Forest Ecology and Management 318 (2014) 110–121

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Refuges for birds in fire-prone landscapes: The influence of fire severity and fire history on the distribution of forest birds

Natasha M. Robinson [a,*], Steven W.J. Leonard [a], Andrew F. Bennett [b], Michael F. Clarke [a]

[a] Department of Zoology, La Trobe University, Melbourne, VIC 3086, Australia
[b] School of Life and Environmental Sciences, Deakin University, Burwood, VIC 3125, Australia

ARTICLE INFO

Article history:
Received 21 October 2013
Received in revised form 4 January 2014
Accepted 7 January 2014
Available online 8 February 2014

Keywords:
Biological legacies
Residual habitat
Fire skips
Black Saturday fire
Foothill forest
Australia

ABSTRACT

Unburnt patches within a fire boundary may act as refuges for fauna, facilitating their survival and persistence within fire-prone landscapes. Unburnt patches can arise due to various processes, including topographic variation, fire behaviour, and fuel reduction from recent burning. However, the value of unburnt patches of differing characteristics to the post-fire persistence of faunal communities has rarely been examined. In this study, we examined the relative importance of fire history and severity in predicting the occurrence of birds in a burnt forest landscape. We conducted surveys in mixed eucalypt forest of south-east Australia, 2–3 years after a high intensity, landscape-scale wildfire (>200,000 ha). Sites ($n = 91$) were selected to encompass fire severity ranging from unburnt patches to stands of crown-burnt forest. Fire history prior to the wildfire was defined as short (<3 years) or long (>20 years) time-since-fire. Unburnt patches of long time-since-fire were important avian refuges, harbouring 20–40% more species, up to 56% more individuals and an assemblage that was distinct from that at all sites burnt by the wildfire, including low severity ground fire. No difference in species richness or composition was detected between sites in unburnt patches of short or long time-since-fire; but bird abundance was ~20% lower in patches of short time-since-fire. Unburnt and ground-burnt patches of short time-since-fire provided habitat for more species and had distinct assemblages from that of severely burnt sites. For sites severely burnt in the wildfire, there was no difference in avifaunal richness, abundance or composition between those burnt twice in rapid succession and those not burnt for >20 years. Together, these results highlight: (1) the particular importance of unburnt vegetation remaining within fire-affected areas as faunal refuges, and (2) the potential for recent planned burns to contribute to refuge habitat if it avoids severe burning in a subsequent wildfire.

1. Introduction

Fire is an important agent of change in many systems globally (Bond and Keeley, 2005). Fire can result in substantial mortality of the existing fauna (Silveira et al., 1999; Lyon et al., 2000; Sanz-Aguilar et al., 2011), especially in the case of large intense wildfires (Newsome et al., 1975; Silveira et al., 1999). Despite this, the most significant impact on fauna often occurs after a fire through loss of habitat and food, and increased predation (Whelan et al., 2002). Requirements for resources that are scarce or unavailable post-fire can place species at risk of reduced fecundity (Brooker and Rowley, 1991) or local extinction (Baker, 1997; Recher et al., 2009). Accordingly, unburnt patches that remain within a fire boundary may have value as faunal refuges that provide immediate shelter and resources for long-term persistence and recovery of animal populations (Whelan et al., 2002; Robinson et al., 2013). Persistence and recovery of populations within a fire boundary are likely to be especially important in the case of large fires for which mortality is often high and distance to outside source populations may be great relative to a species' dispersal ability (Turner et al., 1998; Whelan et al., 2002; Brown et al., 2009).

All fires, even large intense events, typically result in some unburnt or less severely burnt areas remaining (Schoennagel et al., 2008); these areas are sometimes referred to as residuals (Schieck and Hobson, 2000), fire skips or isolates (Stuart-Smith et al., 2002). The processes, either stochastic or deterministic, that contribute to fire heterogeneity differ in the type of habitat that is left unburnt. For example, natural variation in topography and fuel barriers (such as rocky screes, rivers) may afford protection from multiple fire events (Mackey et al., 2002; Bradstock et al., 2005; Burton et al., 2008). Vegetation remaining in such locations may be much

* Corresponding author. Mobile: +61 413 687 675.
E-mail addresses: nm3robinson@students.latrobe.edu.au (N.M. Robinson), s.leonard@latrobe.edu.au (S.W.J. Leonard), andrew.bennett@deakin.edu.au (A.F. Bennett), m.clarke@latrobe.edu.au (M.F. Clarke).

http://dx.doi.org/10.1016/j.foreco.2014.01.008
0378-1127/

older than that in the surrounding landscape (Burton et al., 2008) and floristically distinct (Clarke, 2002), and therefore harbour fauna not found in the broader fire-prone landscape (Gandhi et al., 2001). Unburnt patches may also arise when fuel reduction from recent burning prevents a patch from being burnt in a subsequent fire (Bradstock et al., 2005). Such patches are characterised by early successional age-classes but, depending on the severity of the prior fire, may contain important habitat components (Bradstock et al., 2005; Pereoglou et al., 2013).

Patches that remain unburnt in fire-prone landscapes are expected to become increasingly important under current predictions of climate change (McKenzie et al., 2004). Weather conditions that contribute to large, high intensity fire events are expected to be more frequent in fire-prone regions such as south-east Australia (Hasson et al., 2009) and north-west USA (McKenzie et al., 2004), resulting in greater coverage and frequency of fire. Land managers may be able to minimise the severity and extent of wildfire through prescribed burning, and creating unburnt patches within or adjacent to the fire boundary (Burrows and Wardell-Johnson, 2004). On the other hand, extreme weather conditions may lead to recently fuel-reduced areas burning again in a subsequent wildfire, resulting in adverse changes to faunal habitats due to short fire intervals (Agee, 1993; Whelan et al., 2002). Indeed, the effects of short fire intervals can push vegetation communities towards new states, that cater for a different faunal assemblage (Fontaine et al., 2009).

In order to understand how faunal communities persist in fire-prone landscapes, we investigated the value to birds of unburnt or ground-burnt patches within the fire boundary of a major wildfire (>200,000 ha), and the relevance of fire history prior to the major fire. Our research was undertaken 2–3 years after the Kilmore East-Murrindindi Fire complex in the foothill forests of Victoria, south-east Australia. These fires began on 7th February 2009 on what became known as Black Saturday. Due to their devastating impact on human life and property, a subsequent inquiry (Teague et al., 2010) recommended that prescribed burning in the state of Victoria be increased from an annual average of 1.7% to a minimum annual rolling target of 5% of public land, with the objective of reducing the recurrence and severity of large wildfires. However, the ecological implications of this new policy are unclear. High levels of prescribed fire may reduce the severity and extent of future fires, and sites where fuel has been reduced by prescribed burning may burn less severely when a major fire occurs (Burrows and Wardell-Johnson, 2004). Conversely, high levels of prescribed fire may also result in a decrease in the extent of suitable habitat for certain animal species that remain in the broader landscape after the major fire (Penman et al., 2007).

We examined the role of residual habitat within a fire boundary by addressing three hypotheses (Table 1) and illustrating our predictions (Fig. 1). First, we hypothesise that unburnt, or ground-burnt only (with canopy still intact), patches within the fire boundary act as refuges for birds. This hypothesis predicts that in unburnt, or ground burnt, patches there will be greater species richness and abundance of birds, and an assemblage that is distinct from that in more severely burnt patches; but similar richness, abundance and composition to sites in continuous forest outside the fire boundary. Second, that among patches of equal fire severity in the 2009 wildfire, those that experienced no fire in the 20 years preceding Black Saturday will have greater species richness and abundance and a different assemblage from patches that were burnt during the three years prior to Black Saturday. This hypothesis predicts that (a) unburnt patches of long time-since-fire (TSF) are better refuges than those of short TSF; and b) patches of long fire interval but burnt by the wildfire provide better habitat than patches burnt twice in rapid succession (short interval). The third hypothesis predicts that patches burnt in the three years preceding Black Saturday (short interval), that escaped severe fire during the wildfire, will have greater species richness and abundance and differing composition than more severely burnt patches of long fire interval (>20 years).

2. Methods

2.1. Study area

On 7th February 2009, two independent fires began burning in the central highlands of Victoria, approximately 100 km north of Melbourne, Australia (Teague et al., 2010). These fires converged to form the Kilmore East-Murrindindi fire complex (Price and Bradstock, 2012); a major fire that burnt 228,000 ha of forest, with fire severities ranging from extreme crown burn through to low

Table 1
Planned comparisons of the relationship between birds and fire treatments, based on *a priori* hypotheses and predictions.

