

Interactions between the superb lyrebird (*Menura novaehollandiae*) and fire in south-eastern Australia

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Abstract

Context. The superb lyrebird *Menura novaehollandiae* is thought to be an important ecosystem engineer that, through its foraging, accelerates the decomposition of litter in *Eucalyptus* forests. Lyrebird foraging is therefore likely to affect forest fuel loads and hence fire behaviour in these fire-prone forests. In turn, fire is likely to reduce the abundance and influence the distribution of lyrebirds.

Aims. Our goal was to determine the impacts of a major bushfire on the habitat and food sources for the superb lyrebird and the effects of foraging activities of lyrebirds on litter fuel and potential fire behaviour in gullies of herb-rich foothill forests.

Methods. The effect of fire on lyrebirds and their habitat in the post-fire environment was examined at the landscape-scale, 2 years after fire; and at the patch-scale, 3 years after fire. Paired exclusion and control plots were also used over a 9-month period to assess the effects of foraging by the lyrebird on litter accumulation and fuel connectivity. Fire-behaviour models were used to determine the potential influence of lyrebird scratchings on fire behaviour.

Key results. At the landscape scale, lyrebirds were present in both unburnt and ground-burnt sites, but not in canopy-burnt sites. Within patchily burnt sites, lyrebirds favoured foraging in unburnt patches. On average, lyrebird foraging reduced litter fuel loads by 25% (1.66 t ha⁻¹) in plots in which they were free to forage, compared with plots from which they were excluded, over a 9-month period. Fire-behaviour modelling showed that lyrebird foraging led to a lower likelihood of fire occurring and less intense fire.

Conclusions. Distinctly different vegetation structure and composition between burnt and unburnt patches appears to influence both the foraging patterns and distribution of lyrebirds. Additionally, foraging by lyrebirds reduces surface fuel loads and fuel connectivity such that fire spread is likely to be inhibited.

Implications. We propose that alternative stable states may emerge in *Eucalyptus* forests as a result of feedback mechanisms among lyrebirds, vegetation and fuel accumulation. Therefore, the ecological role of lyrebirds is an important consideration in forest fuel management and conservation in these extensive, fire-prone forests in south-eastern Australia.

Additional keywords: alternative stable states, disturbance ecology, fire, forest fuels, lyrebird.

Received 26 August 2013, accepted 20 July 2014, published online 11 September 2014

Introduction

Fire is an important disturbance in many ecosystems, and its influence on the distribution of organisms and communities across scales from the global (Bond and Keeley 2005) to the local (Soulé *et al.* 2004) is well documented. However, variation in flammability among vegetation types and the activities of animals can affect fire behaviour and fire regimes (Gill 1981; Leonard *et al.* 2010). Where these fire-biotic interactions occur, synergies and feedbacks may emerge, producing outcomes that would not be predicted by considering the effects of the factors in isolation (Kirkpatrick *et al.* 2011).

Herbivory is the best documented faunal activity interacting with fire (Van Langevelde *et al.* 2003) and it is argued that, in some systems, these disturbances are so tightly inter-related that they should be regarded as a single disturbance process

(Fuhlendorf *et al.* 2009). Herbivores can reduce the likelihood of fire through the consumption of potential fuel (Nader *et al.* 2007), while selective herbivory may increase vegetation flammability (Leonard *et al.* 2010). Animal activities other than herbivory that affect the quantity, distribution or flammability of vegetation would also be expected to affect fire behaviour and regimes. However, these remain largely unstudied, apart from a few examples. Bioperturbation by leaf cutter ants has been observed to inhibit spread of low-intensity fires (Carvalho *et al.* 2012). Male great bower birds (*Chlamydera nuchalis*) remove litter from around their bowers, reducing the likelihood that they will burn (Mikami *et al.* 2010).

Animal species that influence the occurrence of fire may be regarded as ecosystem engineers, in that they (indirectly) alter the availability of resources for themselves and other species

(Lawton 1994). In environments subject to periodic, large intense fires (Archibald *et al.* 2013), resources associated with areas that escape burning or experience low-intensity fire are likely to be limiting, at least for some time post-fire (Robinson *et al.* 2013). Therefore, animal activities that promote the occurrence of these areas may have profound importance.

The *Eucalyptus*-dominated forests of south-eastern Australia are one of the most-fire prone environments globally, owing to rapid accumulation of highly flammable fuel (Gill and Catling 2002; Bradstock 2008). The dynamics of surface fuel available for consumption by fire are related to the balance between the accumulation and the breakdown of litter (Walker 1981). In addition to the amount of fuel present, the horizontal and vertical connectivity of fuels is also important in influencing fire behaviour (O'Donnell *et al.* 2011).

