape and does its importance differ between different kinds of plants and animals?

We conducted targeted surveys at 2-3 years post-bushfire for:

- birds
- mammals
- invertebrates
- vegetation structure
- vascular plants
- bryophytes

Bryophytes and fire

Forty species of bryophytes (32 species of mosses, 8 liverworts) were detected at sites in dry forest, surveyed 1-2 years post-fire. Most species (n = 28) were recorded at one or two sites only. Fire severity had a strong influence on both the bryophyte richness and composition of bryophytes. Forest sites that were unburnt, or had only the understorey burnt, had more species than sites with canopy scorch or canopy burn. In particular, unburnt sites had a distinctive bryophyte community that differed markedly from all types of burnt sites.

Effects of fire severity

Birds

A total of 79 bird species was recorded during surveys. The number of species and the abundance of birds was lower at sites that were burnt more severely.

The composition of bird communities also was influenced by fire severity. Some species, such as the Flame Robin that favours open habitat, were more common in severely burnt sites, while other species such as Eastern Spinebill, Eastern Yellow Robin and Silvereye, were more common in unburnt sites.

Mammals

Six species of arboreal mammals were observed during surveys, all in low density. The overall abundance of arboreal mammals, and of the Greater Glider, were lower in severely burnt sites (crown scorch or crown burn), but did not differ between unburnt sites and ground-burnt sites. In severely burnt forest, isolation was important. Arboreal mammals were more common with increasing amounts of unburnt or ground-burnt forest nearby (within 1 km radius).

Terrestrial mammals overall did not show strong responses to fire severity at 2-3 years post-fire. However, the Bush Rat was more common in severely burnt sites than in unburnt sites, while the Agile Antechinus was more common in unburnt sites than ground-burnt sites.

Invertebrates, leaf litter and fire

Invertebrates play a key role in breaking down leaf litter in forests. This is important for nutrient cycling and also reduces fuel build up.

Severe fire results in complete loss of habitat for litter-feeding and declining macro-invertebrates. For moisture-dependent wingless species, such as native woodlice, this may result not only in local extinction, but may inhibit their capacity for recolonisation after fire. Litter-feeding invertebrates, including beetles, were less abundant and less diverse in more severely burnt sites three years after fire. Fire had a negative effect on a number of invertebrate families, including earwigs, millipedes, native woodlice, new beetles and non-biting midges.

Some invertebrates appear to depend on long unburnt sites to persist in the landscape. One family of native woodlice was found only in deep drifts of leaf litter at long unburnt sites. This suggests that this group is vulnerable to both bushfires and planned burns.
Gullies and slopes

Topography is a major source of variation in the landscape, with slope, aspect and landscape position influencing soils, vegetation and fire behaviour. Gullies are important habitat features: they often are more productive, and contain more complex vegetation and a higher abundance of foliage logs and trees than adjacent slopes. We investigated the effect of the interaction of fire and topography on plants and animals by comparing responses between gullies and slopes.

Birds

Severe fire is sometimes thought to have an homogenising effect on landscapes, reducing all sites to a common baseline. We hypothesised that with increasing fire severity, the differences in habitat attributes, and hence bird communities, between gullies and slopes would be diminished. This was not the case. Across all fire severity classes, gullies had a) more bird species, and b) more birds than slopes.

Logs

Logs are important habitat features in forests. Fire can both create logs (by causing tree collapse) and remove them (by burning). We found that large logs (>40 cm diameter) were more common in gullies than on slopes. There were fewer small logs in gullies subject to severe fire, but otherwise there was no net effect of fire on the abundance of logs in either gullies or slopes.

Mammals

Arboreal mammals tended to be more abundant in gullies than on slopes, probably because gullies often have more large trees than slopes. The relationships of ground-dwelling mammals to topography were mixed. Some, such as the Bush Rat, were detected more commonly in gullies than on slopes, while the reverse was the case for detections of the Black Wallaby and Common Wombat. The Agile Antechinus was generally more likely to be recorded in gullies, except at ground-burnt sites, where it was more commonly present on slopes.

Do lyrebirds create fire breaks?

The Superb Lyrebird is an iconic species, well known for its mimery and spectacular plumage. By singing through fuel litter when foraging, lyrebirds play an important role in decomposition and nutrient cycling. By using exclusion plots, we found that lyrebirds reduced litter fuel loads by 1.68 t/ha or 25%, on average, over a nine month period. Lyrebird foraging also inhibited shrubs and fern establishment, reducing horizontal and vertical fuel continuity. The reduction in litter fuel load by lyrebirds was predicted to result in significantly lower flame heights and fire rate of spread (using the MacArthur M4 fire behaviour model).