Hypotheses and predictions	Planned comparison
1. Unburnt, or ground burnt, patches are refuges for birds within burned landscapes (a) Unburnt patches have similar species richness, abundance and composition to reference sites outside the fire boundary (b) Unburnt, or ground burnt, patches have greater species richness, abundance and a distinctive composition compared with more severely burnt patches	Within each class of short and long TSF (or interval) prior to the 2009 fire: • Unburnt compared with reference • Unburnt compared with: ground burnt, crown scorch, crown burnt • Ground burnt compared with: crown scorch, crown burnt
2. Within a given severity class, patches of long TSF (or interval) provide better habitat than patches of short TSF (or interval) (a) Unburnt patches of long TSF have greater species richness, abundance and a distinctive composition compared with unburnt patches of short TSF (b) Patches burnt by the wildfire of long fire interval have greater species richness, abundance and distinctive composition compared with patches burnt twice in rapid succession (short interval)	Within each severity class: • Long TSF (or interval) compared with short TSF (or interval)
3. Patches recently burnt prior to Black Saturday that subsequently escaped the wildfire (or were ground burnt) provide better habitat than more severely burnt vegetation of long fire interval (a) Unburnt, or ground burnt, patches of short TSF (or interval) have greater species richness and abundance and distinctive composition compared with more severely burnt patches of long fire interval	Unburnt of short TSF compared with: • Ground burnt of long interval • Crown scorch of long interval • Crown burnt of long interval Ground burnt of short interval compared with: • Crown scorch of long interval • Crown burnt of long interval

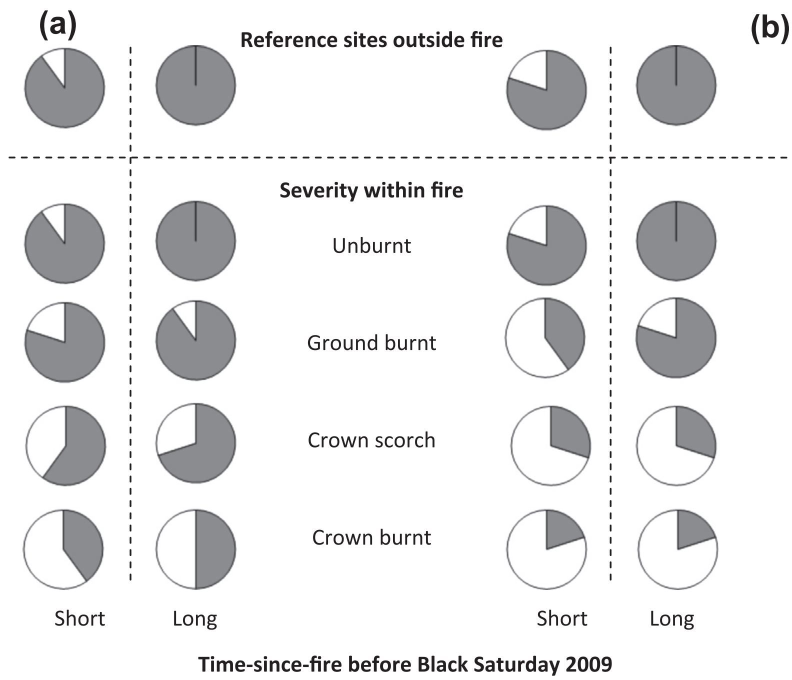

Fig. 1. Predictions of proportional (a) species richness and (b) abundance amongst fire severity and fire interval categories, in relation to a reference site of long TSF.

severity ground burns and unburnt patches. Our study focused on the foothill forests and associated gully systems, which comprise approximately half the area of the fire complex. Messmate (*Eucalyptus obliqua*), narrow-leaved peppermint (*Eucalyptus radiata*) and broad-leaved peppermint (*Eucalyptus dives*) are the dominant tree species across these vegetation communities, with smaller trees of silver wattle (*Acacia dealbata*) and Australian blackwood (*Acacia melanoxylon*) in the sub canopy. Foothill forest vegetation occurs predominately on slopes and is characterised by a sparse to dense understorey often dominated by bracken fern (*Pteridium esculentum*). Gullies are typified by a dense layer of medium to tall shrubs that include musk daisy bush (*Olearia argophylla*), hazel pomaderris (*Pomaderris aspera*) and prickly currant-bush (*Coprosma quadrifida*), tree ferns (*Dicksonia antarctica*, *Cyathea australis*), along with herbs and grasses. The majority of the area under investigation is forested public land (∼80%) that is managed for timber harvesting (mainly single tree selection), conservation and recreation. Our study deliberately avoided areas recently logged (i.e. within the last 30 years) or with a known history of clear felling.

Ninety-one sites were selected inside and adjacent to the boundary of the fire complex, following stratification according to fire history and fire severity. All study sites consisted of 5 ha of forest and were comprised of a gully and adjacent slope. Reference sites were situated in extensive unburnt forest at least 1.2 km beyond the fire edge. As far as possible, sites within fire history/severity combinations were dispersed across the study area in order to minimise regional bias. In general, sites were greater than 1500 m apart, although in a few cases it was necessary to relax this rule in order to achieve sufficient replication of fire history/severity combinations (minimum site separation = 440 m). This investigation is part of a larger study on the relationships between plant and animal communities and the spatial properties of fire within foothill forest landscapes.

2.2. Fire history

Sites were selected to represent two levels of fire history, assumed to reflect differences in habitat quality (and fuel loads) related to fire interval or TSF. For sites that burnt on Black Saturday, fire history relates to the fire interval prior to the wildfire. For sites that escaped burning on Black Saturday, fire history is described by time-since-last-fire (TSF). 'Short fire interval' (or TSF) was defined as being burnt <3 years prior to the 2009 wildfire. In foothill forests, prescribed burning can restrict wildfire and reduce fire severity for 4–5 years, with decreasing benefits up to 10 years, at which point effectiveness is negligible (McCarthy and Tolhurst, 2001; Price and Bradstock, 2012). 'Long fire interval' (or TSF), greater than 20 years since last known fire, was used to define sites in the second level: by this age, vegetation has reached vigorous maturity although habitat elements such as tree hollows may take much longer to develop (Cheal, 2010). Precise determination of longer intervals was not possible due to inadequate and inconsistent historical mapping of fires.

2.3. Fire severity

Fire severity was classified into four classes: (a) unburnt, no evidence of fire in either the understory or canopy; (b) ground burnt, understory mostly burnt but canopy unburnt; (c) crown scorch, understory burnt and canopy scorched, and; (d) crown burnt, both understory and canopy burnt. A broad overview of these classes was obtained by severity mapping based on the change in vegetation before and after the 2009 fires, by calculation of the Normalised Burn Ratio using Landsat/SPOT imagery (DSE, 2009b). Greater accuracy in discriminating between severity classes, especially between unburnt and ground burnt, was achieved by interrogating 15 cm resolution aerial photographs (DSE, 2009a), in combination with ground-truthing the fire severity of all study sites 16–18 months post-fire.

2.4. Bird surveys

Birds were surveyed at 91 sites for four survey rounds each, between October 2010 and April 2012, except for one site that was only sampled thrice due to inaccessibility during one survey round. Surveys occurred during two spring breeding periods (September–December) and two late summer-autumn periods (late January–April). Within a site on each survey round, two point counts were conducted in a gully section and two on an adjacent slope. All birds detected aurally or visually over a 15 min period within 30 m of the point were identified and counted, excluding birds that did not land in this area. Birds recorded outside the 30 m radius but within the 5 ha site and time period contributed to site species richness. Points were typically 70–100 m apart, and located to ensure placement in appropriate vegetation type and to maximise distance to transitions in fire treatments. Surveys were conducted throughout the day from 30 min after sunrise until dusk, but not under persistent rain, wind or temperatures above 30 °C. The time of day when surveys were conducted was balanced across treatment classes during the four rounds of surveys. NMR conducted all surveys.

2.5. Statistical analysis

Avian species richness, abundance and assemblage composition were compared across sites of differing combinations of fire severity and fire history. Species richness was defined as the total number of bird species detected at a site over the four survey rounds. Mean abundance of each species at a site was calculated using only records of birds detected within 30 m of a point, with the four point-count values (i.e. from gully and slope) pooled across a site, and averaged over the four survey rounds. Analyses of the composition of the assemblage of birds at a site was based on the proportion of survey rounds during which each species was detected anywhere within a site. Using such a reporting rate to quantify species occurrence diminishes the influence of flocking species over species typically recorded as singletons. All species were included in multivariate analyses (and contributed to overall test results), but only those species recorded in more than 10 sites were examined individually for differences across treatment types.