The superb lyrebird (*Menura novaehollandiae*) occurs commonly in *Eucalyptus* forests within a natural range extending from southernmost Queensland to south-central Victoria (Sibley 1974). Lyrebirds forage for invertebrates by raking through litter with their powerful legs and large feet. This activity is known to have a major impact on litter dynamics in *Eucalyptus* forests and has been recorded as moving up to 200 t ha⁻¹ of litter and top soil every year (Ashton and Bassett 1997). The burial of fresh leaf litter by lyrebirds accelerates its decomposition and disintegration, as material is less likely to dry out and is brought into close contact with soil microorganisms and invertebrates (Ashton and Bassett 1997). During the warmer months, when wildfires are most likely (Gill and Catling 2002), foraging is intense within and along the margins of gullies (Robinson and Frith 1981), possibly reducing the accumulation of surface fuels and disrupting fuel connectivity. This creates the potential for lyrebirds to reduce surface fuel loads, which may have the effect of inhibiting or suppressing the movement of fire.

This study examined the interaction between lyrebird foraging activities and fire in *Eucalyptus* forests, north-east of Melbourne, Victoria. The study was carried out in 2011–12 within the area affected by the Kilmore East–Murrindindi fires, which occurred north-east of Melbourne, Victoria (37°49'S, 145°41'E) in February 2009 (Teague *et al.* 2010). In particular, we examined (1) how fire severity can influence lyrebird distribution at the landscape-scale, (2) how fire affects lyrebird foraging areas and food availability at the patch-scale, (3) the effects of lyrebird foraging on surface fuel loads and (4) how lyrebird foraging activity could affect fire behaviour.

Materials and methods

Study area

The study region experiences a temperate climate, with warm–hot summers and cool winters. Mean annual rainfall for the region is ~1059 mm (Bureau of Meteorology 2012). The catastrophic wildfires that occurred on 7 February 2009 in south-eastern Australia burned over 450 000 ha and resulted in 173 human fatalities (Cruz *et al.* 2012). The Kilmore East–Murrindindi fire was the most significant of these fires, extending over 250 000 ha, creating a mosaic of burn severities (Cruz *et al.* 2012; Leonard *et al.* 2014). The major vegetation types within these forests are dry open slopes interspersed with damp gullies. Dry slopes

typically support plant species and fuel components that have a high tendency to propagate fire whereas species from gully habitats are often less flammable (Dickinson and Kirkpatrick 1985). *Eucalyptus dives*, *E. obliqua*, *E. radiata*, and/or *E. globulus* are dominant canopy species. Gully understoreys are mostly dominated by mesic shrub species such as *Olearia argophylla*, *Coprosma quadrifida* and ferns (e.g. *Cyathea australis*, *Dicksonia antarctica*). The understorey on slopes is mostly dominated by a dense layer of *Pteridium esculentum*, with a sparse or absent shrub layer.

Experimental design and methods

Lyrebird distribution in a post-fire landscape

To determine the effects of fire on lyrebird distribution 2 years after fire at the landscape scale, 73 sites were selected across the Kilmore East–Murrindindi fire complex that represented one of three classes of fire severity. These classes included the following: 'canopy burnt' ($n = 12$), where intense fire burnt the crown of trees as well as the understorey and ground layers; 'ground burnt' ($n = 28$), where fire burnt near-surface elevated vegetation and surface fuels but left the canopy intact; 'unburnt' ($n = 33$), all strata of vegetation remained unburnt following the fire. All sites consisted of at least 5 ha of consistent fire severity, were at least 1 km apart and consisted of a gully and adjacent slope. At each site, a 50-m transect was placed within the gully. At 1-m intervals along the transect, a structure pole (200 cm long, 3 cm diameter) held vertically was used to assess vegetation cover and the presence of lyrebird scratchings. Plant life-forms (forbs, grasses, ferns, shrubs, regenerating eucalypts, trees) touching the pole were recorded in three height strata (0–0.5 m, 0.51–1 m, 1.01–2 m above the ground). Vegetation cover was assessed on an overlapping basis, so the sum at a given point could exceed 100%. Sites were recorded as having scratching present if a fresh lyrebird scratching was intercepted at any survey point along the transect by the structure pole. These scratchings typically consisted of several square metres of freshly disturbed litter and topsoil and were distinct from diggings by any other animals within the study area. Scratchings lose their freshly disturbed appearance rapidly because of litter fall and the effects of rain, and therefore we could be confident that recent scratchings were indicative of lyrebird presence within, at most, days before observations being made. The association of lyrebird scratching with fire-severity classes was examined using a Chi-squared test. The response variable was the presence or absence of lyrebird scratching at each site. Differences in the cover of vegetation strata between fire-severity classes were examined using MANOVA, followed by univariate ANOVA to test for differences in individual vegetation strata.