Lyrebird foraging was concentrated in unburnt gullies. We propose a positive feedback loop, whereby lyrebird foraging decreases the likelihood and/or severity of fire, and maintains their favoured foraging habitat. Dense plant regeneration after severe fire may inhibit lyrebird foraging, leading to build-up of litter, and dense shrub and fern growth, promoting further fire.

How does planned burning influence the effects of a large bushfire?

A major focus of the study was to shed light on the interactions of planned burning and bushfire. With bushfires predicted to become more frequent and severe as climate change takes effect, planned burning increasingly is seen as a means of reducing the negative impacts of bushfire on both human assets and ecological values. However, the ecology of planned burning remains poorly understood.

Planned burning and unburnt patch occurrence

Most of the 85 unburnt forest patches identified within the fire boundary were in gullies vegetated by wet eucalypt forest or rainforest. In general, time since fire (a surrogate for fuel load) had limited influence on whether patches burnt or not. However, in dry eucalypt forest, while gullies were still less likely to burn, recent planned burning decreased the chances of a site burning in the bushfire. This difference appears to be due to variation in fuel accumulation rates amongst forest types. In wet eucalypt forest and rainforest, fuels build up rapidly after fire, such that there is no window during which low fuel loads prevent fire. In dry eucalypt forest, fuel loads are low enough to inhibit fire spread for around four years post-fire. It is important to note that no unburnt patches remained in areas burnt under extreme weather conditions prior to or immediately after the wind change on 7th February 2009, irrespective of whether they had been recently burnt or not.

Planned burning is likely to contribute to the retention of unburnt patches during bushfire in dry eucalypt forest only under moderate fire weather conditions. While fuel reduction can reduce the chance of a patch burning during bushfire, it also simplifies vegetation structure. This will diminish the quality of patches as refuges for species that depend on complex habitat structure.

Appendix 3

Conclusions

1. Large, severe bushfires can have a profound effect on wildlife and ecosystems, but that effect is not uniform. Variability in fire severity contributes to landscape heterogeneity (patchiness) after fire.

2. Unburnt patches of forest arose mainly due to the effects of topography and vegetation type on fuel moisture and were more common in gullies with rainforest and wet forest, than in drier foothill forests. In dry forests, recent (<4 yr) prior burning contributed to the formation of unburnt patches under low intensity bushfire, but across the region these were fewer than those arising ‘naturally’. In extreme fire conditions, no unburnt patches remained.

3. Surveys of the flora and fauna 2-3 years post-fire revealed rapid recovery, with most species present within the burned landscape, albeit frequently in lower abundance.

4. Fire severity is a key influence on the post-fire status of plants and animals. Greatest impacts generally occurred at sites that were severely burnt (crown scorch, crown burn).

5. Unburnt forest patches have an important role as refuges for fauna. They often supported a greater richness and abundance, and distinct composition, for faunal groups, compared with burnt sites. Old unburnt patches, in particular, may harbour a greater abundance of wildlife following severe bushfire.

6. Increased levels of planned burning could result in more unburnt patches in dry forest exposed to bushfire, under moderate weather conditions. These have a simplified vegetation structure compared with long unburnt patches and so their value to wildlife may be limited. Planned burning potentially could be used strategically to protect long-unburnt stands, enhancing and preserving these valuable components of landscape heterogeneity. Given limited resources for fire management, planned ecological burning could target areas of relative topographic uniformity where ‘natural’ occurrence of unburnt patches is less likely to occur.

Further Research

Direct effects of fire on fauna

It is often assumed that animals will flee an approaching fire and seek refuge to avoid harm. Little is known of the ability of different species to escape the direct effects of fire, or to survive in the post-fire landscape. Ignorance of how fauna use refuges, both during and immediately following a fire, impairs our ability to identify landscape features that function as refuges.

Succession patterns

A shortage of sites of known age (time since last burnt) across a century or more, constrains our ability to document change in the structure of foothill forests, and their fauna, following severe fire.

Interaction of drought and bushfire

Severe bushfires commonly are preceded by drought. The effect of preceding drought on populations of plants and animals and its impact on their recovery after fire is poorly understood.

Tree hollows

Many species require tree hollows for shelter and breeding (e.g. possums, parrots, bats). Little is known about the time for hollows to develop, or the impacts of fire in the creation and loss of hollows, in foothill forests.

Effects of introduced species

Introduced pest species, like foxes, cats and deer, were widespread throughout the post-fire landscape. The magnitude of their impact upon recovering vegetation and wildlife populations is poorly understood.

Further information


Publications


Photo credits

Rohan Clarke (birds and sugar glider), Woodhouse photos(p. 5) by Alastair Robertson and Maria Minor, Massey University

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