A two-factor ANOVA, with type III sums of squares, was used to test the main effects of fire history and fire severity and their interaction on species richness and abundance. ANOVA models were analysed using the R packages car, MASS and nnet (Venables and Ripley, 2002; Logan, 2010; Fox and Weisberg, 2011; Wang et al., 2012). Using the $MS_{residual}$ generated from the ANOVA models (see Appendix A), planned comparisons based on our hypotheses were made using the package biology (Logan, 2010) (Table 1). The number of comparisons was small (but not orthogonal) and thus no post-hoc adjustments were made to significance levels (Quinn and Keough, 2002).

Assemblage composition and variation in the occurrence of individual species were analysed in relation to fire history, fire severity and their interaction, by using multivariate general linear models and unadjusted *P* values in the package mvabund (Wang et al., 2012) (see Appendix A). Using the same approach, pairwise planned comparisons at multivariate and individual species levels were conducted between fire severity/interval classes. Species with significance levels between 0.01 and 0.05 were interpreted cautiously to avoid family-wise Type 1 error (Quinn and Keough, 2002). All analyses were completed in R version 2.15.1.

3. Results

A total of 14,961 birds from 79 species were detected across 91 sites; Appendix B lists common and scientific names. The taxonomy for bird species follows Christidis and Boles (2008). Fifty species were present in more than 10 sites and were further analysed at an individual level.

3.1. Are unburnt patches refuges for birds within burnt landscapes?

Two to three years after the wildfire, unburnt sites generally supported a greater richness and abundance of birds than sites in the surrounding burnt landscape (Figs. 2 and 3, and Table 2). Overall, severely burnt sites were associated with lower species richness and changes in composition across both TSF treatments, and lower abundance compared with unburnt sites of long TSF (Figs. 2 and 3, and Table 2). Unburnt sites in the midst of burnt landscapes supported a similar richness, abundance and assemblage composition of birds to external reference sites surrounded by extensive unburnt habitat (Figs. 2 and 3, and Table 2). There were, however, significant differences in occurrence of some species between unburnt sites within the fire boundary and external reference sites for each fire history treatment (Table 3). For sites of long TSF, three species had greater reporting rates at reference sites outside the fire boundary than for unburnt sites within the boundary. However, one species, superb lyrebird, had a higher reporting rate in long unburnt patches within the fire boundary (Table 3). For sites that had been recently burnt prior to Black Saturday, two species (eastern spinebill, silvereye) had a higher reporting rate in reference sites outside the fire, whereas grey fantail was higher at unburnt sites within the fire boundary (Table 3).

Unburnt sites within the fire boundary with long TSF had a higher species richness and abundance than all categories of burnt vegetation of similarly long TSF history prior to 2009, including the low severity class of ground burnt (Figs. 2 and 3, and Table 2). On average, there were almost 20% more species and 47% more individual birds in unburnt sites than in ground burnt sites; this difference increased to almost 40% more species and 56% more birds compared with crown burnt sites. The assemblage composition within these unburnt sites also differed significantly from that in all three categories of burned sites (Table 2), and 17 species had significant differences across this range (Table 3). Five species (eastern spinebill, laughing kookaburra, eastern yellow robin, superb lyrebird, and silvereye) were more frequently observed in unburnt sites compared with all categories of burn (Table 3). A further ten species showed decreases in reporting rates in the more severe categories of crown scorch and crown burn, compared with unburnt patches within the fire boundary. In contrast, flame robin and scarlet robin responded positively to burnt habitat.

Within sites burnt less than three years prior to the 2009 wildfire, the differences between unburnt and burnt sites were less dramatic. No difference in abundance was detected; similar numbers of birds were found in unburnt sites that had been recently burnt prior to Black Saturday as in ground burnt, crown scorch and crown burnt sites (Fig. 3, and Table 2). There was no difference in species richness, assemblage composition and reporting rates of individual species between unburnt and ground burnt sites (Fig. 2, and Table 2). Unburnt sites were distinct in richness and composition only from sites subject to high severity classes of

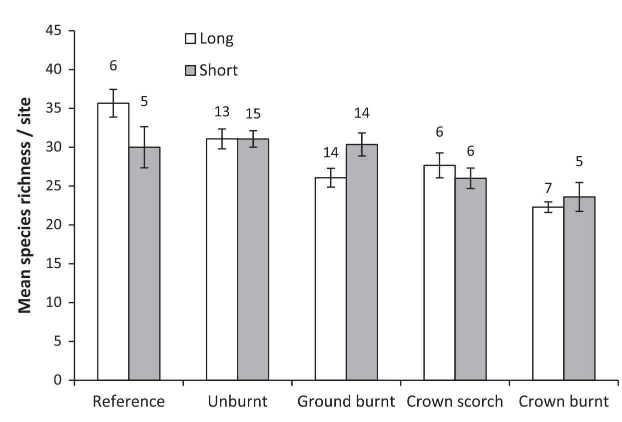

Fig. 2. Comparison of the mean species richness of birds in relation to fire severity and fire interval (or TSF), with standard error. Values shown above the bars are the sample sizes of sites in each category.

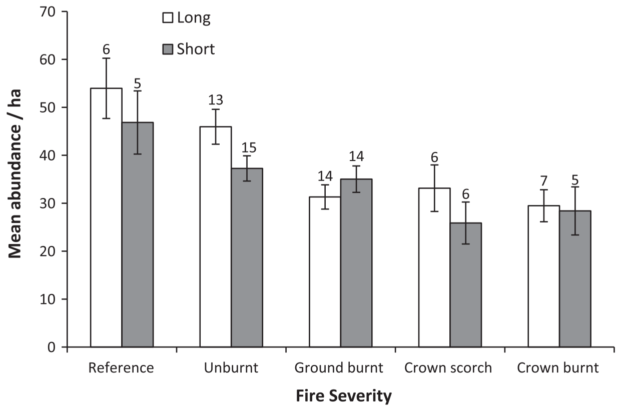

Fig. 3. Comparison of the mean bird abundance per hectare in relation to fire severity and fire interval (or TSF), with standard error. Values shown above the bars are the sample sizes of sites in each category.

crown scorch or burnt (Fig. 2, and Table 2). On average, 19% more species were detected in unburnt compared with crown scorch sites; this difference increased to almost 32% more species when compared with crown burnt sites. Eleven species had significantly different reporting rates between unburnt and either crown scorch or crown burnt sites (Table 3). Of these species, nine occurred more frequently in unburnt sites that had been recently burnt prior to Black Saturday than in either crown scorch or burnt sites with similar history. However, flame robin and eastern whipbird were more common in severely burnt sites.

3.2. Are ground burnt patches refuges for birds within burnt landscapes?

Distinctions between ground burnt sites and more severely burnt sites were less pronounced than were those for unburnt patches. However, the composition of the avifauna of ground burnt sites did differ from that of the most extreme severity class; crown burnt sites (Table 2).

Ground burnt sites with a long fire interval (i.e. not burnt in the preceding 20 years) supported an avifauna that differed from unburnt sites of similar fire history; but did not differ in species richness and abundance from severely burnt classes of crown scorch and crown burnt (Figs. 2 and 3, and Table 2). Composition (Table 2) and individual species reporting rates (Table 3) differed between ground burnt and crown burnt sites. Eight species had higher reporting rates in ground burnt sites compared with higher severity classes (Table 3). Conversely, three species (flame robin, buff-rumped thornbill, eastern whipbird) were more common in either crown scorch or crown burnt sites (Table 3).

For sites with a short fire interval (i.e. burnt <3 years prior to Black Saturday), there was no discernible difference between sites that were unburnt in the wildfire and those that were ground burnt (Figs. 2 and 3, and Table 2). Furthermore, there was no difference in abundance and composition between ground burnt sites and both crown scorch and crown burnt sites (Figs. 2 and 3, and Table 2). There was, however, a greater richness in ground burnt sites than crown burnt sites, with 29% more species detected in ground burnt sites. Six species had significantly higher reporting rates in ground burnt compared to either crown scorch or crown burnt sites, whereas only flame robin increased with increasing severity class (Table 3).

3.3. Are unburnt patches of long TSF better refuges than unburnt patches of short TSF?

Unburnt patches of long TSF supported 23% greater abundance of birds than unburnt patches that were burnt less than three years prior to the wildfire (Fig. 3, and Table 4). In contrast, there was no difference detected in species richness (Fig. 2, and Table 4) between unburnt patches of differing fire history classes. Differences in composition between unburnt patches of short and long TSF just failed to reach significance at the 5% level (Table 4). Five species had significantly higher reporting rates in long unburnt patches than in unburnt patches of recent fire history (Table 5).