Distribution of lyrebird foraging within partially burnt sites

To examine the relationship of lyrebird foraging to prior fire, 10 sites were selected that contained both burnt and unburnt patches within a single gully. Lyrebirds were known to be present at all 10 sites. Sites were at least 1 km apart. Using a GIS overlay, five points were located within a burnt patch, and a further five in an unburnt patch within each site. Burnt and unburnt patches were no more than 100 m apart, and points within patches were at least

50 m apart. At each point, the ground within a 5-m radius was categorised as being scratched or not scratched by a lyrebird. In addition to scratchings, the dominant plant species and the percentage cover of vegetation strata at 0–0.1 m, 0.11–0.5 m, 0.51–1 m, 1.01–2 m, and >2 m were visually estimated within a 5-m radius at each point.

The strength of association between lyrebird scratchings and patch burnt/unburnt status within sites was analysed using generalised estimating equations (GEEs). GEEs are an extension of generalised linear models that account for correlation between observations (Quinn and Keough 2002). The response variable in this model was the presence or absence of scratching at each point. Patch burn status was fitted as a categorical predictor and vegetation cover as a continuous predictor. Prior to the selection of vegetation cover as a covariate, GEEs were used to determine whether percentage vegetation cover was co-linear with patch burn status. In this model, a linear regression was used and vegetation cover of individual vegetation stratum was selected as the response variable and patch burn status as the predictor variable. All vegetation strata were found to be co-linear with fire history and were therefore not included in models as covariates. Differences in vegetation strata between burnt and unburnt patches were analysed using MANOVA.

Lyrebird food availability in post-fire patches

The importance of unburnt gullies as sources of food for lyrebirds was assessed at five sites containing patches of both burnt and unburnt gully vegetation. Burnt and unburnt patches were ~100 m apart. Within each site, five subsamples of leaf litter and soil were collected along a 50-m transect at 10-m intervals in burnt gully vegetation, and a further five samples were collected along a transect in unburnt gully vegetation. Each subsample was collected using an 11-cm-diameter cylinder pipe, which was gently inserted into the ground 5 cm deep, thus removing a core of litter and soil. Subsamples were combined into separate sealed bags for burnt and unburnt patches, respectively, at each site.

The leaf litter/soil samples were placed in Tullgren funnels for 72 h for extraction of invertebrates, within 12–15 h after collection. To ensure that all macro-invertebrates were collected, each sample was visually searched for 15 min after Tullgren extraction. The extracted invertebrates were sorted under a binocular microscope. Invertebrates were classified to class (Arachnida, Gastropoda, Chilopoda, Diplopoda), subclass (Oligochaeta, Collembola) or order (Coleoptera, Diptera, Hemiptera, Hymenoptera, Isoptera, Lepidoptera). Dry mass (biomass) values were obtained for each invertebrate sample after oven-drying at 70°C for 72 h. Differences in invertebrate abundances and biomass between burnt and unburnt samples were examined using paired Student's *t*-tests.

The effect of excluding lyrebirds on litter accumulation

In June 2011, paired 1 × 1 m quadrats were set up in unburnt gully vegetation at 18 sites, to determine the effects of lyrebird activity on litter accumulation. Paired quadrats were placed ~5 m apart at a location deemed typical of the site in terms of litter depth, vegetation and lyrebird activity. One quadrat within each pair was randomly assigned to be enclosed within a 2 × 2 × 1.5 m chicken-wire fence, which excluded lyrebirds, with the other

member of the pair left open to lyrebird foraging. Measurements taken before erection of exclusion fences revealed no significant difference in average litter depth (paired Student's *t*-test, $t=1.3$, d.f.=17, $P=0.222$) or mean cover of bare ground (paired Student's *t*-test, $t=0.8$, d.f.=17, $P=0.440$) between treatments. Quadrats were marked with steel nails at each corner.

At the beginning of the experiment, litter depth (cm) was measured at five random points within each quadrat and the average depth per quadrat was calculated. The number and average height (cm) of seedlings of understorey species and ground ferns (*Pteridium esculentum*, *Calochlaena dubia*) were recorded within each quadrat. The percentage area of bare ground was also recorded. After approximately 9 months (June 2011 – February 2012), all measurements were repeated within each quadrat. Additionally, all leaf litter and twigs (woody material less than 15 mm in diameter) were collected from each quadrat. Samples were oven-dried at 70°C for 24 h and weighed. MANOVA were used to determine differences in litter mass, litter depth, bare ground cover and the change in the number and height of seedlings and ground ferns (final value – initial value) between fenced and unfenced quadrats.