Reference sites of long and short TSF did not differ in abundance or composition (Table 4). However, species richness of those with long TSF was greater than those burnt less than three years prior (Fig. 2, and Table 4), representing almost 19% more species in reference sites of long TSF. Two species (eastern whipbird, superb fairy-wren) had higher reporting rates in long TSF reference sites than those that had been burnt less than three years prior (Table 5).

3.4. Do patches burnt by the wildfire of long fire interval provide better habitat than patches burnt twice in rapid succession (short interval)?

Contrary to predictions (Table 1), no significant negative effect of twice burning was detected at the individual or community level. Species richness, abundance and composition in sites recently burnt prior to Black Saturday that were re-burnt in the wildfire were equal to, if not greater than, sites of comparable severity and long fire interval. Ground burnt sites of differing fire intervals did not differ in abundance and composition (Fig. 3, and Table 4);

Table 2
Results of planned comparisons for species richness ($MS_{Residual}$ = 19.9, df = 1, 81), abundance ($MS_{Residual}$ = 10.2, df = 1, 81) and assemblage composition (df = 1, Residual df) between severity classes, within each fire interval class (long or short).

	Species richness		Abundance		Composition		
	F	*P*	F	*P*	Res. df	LR	*P*
Long interval:							
Reference vs Unburnt	0.21	0. 651	0.01	0.916	17	90.52	0.253
Unburnt vs Ground burnt	8.46	**0.005**	11.28	**0.002**	25	126.2	**0.015**
Unburnt vs Crown scorch	4.35	**0.040**	7.36	**0.008**	23	197.4	**<0.0001**
Unburnt vs Crown burnt	15.83	**0.0002**	10.52	**0.002**	18	266.5	**<0.0001**
Ground burnt vs Crown scorch	2.11	0.150	1.91	0.171	18	81.21	0.193
Ground burnt vs Crown burnt	0.27	0.603	0.52	0.472	19	160.4	**0.001**
Short interval:							
Reference vs Unburnt	1.60	0.210	0.31	0.579	18	75.59	0.348
Unburnt vs Ground burnt	0.24	0.625	0.30	0.585	27	57.43	0.658
Unburnt vs Crown scorch	5.78	**0.018**	3.12	0.081	19	131.1	**0.02**
Unburnt vs Crown burnt	8.80	**0.004**	1.89	0.173	18	125.2	**0.026**
Ground burnt vs Crown scorch	3.36	0.071	1.23	0.271	18	94.93	0.117
Ground burnt vs Crown burnt	5.66	**0.020**	0.47	0.495	17	98.44	0.112

Note: Statistically significant results ($P < 0.05$) are shown in bold.

Table 3
Results of planned comparisons of the reporting rates of individual species between fire severity classes, within each fire interval class (long or short). Level of significance is indicated as 0–0.001***, 0.001–0.01**, 0.01–0.05*, followed by the severity class of higher value.

Species	TSF	Reference (RF) vs	Unburnt (UB) vs			Ground burnt (GB) vs	
		Unburnt (UB)	Ground burnt (GB)	Crown scorch (CS)	Crown burnt (CB)	Crown scorch (CS)	Crown burnt (CB)
Eastern spinebill	Long		**UB	***UB	***UB		***GB
	Short	*RF		***UB	***UB	**GB	*GB
Laughing kookaburra	Long		*UB	***UB	***UB		
	Short			**UB	**UB		
Eastern yellow robin	Long		*UB	**UB	***UB		
	Short			*UB			
Superb lyrebird	Long	*UB	**UB	**UB	***UB		*GB
	Short				*UB		*GB
Silvereye	Long		**UB	**UB	*UB		
	Short	**RF					
Gang-gang cockatoo	Long			*UB	**UB		*GB
	Short			**UB	**UB	*GB	
White-throated treecreeper	Long				***UB		**GB
	Short			*UB		*GB	
Rose robin	Long			***UB	**UB		
	Short						
Red wattlebird	Long			*UB			
	Short					*GB	
Brown thornbill	Long				***UB		**GB
	Short						
Superb fairy-wren	Long				*UB		
	Short						
Golden whistler	Long				*UB		
	Short						
Rufous whistler	Long				**UB		
	Short				**UB		*GB
White-browed scrubwren	Long				**UB		*GB
	Short						
Pied currawong	Long				*UB		
	Short				**UB		
Scarlet robin	Long			**CS			
	Short						
Flame robin	Long			**CS	***CB		***CB
	Short			**CS	*CB	*CS	
Crimson rosella	Long						
	Short				*UB		
Eastern whipbird	Long	**RF				*CS	
	Short				*CB		
Grey shrike-thrush	Long						*GB
	Short						
Grey butcherbird	Long						*GB
	Short						
Buff-rumped thornbill	Long						*CB
	Short						
Australian king-parrot	Long	*RF					
	Short						
Olive-backed oriole	Long	*RF					
	Short						
Grey fantail	Long						
	Short	*UB					

but, species richness was greater in ground burnt sites recently burnt prior to 2009 than in ground burnt sites of long fire interval (Fig. 2, and Table 4). There were, on average, 16% more species found in ground burnt sites of short fire interval, and two species were detected significantly more often in such sites than in ground burnt sites of long fire interval (Table 5). Within crown scorch and crown burnt classes, there were no differences in richness (Fig. 2, and Table 4), abundance (Fig. 3, and Table 4) or composition (Table 4) between the two fire interval classes. Only one species, white-naped honeyeater, differed in reporting rate; it was found more often in crown scorch sites that had been recently burnt prior to 2009 (Table 5).

3.5. Do unburnt patches of short TSF provide better habitat than more severely burnt patches of long fire interval?

Unburnt sites that were recently burnt prior to Black Saturday were found to be important for a distinct suite of species not found

Table 4
Results of planned comparisons for species richness ($MS_{Residual}$ = 19.9, df = 1, 81), abundance ($MS_{Residual}$ = 10.2, df = 1, 81) and assemblage composition (df = 1, Residual df) between fire interval classes, within each severity treatment.

	Species richness		Abundance		Composition		
	F	*P*	*F*	*P*	Res. df	LR	*P*
Long vs short interval:							
Reference	4.402	**0.039**	1.081	0.302	9	84.28	0.302
Unburnt	0.000	0.995	4.11	**0.0459**	26	112.7	0.058
Ground burnt	6.463	**0.0129**	0.754	0.388	26	85	0.164
Crown scorch	0.419	0.519	1.236	0.27	10	87.53	0.187
Crown burnt	0.253	0.616	0.027	0.871	10	57.15	0.427

Note: Statistically significant results ($P < 0.05$) are shown in bold.

in higher severity classes of long fire interval. Species richness within these unburnt sites was significantly greater than ground burnt and crown burnt sites of long fire interval, but not of crown scorch sites (Fig. 2, and Table 6). Composition within unburnt sites of short fire interval was different only from crown burnt of long fire interval (Table 6). No positive or negative effect of these unburnt sites was found in relation to the abundance of birds (Fig. 3, and Table 6). Once a site was burnt, either by the 2009 fire or three years prior, abundance did not decline further with increasing severity. At the individual species level, 18 species had significantly different reporting rates between unburnt sites of short fire interval and more severely burnt sites of long fire interval (Table 7). All except two species had higher reporting rates in these unburnt sites than in more severely burnt sites.

3.6. Do ground burnt patches of short fire interval provide better habitat than more severely burnt patches of long fire interval?

Ground burnt sites of short fire interval did not differ in abundance (Fig. 2), richness or composition from crown scorch sites of previously long TSF (Table 6); but had a greater species richness (36% more species) and differed in composition from crown burnt sites (Fig. 2, and Table 6). In addition, 18 species were recorded more often in ground burnt sites of short fire interval than in either crown scorch or crown burnt sites of long fire interval (Table 7). Two species, flame robin and superb fairy-wren, increased their presence in sites of higher fire severity.

4. Discussion

Unburnt patches within the fire boundary supported higher species richness and an assemblage composition that was distinct from severely burnt sites. No differences in species richness or composition were detected between unburnt patches of long or short time-since-fire; but abundance in unburnt patches of long TSF was significantly greater than that of short TSF, and all remaining treatments within the fire boundary. Between severely burnt sites of long or short TSF, there were no differences in bird richness, abundance or composition. Unburnt, and less severely burnt, patches of short TSF supported a greater number of species and a distinct suite of species to that of severely burnt sites.

Table 6
Results of planned comparisons for species richness ($MS_{Residual}$ = 19.9, df = 1, 81), abundance ($MS_{Residual}$ = 10.2, df = 1, 81) and assemblage composition (df = 1, Residual df) between unburnt or ground burnt patches of short fire interval and more severely burnt patches of long interval.