Fire-behaviour modelling

To assess how changes in surface fuel load as a result of lyrebird foraging might affect fire behaviour, the litter mass values from the 18 paired quadrats were used as fuel-load inputs for the McArthur Mk5 Forest Fire Behaviour model (Noble *et al.* 1980). Differing values for air temperature, relative humidity and wind speed were entered into the model to represent extreme, high, and low to moderate fire danger days (Appendix 1). Slope was held constant at 0 degrees. The modelled fire-behaviour variables were all highly correlated ($r > 0.9$), both within and across fire-danger categories. Therefore, we chose flame height as representative of fire behaviour. Flame height is related to both fire intensity (i.e. energy output; Byram 1959) and fire severity (i.e. impact on vegetation; Alexander and Cruz 2012). Differences in flame height in the presence/absence of lyrebirds were examined using paired Student's *t*-tests.

All statistical analyses were carried out using SPSS 18 (SPSS Statistics 2009), except for MANOVA, which was performed using R 2.15 (R Core Development Team 2013).

Results

Lyrebird distribution in a post-fire landscape

No lyrebird scratchings were recorded in any of the 12 canopy-burnt sites; whereas 8 of the 28 ground-burnt sites and 12 of the 33 unburnt sites showed evidence of lyrebird scratching (Pearson $\chi^2 = 5.9$, d.f. = 2, $P = 0.053$).

Vegetation structure varied among fire-severity classes (MANOVA results: Pillai trace = 0.55, d.f. = 2, $F = 8.78$, $P < 0.001$). Vegetation cover in canopy-burnt sites was higher than in ground-burnt and unburnt sites in the 0.5–1 m and 1–2 m strata and higher than in unburnt sites in the 0–0.5 m stratum (Table 1).

Lyrebird foraging and food availability in post-fire patches

Lyrebirds were significantly more likely to forage in unburnt than in burnt patches within patchily burnt gullies (generalised

estimating equation: $\beta = 2.60 \pm \text{s.e. } 0.60$, Wald $\chi^2 = 25.60$, $P < 0.001$). Lyrebird scratchings were observed at 92% of points within unburnt patches, compared with 38% of points within burnt patches. However, no significant differences were found in mean litter invertebrate biomass (mean \pm s.e.; burnt = 0.061 ± 0.023 g, unburnt = 0.080 ± 0.054 g; $P = 0.246$) or abundance (burnt = 49.80 ± 23.33 , mean unburnt = 51.40 ± 39.12 ; $P = 0.943$) between burnt and unburnt patches. Oligochaete worms were the most abundant invertebrate found in unburnt patches, whereas dipteran fly larvae and oligochaete worms were the most abundant in burnt patches.

Vegetation structure within gullies differed considerably between burnt and unburnt forest patches (MANOVA results: Pillai trace = 0.87, d.f. = 1, $F = 18.41$, $P < 0.001$). Burnt gully patches had substantially higher cover than did unburnt patches in strata up to 2 m in height, whereas the reverse occurred for the >2 m stratum (Table 2). In burnt areas, *Pteridium esculentum* and *Goodenia ovata* were the dominant species between 0.11 and 0.5 m, whereas *Pomaderris aspera* and *Bedfordia arborescens* formed dense stands between 0.51 and 2 m tall. In unburnt forest patches, vegetation cover was relatively sparse between 0 and 2 m, representing a more open forest floor.

Litter accumulation and lyrebird exclusion

After 9 months, litter mass was significantly greater within the fenced than unfenced quadrats (Table 3). Litter was deeper in fenced than in unfenced quadrats, although this difference was marginally non-significant (Table 3). Additionally, mean percentage cover of bare ground of unfenced quadrats was almost nine times greater than for fenced quadrats (Table 3).

On average, plots in which lyrebirds were free to forage contained 1.66 t ha^{-1} less litter, than did plots in which they were excluded from foraging. The greatest difference in litter mass between paired quadrats within a site was 7.58 t ha^{-1} .