	Species richness		Abundance		Composition		
	F	*P*	F	*P*	Res. df	LR	*P*
Unburnt of short vs							
Ground burnt	9.08	**0.003**	2.00	0.161	27	94.55	0.108
Crown scorch	2.49	0.118	0.57	0.453	19	107.2	0.066
Crown burnt	18.50	**<0.0001**	2.26	0.137	20	227.9	**<0.000**
Ground burnt of short vs							
Crown scorch	1.53	0.22	0.12	0.734	18	84.85	0.174
Crown burnt	15.28	**<0.0002**	1.12	0.293	19	178.1	**<0.000**

Note: Statistically significant results ($P < 0.05$) are shown in bold.

4.1. Unburnt patches of long time-since-fire are refuges for birds

Two to three years post-fire, unburnt patches of long TSF provided refuge for birds that were either absent, or less frequently recorded, in the surrounding fire-affected landscape (Fig. 4). Fifteen species were more frequently recorded at sites in unburnt patches of long TSF within the fire boundary when compared with sites burnt either in the 2009 wildfire, or less than three years prior. High densities within the fire boundary were restricted to unburnt patches of long TSF, and were comparable to densities outside the fire boundary.

Late successional patches within younger pyrogenic landscapes have unique habitat attributes (Camp et al., 1997; DeLong and Kessler, 2000) that can determine fauna distributions for many years to centuries post-fire (Loyn, 1998; Gandhi et al., 2001; Hingston and Grove, 2010). Within the forest type that we studied, older vegetation characteristics such as flowering, fruiting and a complex structure of shrubs, logs and deep leaf litter become apparent with periods greater than 20 years since fire and continue to develop for many years after (Department of Sustainability and Environment, 2003; Cheal, 2010). Our sites of long TSF were fire-free for at least 20 years but could have been much older, as gullies have an inherent capacity to repeatedly escape fire (Bradstock et al., 2005; Leonard et al., 2014). Evidence of mature food plants and richer food sources in unburnt patches of long TSF is suggested by the greater numbers of nectarivores (e.g. eastern spinebill) and frugivores (e.g. silvereye) found within these sites than in burnt sites, along with species that forage for invertebrates in the leaf litter (e.g. superb lyrebird, eastern yellow robin) and feed on small ground dwelling vertebrates (e.g. laughing kookaburra). Canopy foragers (e.g. gang-gang cockatoo, rose robin) were also more common in unburnt sites. The high habitat value of these unburnt

Table 5
Results of planned comparisons of the reporting rates of individual species between fire interval classes, within each severity treatment. Level of significance is indicated as 0–0.001***, 0.001–0.01**, 0.01–0.05*, followed by interval class of higher value.

Species	Long compared to short interval, within:			
	Reference	Unburnt	Ground burnt	Crown scorch
Eastern whipbird	*Long	*Long		
Superb fairy-wren	*Long			
Eastern spinebill		***Long		
Eastern yellow robin		*Long		
Rose robin		**Long		
Silvereye		*Long		
Buff-rumped thornbill			*Short	
White-eared honeyeater			**Short	
White-naped honeyeater				*Short

Table 7
Results of planned comparisons of the reporting rates of individual species between unburnt or ground burnt patches of short TSF (or interval) and more severely burnt patches of long interval. Level of significance is indicated as 0–0.001***, 0.001–0.01**, 0.01–0.05*, followed by class of higher value.

	Unburnt (UB) of short TSF vs sites of long interval &			Ground burnt (GB) of short interval vs sites of long interval &	
	Ground burnt (GB)	Crown scorch (CS)	Crown burnt (CB)	Crown scorch (CS)	Crown burnt (CB)
Gang-gang cockatoo	*UB	**UB	**UB		**GB
Eastern spinebill		*UB	***UB		**GB
Superb lyrebird		*UB	**UB	*GB	*GB
Crimson rosella		*UB	*UB		*GB
Rufous whistler	*UB		**UB		**GB
Pied currawong	*UB		**UB		*GB
White-throated treecreeper			***UB		**GB
Grey shrike-thrush			***UB		**GB
Grey butcherbird			*UB		*GB
Laughing kookaburra			**UB		
Eastern yellow robin			**UB		**GB
White-eared honeyeater	*UB			*GB	
Grey fantail			**UB		*GB
White-browed scrubwren			*UB		*GB
Grey currawong		*UB		*GB	
Lewin's honeyeater	*UB				
Brown thornbill					**GB
Olive-backed oriole					*GB
Scarlet robin					*GB
Superb fairy-wren				*CS	
Flame robin			***CB		**CB
Eastern whipbird		*CS		*GB	

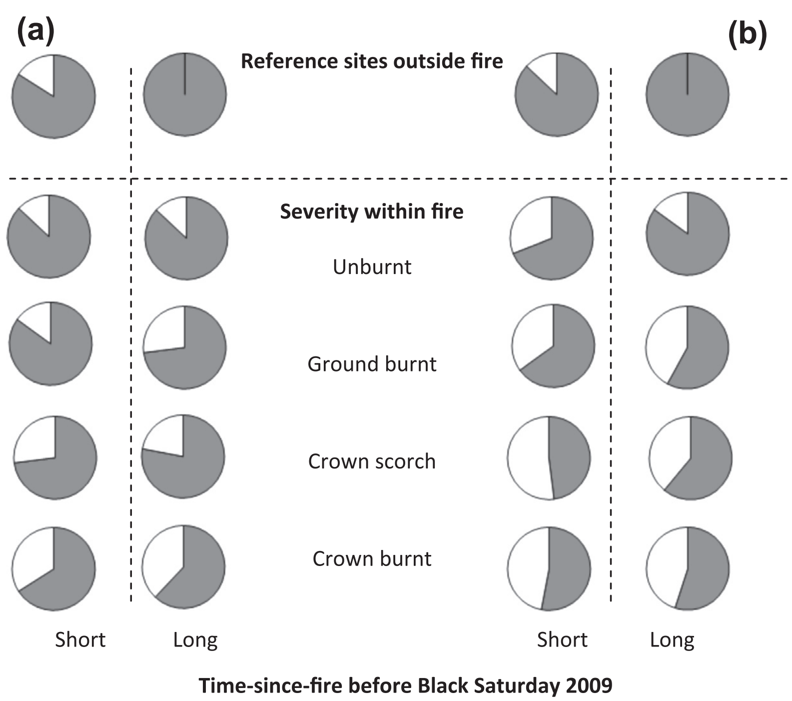

Fig. 4. Results of proportional (a) species richness and (b) abundance amongst fire severity and fire interval categories, in relation to a reference site of long TSF.

patches of long TSF is further demonstrated by greater reporting rates of particular species (e.g. superb lyrebird) relative to similar reference habitat outside the fire. These results suggest that the superb lyrebird may have survived the fire *in situ* but then moved into these long unburnt patches, augmenting their density. Overall high numbers of birds found within unburnt patches of long TSF may confer greater resilience to current and future populations within the fire-affected landscape, especially if subjected to further disturbance in the recovery phase (Recher et al., 2009). As such, these patches may have ongoing importance for species requiring mid-late successional habitat, enabling their persistence in fire prone landscapes (e.g. Gandhi et al., 2001; Lindenmayer et al., 2009).

4.2. Recently burnt patches can act as future refuges

Recently burnt areas can act as avifaunal refuges in a subsequent large intense wildfire, providing the patches avoid canopy-consuming fire. More species of birds used unburnt and ground burnt patches of short fire interval than more severely burnt patches of long interval, yet some species benefitted from increasing severity (e.g. flame robin). Overall, greater fire severity led to declines in species richness and occurrence of many species, regardless of fire history prior to 2009. Moreover, despite being characterised by a less mature seral stage, total richness in unburnt patches of short TSF did not differ from unburnt patches of long TSF. However, greater numbers of birds and high occurrences of certain species suggest that long unburnt patches provide better refuge habitat than unburnt patches that been recently burnt.

Prescribed burning may have a role in maintaining existing habitat patches as refuges and in creating future refuges for fauna (Bradstock et al., 2005; Penman et al., 2007; Leonard et al., 2014). Patchy mosaic burning can maintain heterogeneity of burnt and unburnt patches in prescribed burnt landscapes (Burrows and Wardell-Johnson, 2004; Penman et al., 2007). Strategic prescribed burning may further act as a buffer against wildfire for important habitat areas (Burrows, 2008). Lastly, recently fuel reduced areas may become future refuges themselves if they resist burning in a subsequent wildfire (Bradstock et al., 2005) but with reduced refuge capacity in the short term (Swengel and Swengel, 2007). However, caution is needed against the latter style of refuge creation as too much burning can lead to an overall decline in the amount of unburnt areas remaining (Penman et al., 2007), without targeted protection of high value areas of long TSF. Refuges created through means other than burning (e.g. mowing) may also be worthy of consideration and have enhanced faunal outcomes (Swengel and Swengel, 2007). However, all such fuel management actions will need to be weighed against their ability to effectively lessen the impact of wildfire under various weather conditions (Price and Bradstock, 2012) and the quality of the resulting habitat.

4.3. The value of unburnt patches within a large wildfire

Unburnt patches are rare in most fires (Eberhart and Woodard, 1987; Román-Cuesta et al., 2009; Leonard et al., 2014), have disproportionate habitat value for fire-sensitive fauna (DeLong and Kessler, 2000), yet few studies have considered their importance to avian communities. Stuart-Smith et al. (2002) compared unburnt patches within a wildfire (<10,000 ha) to burnt vegetation five years post-fire but, in contrast to our study, found no difference between the two habitats in terms of species richness, abundance and diversity, possibly due to limited statistical power ($n = 4$). Two other North American studies noted the elevated habitat value of unburnt patches compared with burnt forest, yet found that bird communities in unburnt patches were dissimilar to continuous old forest (Seip and Parker, 1997; Schieck and Hobson, 2000). Our study, on the other hand, indicates that the assemblage composition in unburnt patches within the fire boundary does not differ substantially from sites of similar fire history located outside.

Unburnt habitat remaining within the fire boundary is likely to be increasingly important in large, severe wildfires, such as the one studied. Severe wildfires can result in high mortality of fauna with greater reliance of surviving individuals on remaining unburnt habitat (Recher et al., 2009). Meanwhile, changes in biological communities may be more pronounced following large fires due to differences in recovery mechanisms, and dispersal abilities (Turner et al., 1998). *In situ* persistence of organisms, in unburnt patches, is expected to facilitate recolonisation of the burnt landscape more easily than individuals colonising from outside the fire (Baker, 2000; Bain et al., 2008; Watson et al., 2012), particularly for species with poor dispersal ability (Turner et al., 1998; Whelan et al., 2002). Unburnt habitat may additionally augment species richness in the surrounding burnt landscape (Watson et al., 2012). Species may utilise burnt habitat but still rely on components of unburnt habitat, such as shelter, for long periods after the fire (Murphy et al., 2010). Accordingly, unburnt habitat within a fire boundary is not only important to birds residing within the patch but is likely to provide benefits to the surrounding avifaunal community. The resilience of avian communities within refuges will be important in safeguarding populations over time, especially in the face of increasing natural and anthropogenic pressures (McKenzie et al., 2004).

4.4. Double burning in rapid succession was not inferior habitat to sites burnt once

Contrary to our predictions, two fires in rapid succession had no detectable negative effect on avifauna compared with a single burn. Severity classes of differing fire interval were similar in abundance, richness and composition; the exception being species richness of ground burnt sites. Our predictions were based on an expected decline in habitat structure and floristic richness (Spencer and Baxter, 2006), and the subsequent decline or change in the avifauna (Fontaine et al., 2009).

Short rotational fires can lead to structural simplification by restricting growth of woody plants and reducing litter and coarse woody debris (Catling, 1991). Residual habitat features such as burnt stems and logs are important for faunal survival and recovery. Yet, even early seral stage specialists can be threatened by too frequent fire (e.g. Pereoglou et al., 2011). To a lesser extent, frequent fire can diminish floristic diversity over time (e.g. Spencer and Baxter, 2006) or eliminate certain functional types (e.g. obligate seeders) from some plant communities (Noble and Slatyer, 1980). However, the forest system studied here may be resilient to two fires that occur more frequently than recommended, particularly if both events are not high intensity (Department of Sustainability and Environment, 2003; Cheal, 2010). In our study, only one site was subjected to two high intensity events, as the majority of recent fire history was due to prescribed burning. Thus, the type of burning prior to Black Saturday may have diminished differences due to short and long fire interval, with the result that fire intervals of burnt sites were less relevant than the degree to which it was burnt.

Surprisingly, ground burnt sites of short fire interval had more species than ground burnt sites of long interval. This counterintuitive result may be explained by considering the degree of habitat change that each category experienced on being ground burnt on Black Saturday. Before the 2009 wildfire, sites of long TSF would have been characterised by complex structure with an associated bird assemblage that was distinct from sites of recent fire history. With the passage of low severity fire in 2009, structure in the understory of both history categories would have been simplified; however, the magnitude of structural change would have been less in sites that had been burnt less than three years prior. For example, ant assemblages are largely resilient to fire in habitats where vegetation change is less pronounced (Barrow et al., 2007). Thus, providing residents survive the fire, the avian assemblage within sites of recent fire history would remain largely the same. In contrast, sites that had not been burnt for more than twenty years would have undergone marked compositional change due to major habitat change. Perhaps the resulting habitat was not completely occupied by the time of our study (Pearman et al., 2008).

5. Conclusion and management implications

Unburnt patches of long TSF provided the best refuge for birds within a large, severely burnt landscape, followed by unburnt and ground burnt patches of short TSF. Refuges of older vegetation are rare (Leonard et al., 2014), their habitat traits can take many years to develop (Camp et al., 1997) and their value to fauna may last for long periods after the disturbance (Gandhi et al., 2001). However, inappropriate management (Lindenmayer et al., 2011) and changes to climate (McKenzie et al., 2004) threaten their persistence in fire-prone landscapes. To a lesser degree, patches that retained intact canopy, regardless of inter-fire interval, also provided valuable habitat. Thus the potential for prescribed burns to act as refuges in a subsequent fire is supported by this study, yet with the caveat that not all recently burnt areas will necessarily retain features that enable them to act as future refuges.

Our findings have important implications for management. Firstly, we recommend the recognition and protection of long unburnt vegetation in the landscape, in particular, vegetation within positions naturally sheltered from fire such as gullies and rocky screes. This would involve locating and identifying places of high habitat value (e.g. Camp et al., 1997; Mackey et al., 2012) and adopting management practises to protect them from wildfire and planned fire or other disturbance. Naturally occurring refuges are inherently less likely to burn (Bradstock et al., 2005). However, further protection could be afforded through fuel reduction in surrounding areas (e.g. Burrows, 2008). Secondly, prescribed burning may be used as a tool to create future refuges. However, prescribed burning can only produce a particular kind of refuge, within particular vegetation types and only under certain fire conditions (Price and Bradstock, 2012).

Not all fauna require unburnt vegetation to survive post-fire (Banks et al., 2011) and some species preferentially seek out burnt habitat (Brotons et al., 2008; Hutto, 2008). However, managing for the needs of pyrophyllic species is easier than catering for the needs of more fire-sensitive faunal species (Clarke, 2008). Wherever possible, old unburnt refuges within fire-prone landscapes should be safeguarded from disturbance, as these will be beneficial to the long-term survival of fire sensitive fauna, particularly in the face of mounting anthropogenic (e.g. logging, fragmentation) and climatic pressures.

Acknowledgements

This research was conducted as part of the Faunal Refuges Project. Funding was provided by the Land and Fire Management Division of the Department of Sustainability and Environment (Vic.). A La Trobe University postgraduate research scholarship supported NMR. Research was carried out in accordance with animal welfare and conservation ethics permits granted by the Victorian government. Thanks to Michelle Bassett and Evelyn Chia for assistance with mapping, site selection and discussions concerning the project, and to Angie Haslem for statistical advice.

Appendix A

Results of tests of the differences in species richness, abundance and assemblage composition in relation to fire history, fire severity and their interaction.

	df	*F*	*P*
Species richness			
History	1, 81	0.12	0.735
Severity	4, 81	9.77	**<0.0001**
History × severity	4, 81	2.79	**0.032**
$MS_{Residual}$	19.9		
Abundance			
History	1, 81	1.08	0.302
Severity	4, 81	7.07	**<0.0001**
History × severity	4, 81	1.26	0.291
$MS_{Residual}$	10.2		
Composition		*(LR)*	
History	1, 89	108.8	0.076
Severity	4, 85	746.1	**<0.0001**
History × severity	4, 81	389.7	0.258

Appendix B

Species detected within study sites, * indicates presence in >10 sites.