Table 1. Results of univariate ANOVA (d.f.=2) tests of differences in vegetation cover among fire-severity classes

Values in severity columns = percentage cover of vegetation strata (mean \pm s.e.). Values followed by the same letter are not significantly different at $P = 0.05$, as indicated by Tukey's *post hoc* comparisons

Vegetation stratum (m)	F	P	Canopy burnt (n=12)	Ground burnt (n=28)	Unburnt (n=33)
0-0.5	3.24	0.04	153.8 \pm 38.8a	115.9 \pm 66.4ab	105.7 \pm 51.9b
0.51-1.0	25.00	<0.001	100.9 \pm 20.6a	42.7 \pm 23.4b	44.7 \pm 28.8b
1.01-2	25.07	<0.001	70.3 \pm 43.7a	14.7 \pm 12.0b	27.5 \pm 19.2b

Table 2. Mean (\pm s.e.) and results of univariate ANOVA for percentage cover of vegetation strata between unburnt (n=50) and burnt (n=50) patches within gullies

Vegetation stratum (m)	Unburnt	Burnt	F	P
0-0.10	11.50 \pm 0.77	34.80 \pm 3.24	17.36	<0.001
0.11-0.50	24.20 \pm 1.64	60.30 \pm 2.75	64.10	<0.001
0.51-1.0	29.20 \pm 2.13	59.70 \pm 2.87	35.12	<0.001
1.01-2	33.80 \pm 2.31	47.80 \pm 3.30	4.97	0.04
>2	60.80 \pm 3.16	19.50 \pm 2.75	31.28	<0.001

There was no overall significant difference in seedling and ground fern variables between fenced and unfenced quadrats (MANOVA results: Pillai trace = 0.09, d.f. = 4, $F = 0.74$, $P = 0.57$). However, there was a trend for seedlings and ground ferns to show a larger height change in lyrebird-excluded quadrats than in quadrats open to lyrebird foraging (Appendix 2).

Fire-behaviour model

Comparison of McArthur fire model outputs indicated that flame height was predicted to be reduced in quadrats exposed to lyrebird foraging under extreme and high fire weather scenarios (Table 4). On days of low to moderate fire-danger risk, flame height was zero (or effectively so) regardless of lyrebird presence.

Discussion

The absence of lyrebird scratchings from canopy-burnt sites suggests that this environment is unsuitable for lyrebirds 2 years after the fire or that they have failed to recolonise such sites following eradication by the fire. This result appears to be at least partly due to the effect of extremely dense regenerating vegetation constraining lyrebird foraging, as has been postulated in other studies (Adamson et al. 1983). However, lyrebird mortality is likely to have been higher in areas subjected to a canopy burn, because escape is difficult from fast-moving, intense fire fronts (Recher et al. 1975; Gill and Catling 2002). It would be expected that birds with limited flying abilities, such as the lyrebird, would experience higher mortality rates than birds with stronger flying abilities during intense fires. The amount of scratching observed in ground burnt and unburnt sites did not differ greatly, which suggested that a less severe fire did not have the same impact as canopy fires on lyrebird habitat or survival. High-intensity fires can often have much longer-term impacts on avifaunal recovery than patchy, low-intensity fires (Loyn 1985).

Many bird species change their behavioural patterns following habitat changes in the post-fire environment (Woinarski and Recher 1997). Surveys of lyrebird scratchings in burnt and unburnt patches indicated that lyrebirds strongly favoured

Table 3. Mean (\pm s.e.) and results of univariate ANOVA for litter variables and bare ground in fenced and unfenced quadrats

	Fenced	Unfenced	F	P
Litter depth (cm)	7.53 \pm 1.27	4.62 \pm 0.75	3.89	0.06
Litter mass (t ha^{-1})	6.59 \pm 0.67	4.94 \pm 0.39	4.47	0.04
Bare ground (%)	1.36 \pm 0.47	11.34 \pm 2.69	13.33	<0.001

Table 4. Mean (\pm s.d.) of fire behaviour parameters as derived from McArthur Mk5 Forest Fire Behaviour model (Noble et al. 1980) and results of paired Student's *t*-tests using litter fuel loads recorded in the presence (LP) and absence (LA) of lyrebirds
FFDI = forest fire danger index; d.f. = 17

FFDI	Flame height (m)		t	P
	LP	LA		
Extreme (91.9)	6.3 \pm 2.8	9.0 \pm 4.8	-2.84	0.01
High (18)	0.72 \pm 0.6	1.5 \pm 1.5	-2.81	0.01
Low to moderate (3.9)	0 \pm 0.1	0.3 \pm 0.6	-0.8	0.43

foraging in unburnt forest. This pattern may be the result of loss of food sources (Sutherland and Dickman 1999) and/or shifts in vegetation structure and composition with burning.