Latin name (common name)
Acanthiza lineata (striated thornbill)*
Acanthiza pusilla (brown thornbill)*
Acanthiza reguloides (buff-rumped thornbill)*
Acanthorhynchus tenuirostris (eastern spinebill)*
Accipiter cirrhocephalus (collared sparrowhawk)
Accipiter fasciatus (brown goshawk)
Alisterus scapularis (Australian king-parrot)*
Anthochaera carunculata (red wattlebird)*
Aquila audax (wedge-tailed eagle)
Artamus cinereus (black-faced woodswallow)
Artamus cyanopterus (dusky woodswallow)
Cacatua galerita (sulphur-crested cockatoo)*
Callocephalon fimbriatum (gang-gang cockatoo)*
Calyptorhynchus funereus (yellow-tailed black-cockatoo)*
Chrysococcyx lucidus (shining bronze-cuckoo)*
Cinclosoma punctatum (spotted quail-thrush)
Climacteris erythrops (red-browed treecreeper)*
Climacteris leucophaea (white-throated treecreeper)*
Colluricincla harmonica (grey shrike-thrush)*
Coracina novaehollandiae (black-faced cuckoo-shrike)*
Coracina tenuirostris (cicadabird)
Corcorax melanorhamphos (white-winged chough)*
Corvus sp. (mostly *C. mellori* little raven)*
Coturnix australis (brown quail)
Cracticus torquatus (grey butcherbird)*
Cuculus pallidus (pallid cuckoo)
Cuculus pyrrhophanus (fan-tailed cuckoo)*
Cuculus variolosus (brush cuckoo)
Dacela novaeguineae (laughing kookaburra)*
Daphoenositta chrysoptera (varied sittella)*
Dicaeum hirundinaceum (mistletoebird)
Emblema temporalis (red-browed firetail)*
Eopsaltria australis (eastern yellow robin)*
Falco longipennis (Australian hobby)
Falcunculus frontatus (crested shrike-tit)
Gerygone olivacea (white-throated gerygone)
Gymnorhina tibicen (Australian magpie)*
Halcyon sancta (sacred kingfisher)*
Leucosarcia melanoleuca (wonga pigeon)
Lichenostomus chrysops (yellow-faced honeyeater)*
Lichenostomus fuscus (fuscous honeyeater)*
Lichenostomus leucotis (white-eared honeyeater)*
Lichenostomus penicilliatus (white-plumed honeyeater)
Malurus cyaneus (superb fairy-wren)*
Meliphaga lewinii (Lewin's honeyeater)*
Melithreptus brevirostris (brown-headed honeyeater)*
Melithreptus lunatus (white-naped honeyeater)*
Menura novaehollandiae (superb lyrebird)*
Microeca leucophaea (jacky winter)
Myiagra cyanoleuca (satin flycatcher)*
Myiagra inquieta (restless flycatcher)
Myiagra rubecula (leaden flycatcher)*
Oriolus sagittatus (olive-backed oriole)*
Pachycephala olivacea (olive whistler)
Pachycephala pectoralis (golden whistler)*
Pachycephala rufiventris (rufous whistler)*
Pardalotus punctatus (spotted pardalote)*

(*continued on next page*)

Appendix B (*continued*)

Latin name (common name)
Pardalotus striatus (striated pardalote)*
Petroica multicolor (scarlet robin)*
Petroica phoenicia (flame robin)*
Petroica rodinogaster (pink robin)
Petroica rosea (rose robin)*
Phaps chalcoptera (common bronzewing)
Philemon corniculatus (noisy friarbird)
Phylidonyris pyrrhoptera (crescent honeyeater)
Platycercus elegans elegans (crimson rosella)*
Platycercus eximius (eastern rosella)
Psophodes olivaceus (eastern whipbird)*
Ptilonorhynchus violaceus (satin bowerbird)
Pycnoptilus floccosus (pilotbird)
Rhipidura fuliginosa (grey fantail)*
Rhipidura rufifrons (rufous fantail)*
Sericornis frontalis (white-browed scrubwren)*
Sericornis magnirostris (large-billed scrubwren)
Strepera graculina (pied currawong)*
Strepera versicolor (grey currawong)*
Turnix varia (painted button-quail)
Zoothera dauma (bassian thrush)
Zosterops lateralis (silvereye)*

References

Agee, J.K., 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, DC.

Bain, D.W., Baker, J.R., French, K.O., Whelan, R.J., 2008. Post-fire recovery of Eastern Bristlebirds (*Dasyornis brachypterus*) is context-dependent. Wildlife Res. 35, 44–49.

Baker, J., 1997. The decline, response to fire, status and management of the Eastern Bristlebird. Pacific Conserv. Biol. 3, 235–243.

Baker, J., 2000. The Eastern Bristlebird: cover-dependent and fire-sensitive. Emu 100, 286–298.

Banks, S.C., Dujardin, M., McBurney, L., Blair, D., Barker, M., Lindenmayer, D.B., 2011. Starting points for small mammal population recovery after wildfire: recolonisation or residual populations? Oikos 120, 26–37.

Barrow, L., Parr, C.L., Kohen, J.L., 2007. Habitat type influences fire resilience of ant assemblages in the semi-arid tropics of Northern Australia. J. Arid Environ. 69, 80–95.

Bond, W.J., Keeley, J.E., 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends Ecol. Evol. 20, 387–394.

Bradstock, R.A., Bedward, M., Gill, A.M., Cohn, J.S., 2005. Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. Wildlife Res. 32, 409–423.

Brooker, M.G., Rowley, I., 1991. Impact of wildfire on the nesting behaviour of birds in heathland. Wildlife Res. 18, 249–263.

Brotons, L., Herrando, S., Pons, P., 2008. Wildfires and the expansion of threatened farmland birds: the Ortolan Bunting *Emberiza hortulana* in Mediterranean landscapes. J. Appl. Ecol. 45, 1059–1066.

Brown, S., Clarke, M.F., Clarke, R., 2009. Fire is a key element in the landscape-scale habitat requirements and global population status of a threatened bird: the Mallee Emu-wren (*Stipiturus mallee*). Biol. Conserv. 142, 432–445.

Burrows, N.D., 2008. Linking fire ecology and fire management in south-west Australian forest landscapes. For. Ecol. Manage. 255, 2394–2406.

Burrows, N.D., Wardell-Johnson, G., 2004. Implementing fire mosaics to promote biodiversity and reduce the severity of wildfires in south-west Australian ecosystems. In: 11th Annual AFAC Conference and Inaugural Bushfire CRC Conference, 7–9th October 2004, Perth, Western Australia.

Burton, P.J., Parisien, M.-A., Hicke, J.A., Hall, R.J., Freeburn, J.T., 2008. Large fires as agents of ecological diversity in the North American boreal forest. Int. J. Wildland Fire 17, 754–767.

Camp, A., Oliver, C., Hessburg, P., Everett, R., 1997. Predicting late-successional fire refugia pre-dating European settlement in the Wenatchee Mountains. For. Ecol. Manage. 95, 63–77.

Catling, P.C., 1991. Ecological effects of prescribed burning practices on the mammals of southeastern Australia. In: Lunney, D. (Ed.), Conservation of Australia's Forest Fauna. Royal Zoological Society of New South Wales, Mosman, pp. 353–363.

Cheal, D., 2010. Growth stages and tolerable fire intervals for Victoria's native vegetation data sets. Fire and Adaptive Management Report No. 84. In: Department of Sustainability and Environment, East Melbourne, Victoria.

Christidis, L., Boles, W.E., 2008. Systematics and Taxonomy of Australian Birds. CSIRO Publishing, Collingwood.

Clarke, P.J., 2002. Habitat islands in fire-prone vegetation: do landscape features influence community composition? J. Biogeogr. 29, 677–684.

Clarke, M.F., 2008. Catering for the needs of fauna in fire management: science or just wishful thinking? Wildlife Res. 35, 385–394.

DeLong, S.C., Kessler, W.B., 2000. Ecological characteristics of mature forest remnants left by wildfire. For. Ecol. Manage. 131, 93–106.

Department of Sustainability and Environment, 2003. Ecological effects of repeated low-intensity fire in a mixed eucalypt foothill forest in south-eastern Australia – summary report (1984–1999). Fire Research Report No. 57. Department of Sustainability and Environment, East Melbourne.

DSE, 2009a. kilmore-murrindindi_2009mar02_air_vis_15cm_mga55.ecw [air photo]. In: Department of Sustainability and Environment, Melbourne, Victoria.

DSE, 2009b. Remote sensing guideline for assessing landscape scale fire severity in Victoria's forest estate. Guideline – reference manual for SOP No. 4. Classification of remotely sensed imagery into fire severity maps. Department of Sustainability and Environment, Melbourne, Victoria.

Eberhart, K.E., Woodard, P.M., 1987. Distribution of residual vegetation associated with large fires in Alberta. Can. J. For. Res. 17, 1207–1212.

Fontaine, J.B., Donato, D.C., Robinson, W.D., Law, B.E., Kauffman, J.B., 2009. Bird communities following high-severity fire: response to single and repeat fires in a mixed-evergreen forest, Oregon, USA. For. Ecol. Manage. 257, 1496–1504.