The consumption of some or all leaf litter by fire can reduce litter fauna populations (Springett 1979) that form the bulk of the lyrebird diet (Robinson and Frith 1981). Within fire-affected sites, there was no difference in litter invertebrate biomass and abundance between burnt and unburnt patches 3 years after fire. Fire can have long-term impacts on litter-dwelling invertebrates because the amount of litter is reduced and habitat structure is lost (York 1999). However, because invertebrates can seek shelter within the soil and unburnt refuges, populations can recover effectively after a single fire event within 3 years (Abbott 1984; Neumann and Tolhurst 1991). The findings of the current study are consistent with these observations.

If food availability is not driving lyrebird foraging preference for unburnt patches, vegetation structure may be an influencing factor. Burnt patches in the present study showed thick vegetation regeneration of species such as *Pteridium esculentum*, *Pomaderris aspera* and *Bedfordia arborescens*, which had formed a dense layer between 0 and 2 m. A well developed tall shrub understorey, greater than 2 m high, was often absent in burnt patches. Conversely, unburnt patches supported an intact tall shrub-understorey and sparse-ground vegetation layers. Unburnt patches in these fire-affected areas may provide important areas of open forest floor on which lyrebirds can forage. If several lyrebirds were to survive a fire event or were to quickly recolonise the site, they could potentially maintain suitable small burnt areas for foraging by uprooting fire-stimulated seedlings and preventing their establishment. Little is known about the behavioural responses of lyrebirds to fire. Adamson *et al.* (1983) suggested that resources available to lyrebirds in forests of the Sydney Basin area are likely to be depleted in the post-fire environment. Lyrebirds have been observed foraging in ash shortly after fire (Loyn *et al.* 1992), so they could be contributing to the maintenance of foraging areas soon after the fire event.

The foraging behaviour of the lyrebird can cause extensive disturbance throughout its habitat (Adamson *et al.* 1983). We found that lyrebirds markedly reduced litter depth and mass by excavating litter and soil as they foraged, which probably accelerated breakdown of organic matter, as postulated by Ashton and Bassett (1997). This can occur over extensive areas. Within our unburnt gully sites, fuel-litter reduction as a result of lyrebird foraging was evident over most of the forest floor, with one site being virtually devoid of litter over an area of several hectares. It has been estimated that lyrebirds can turn over the whole forest floor in a 2-year period (Ashton 1975; Ashton and Bassett 1997).

The effects of lyrebirds on forest litter levels translate into a reduction in potential fuel. The decomposition rate of surface fuels is influenced by factors including climate, substrate quality and soil organisms (Ashton 1975; González and Seastedt 2001), but is accelerated by lyrebird scratchings (Ashton and Bassett 1997). The continual disturbance of the litter layer by lyrebirds in *Eucalyptus* forests (Ashton 1975) may be reducing surface fuel loads over large areas. The absence of lyrebirds could result in a faster build-up of litter material and greater surface fuel availability for potential fires.

In addition to effects of lyrebird foraging on surface fuel accumulation, scratchings may reduce the connectivity of fuels. Lyrebird scratchings increased the extent of bare-ground patches on the forest floor, which is likely to disrupt connectivity of the surface fuel layer. Horizontal fuel continuity is necessary to allow a fire to spread laterally (Gould *et al.* 2007) and anthropogenic fuel treatments such as fire breaks interrupt surface fuel continuity to suppress and mitigate fire (Agee *et al.* 2000; Mooney 2010). The bare ground created by lyrebird foraging provides litter-free niches for the establishment of seedlings and ferns (Ashton and Bassett 1997). However, frequent disturbance by lyrebirds can also prevent the establishment of some germinating plant species (Howard 1973). Although we found that the presence or absence of lyrebird activity did not change the number of seedlings or ground ferns significantly, we observed a trend for seedlings present on scratched sites to be shorter than those free of lyrebird disturbance. Uprooted plants were frequently found in lyrebird scratchings (Appendix 3).

These results suggest that although lyrebird foraging may promote seed germination, frequent disturbance prevents plants from establishing and growing. This is consistent with the conclusion of Ashton and Bassett (1997) that lyrebirds can maintain open foraging areas through their own activity. Importantly, these areas are likely to be reduced in ferns, grasses and shrubs that commonly support the near-surface and elevated fuel layers of the fuel complex (Gould *et al.* 2007). These layers provide vertical fuel continuity, and contribute to the fire rate of spread and flame height (Whelan and York 1998; Gould *et al.* 2007). Lyrebird foraging areas may therefore suppress the horizontal and vertical spread of fire, limiting the extent and severity of fire events.

Our modelling suggests that the reduction in litter fuel loads brought about by lyrebird foraging has the potential to result in markedly subdued fire behaviour relative to that predicted in the absence of lyrebirds. While we measured the effects of lyrebird foraging on fuel loads only over a small area, litter levels within the scratched quadrats appeared typical of those in the surrounding area. As mentioned above, litter fuel-load reduction by lyrebirds was observed to be extensive and marked within unburnt gully sites. Therefore, lyrebird foraging may produce at least a localised (i.e. patch scale) reduction in fire severity. Previous studies have found that a range of different animal activities can reduce fuel loads and inhibit the spread of low-intensity fire (McNaughton 1992; Carvalho *et al.* 2012). In the tropical savannas of northern Australia, the great bowerbird (*Chlamydera nuchalis*) establishes an area of little fuel, a 'firebreak', around its bowers (Mikami *et al.* 2010). Other animals that reduce or disturb leaf-litter structure, such as malleefowl (*Leipoa ocellata*) and burrowing bettongs (*Bettongia lesueur*) in arid zones of Australia, could have similar effects on the fuel complex. Results of the current study suggest that lyrebird foraging could produce similar patches of reduced fuel that influence the extent and severity of fire.

The interactions among lyrebird foraging, vegetation structure and fire can be characterised in terms of a feedback system. Positive feedback systems are critical in maintaining stable community structure and preventing state shifts (Stone and Berman 1993). We have identified two positive feedback

loops that may occur following fire as a disturbance, and potential for the lyrebird to contribute to the maintenance of stable states (Fig. 1). Within this model, the effects of a high-severity fire and a low-severity fire or no fire scenario are represented. Following high-severity fire, lyrebird numbers may be severely reduced as a direct result of being killed by the fire. Less invertebrate food (Springett 1979; York 1999) and loss of foraging areas as a result of thick vegetation regrowth (Gill 1981) in the post-fire environment would likely lead to further declines in lyrebird numbers. The absence of lyrebirds allows the build-up of high fuel loads, which in turn increases the likelihood of high-severity fire in the future (Bradstock 2008). Consequently, this state would remain lyrebird-free and the positive feedback loop continues.

In the alternative state, lyrebirds persist in unburnt or patchily burnt areas. Litter invertebrates can persist in unburnt patches and micro-refuges (Neumann and Tolhurst 1991), thereby supplying lyrebirds with a food source in the post-fire environment. Low-intensity fires do not trigger the same dramatic seedling succession as do canopy-burn fires (Gill 1981), so lyrebirds can continue to forage on the forest floor and disturb the litter layer by their scratching. The continual disturbance of the forest floor may

create a positive feedback loop that reduces fuel loads and disrupts fuel connectivity, thus limiting the extent and severity of the fire and increasing the likelihood of an area remaining unburnt in the future. Lyrebirds are in effect maintaining a suitable habitat for themselves through their own activity.

It is important to predict and identify alternative states because shifts can represent catastrophic changes in communities (Scheffer *et al.* 2001). In this model, fire severity is driving state shifts from lyrebird-suitable habitat to unsuitable habitat. Another possible driver of state shifts is the loss of lyrebirds from the ecosystem through predation. Introduced foxes (*Vulpes vulpes*) and cats (*Felis catus*) pose significant threats to lyrebird populations, in particular along the urban boundary (Lill 1980). Uncontrolled feral-predator numbers could remove the lyrebird from the system, and therefore contribute to a state change. Lyrebird populations subjected to an environment of increased predation rates and high-severity fire would likely be severely reduced or lost. The loss of lyrebirds from forests adjacent and within urban areas could result in higher fuel loads and an increased likelihood of wildfires threatening human life.