Fox, J., Weisberg, S., 2011. An (R) Companion to Applied Regression. Sage, Thousand Oaks, CA.

Gandhi, K.J.K., Spence, J.R., Langor, D.W., Morgantini, L.E., 2001. Fire residuals as habitat reserves for epigaeic beetles (Coleoptera: Carabidae and Staphylinidae). Biol. Conserv. 102, 131–141.

Hasson, A.E.A., Mills, G.A., Timbal, B., Walsh, K., 2009. Assessing the impact of climate change on extreme fire weather events over southeastern Australia. Clim. Res. 39, 159–172.

Hingston, A.B., Grove, S., 2010. From clearfell coupe to old-growth forest: succession of bird assemblages in Tasmanian lowland wet eucalypt forests. For. Ecol. Manage. 259, 459–468.

Hutto, R.L., 2008. The ecological importance of severe wildfires: some like it hot. Ecol. Appl. 18, 1827–1834.

Leonard, S.W.J., Bennett, A.F., Clarke, M.F., 2014. Determinants of the occurrence of unburnt forest patches: potential biotic refuges within a large, intense wildfire. For. Ecol. Manage. 314, 85–93.

Lindenmayer, D.B., MacGregor, C., Wood, J.T., Cunningham, R.B., Crane, M., Michael, D., Montague-Drake, R., Brown, D., Fortescue, M., Dexter, N., Hudson, M., Gill, A.M., 2009. What factors influence rapid post-fire site re-occupancy? A case study of the endangered Eastern Bristlebird in eastern Australia. Int. J. Wildland Fire 18, 84–95.

Lindenmayer, D.B., Hobbs, R.J., Likens, G.E., Krebs, C.J., Banks, S.C., 2011. Newly discovered landscape traps produce regime shifts in wet forest. Proc. Natl. Acad. Sci. 108, 15887–15891.

Logan, M., 2010. Biostatistical Design and Analysis Using R: A Practical Guide. Wiley-Blackwell.

Loyn, R.H., 1998. Birds in patches of old-growth ash forest, in a matrix of younger forest. Pacific Conserv. Biol. 4, 111.

Lyon, L.J., Telfer, E.S., Schreiner, D.S., 2000. Direct effects of fire and animal responses. In: Smith, J.K. (Ed.), Wildland Fire in Ecosystems: Effects of Fire on Fauna. United States Department of Agriculture, Ogden, pp. 17–23.

Mackey, B., Lindenmayer, D.B., Gill, A.M., McCarthy, M.A., Lindesay, J., 2002. Wildfire, Fire & Future Climate: A Forest Ecosystem Analysis. CSIRO Publishing, Collingwood.

Mackey, B.G., Berry, S., Hugh, S., Ferrier, S., Harwood, T., Williams, K., 2012. Ecosystem greenspots: identifying potential drought, fire and climate change micro-refuges. Ecol. Appl. 22, 1852–1864.

McCarthy, G.J., Tolhurst, K.G., 2001. Effectiveness of broadscale fuel reduction burning in assisting with wildfire control in parks and forests in Victoria. Research Report No. 51. Department of Natural Resources and Environment.

McKenzie, D., Gedalof, Z.E., Peterson, D.L., Mote, P., 2004. Climatic change, wildfire, and conservation. Conserv. Biol. 18, 890–902.

Murphy, S.A., Legge, S.M., Heathcote, J., Mulder, E., 2010. The effects of early and late-season fires on mortality, dispersal, physiology and breeding of red-backed fairy-wrens (*Malurus melanocephalus*). Wildlife Res. 37, 145–155.

Newsome, A.E., McIlroy, J., Catling, P.C., 1975. The effects of an extensive wildfire on populations of twenty ground vertebrates in south-east Australia. Proc. Ecol. Soc. Aust. 9, 107–123.

Noble, J.C., Slatyer, R.O., 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Plant Ecol. 43, 5–21.

Pearman, P.B., Guisan, A., Broennimann, O., Randin, C.F., 2008. Niche dynamics in space and time. Trends Ecol. Evol. 23, 149–158.

Penman, T.D., Kavanagh, R.P., Binns, D.L., Melick, D.R., 2007. Patchiness of prescribed burns in dry sclerophyll eucalypt forests in south-eastern Australia. For. Ecol. Manage. 252, 24–32.

Pereoglou, F., Macgregor, C., Banks, S.C., Ford, F., Wood, J., Lindenmayer, D.B., 2011. Refuge site selection by the eastern chestnut mouse in recently burnt heath. Wildlife Res. 38, 290–298.

Pereoglou, F., Lindenmayer, D.B., MacGregor, C., Ford, F., Wood, J., Banks, S.C., 2013. Landscape genetics of an early successional specialist in a disturbance-prone environment. Mol. Ecol. 22, 1267–1281.

Price, O.F., Bradstock, R.A., 2012. The efficacy of fuel treatment in mitigating property loss during wildfires: insights from analysis of the severity of the catastrophic fires in 2009 in Victoria, Australia. J. Environ. Manage. 113, 146–157.
Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge.
Recher, H.F., Lunney, D., Matthews, A., 2009. Small mammal populations in a eucalypt forest affected by fire and drought. I. Long-term patterns in an era of climate change. Wildlife Res. 36, 143–158.
Robinson, N.M., Leonard, S.W.J., Ritchie, E.G., Bassett, M., Chia, E.K., Buckingham, S., Gibb, H., Bennett, A.F., Clarke, M.F., 2013. Refuges for fauna in fire-prone landscapes: their ecological function and importance. J. Appl. Ecol. 50, 1321–1329.
Román-Cuesta, R.M., Gracia, M., Retana, J., 2009. Factors influencing the formation of unburned forest islands within the perimeter of a large forest fire. For. Ecol. Manage. 258, 71–80.
Sanz-Aguilar, A., Anadón, J.D., Giménez, A., Ballestar, R., Graciá, E., Oro, D., 2011. Coexisting with fire: the case of the terrestrial tortoise *Testudo graeca* in mediterranean shrublands. Biol. Conserv. 144, 1040–1049.
Schieck, J., Hobson, K.A., 2000. Bird communities associated with live residual tree patches within cut blocks and burned habitat in mixedwood boreal forests. Can. J. For. Res. 30, 1281–1295.
Schoennagel, T., Smithwick, E.A.H., Turner, M.G., 2008. Landscape heterogeneity following large fires: insights from Yellowstone National Park, USA. Int. J. Wildland Fire 17, 742–753.
Seip, D.R., Parker, K., 1997. Use of Wildlife Tree Patches by Forest Birds in the Sub-boreal Spruce (SBS) Zone. Forest Resources & Practices Team, Prince George, BC.
Silveira, L., De Almeida Jácomo, A.T., Diniz Filho, J.A.F., Rodrigues, F.H.G., 1999. Impact of wildfires on the megafauna of Emas National Park, central Brazil. Oryx 33, 108–114.
Spencer, R.-J., Baxter, G.S., 2006. Effects of fire on the structure and composition of open eucalypt forests. Austral Ecol. 31, 638–646.
Stuart-Smith, K., Adams, I.T., Larsen, K.W., 2002. Songbird communities in a pyrogenic habitat mosaic. Int. J. Wildland Fire 11, 75–84.
Swengel, A.B., Swengel, S.R., 2007. Benefit of permanent non-fire refugia for Lepidoptera conservation in fire-managed sites. J. Insect Conserv. 11, 263–279.
Teague, B., McLeod, R., Pascoe, S., 2010. 2009 Victorian Bushfires Royal Commission: Final Report. Parliament of Victoria, Melbourne.
Turner, M.G., Baker, W.L., Peterson, C.J., Peet, R.K., 1998. Factors Influencing succession: lessons from large, infrequent natural disturbances. Ecosystems 1, 511–523.
Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S. Springer, New York.
Wang, Y., Naumann, U., Wright, S.T., Warton, D.I., 2012. Mvabund – an R package for model-based analysis of multivariate abundance data. Methods Ecol. Evol. 3, 471–474.
Watson, S.J., Taylor, R.S., Nimmo, D.G., Kelly, L.T., Clarke, M.F., Bennett, A.F., 2012. The influence of unburnt patches and distance from refuges on post-fire bird communities. Anim. Conserv. 15, 499–507.
Whelan, R.J., Rodgerson, L., Dickman, C.R., Sutherland, E.F., 2002. Critical life cycles of plants and animals: developing a process-based understanding of population changes in fire-prone landscapes. In: Bradstock, R.A., Williams, J., Gill, A.M. (Eds.), Flammable Australia: the Fire Regimes and Biodiversity of a Continent. Cambridge University Press, Cambridge, pp. 94–124.