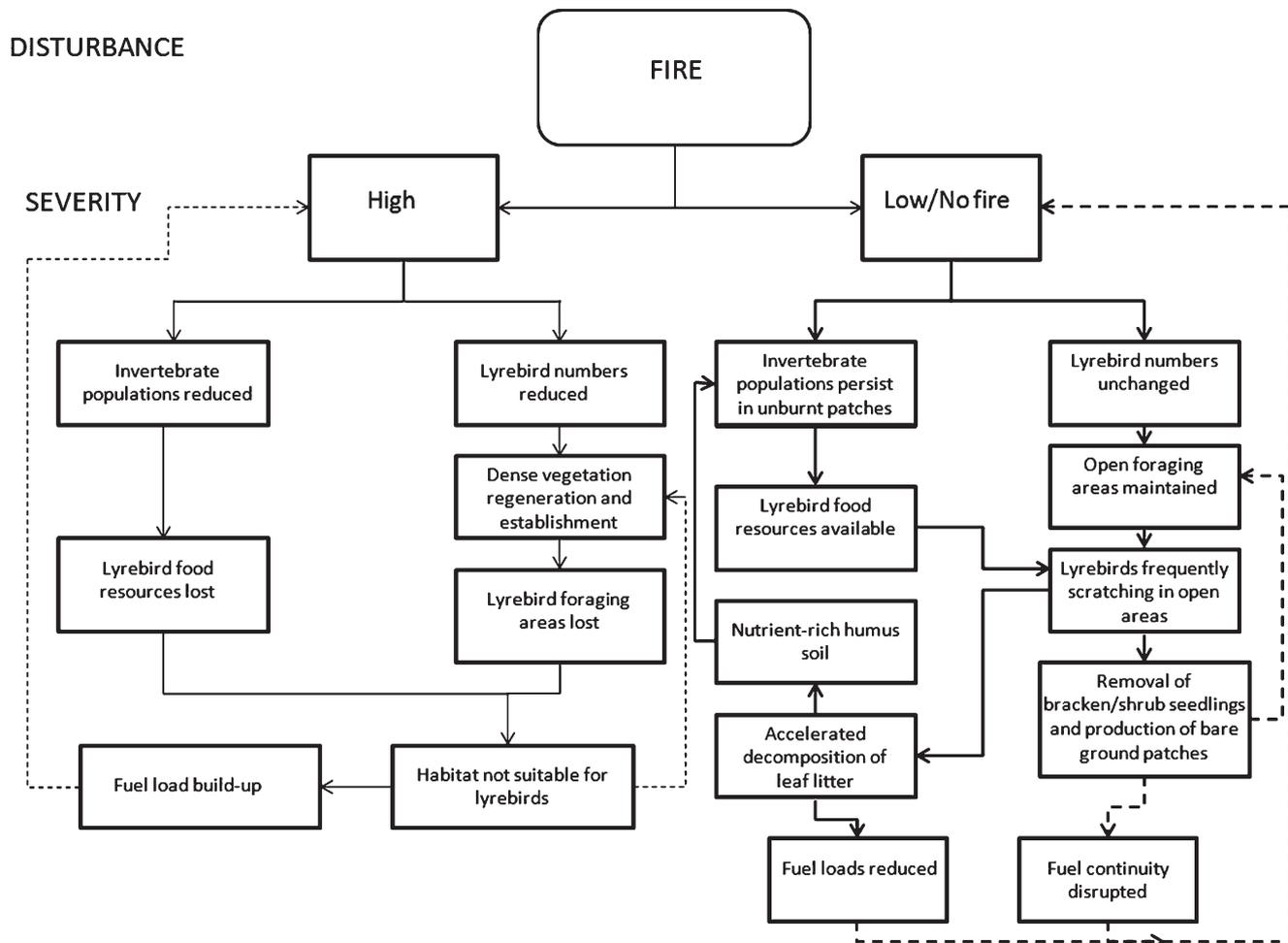


Fig. 1. Conceptual model representing the possible feedback loops arising because of interaction of fire and lyrebird disturbance. Thick solid lines indicate known ecological links that may support the persistence of lyrebirds. Thin solid lines indicate known ecological links that may negatively affect lyrebirds. Dash type lines indicate links in need of further support.

The current study investigated the effects of fire on lyrebird distribution and habitat only 2–3 years after fire. It has been speculated that lyrebirds have a preference for young (≤ 50 years old) even-aged eucalypt forests because they are almost devoid of ground vegetation (Ashton and Bassett 1997). Conversely, mature-age forests at Wallaby Creek, Victoria, were identified as having decreased tree density and dense ground-fern covers (Ashton 1976), and so were thought not to represent favourable lyrebird habitat (Ashton and Bassett 1997). Findings from the current study suggest that recently burnt eucalypt forests also do not provide ideal lyrebird habitat. On an ecological time scale, these studies imply that eucalypt forests aged between ~20 and 80 years provide the most ideal conditions for lyrebird populations to flourish. Further studies comparing large numbers of sites of differing ages post-fire could test this hypothesis.

The present study has provided evidence that the foraging effects of the lyrebird can decrease fuel availability and disrupt fuel connectivity, thus reducing fire potential within biodiversity-rich gullies. Gullies often remain unburnt following fire because of microclimatic effects on fuel moisture (Leonard *et al.* 2014) and form important fire refuges for biota (Collins *et al.* 2012). However, lyrebird disturbance may also be a contributing factor in the increased likelihood of gullies remaining unburnt. Lyrebirds may therefore perform an important ecological role by assisting in the creation of fire refuges (Robinson *et al.* 2013). Fire refuges are likely to become increasingly important in the future because climate predictions suggest that Australia will experience an increase in the frequency of large severe wildfires (Bradstock 2008). This may have significant impacts on forest communities as they could be pushed into lyrebird-free, highly flammable states.

Increased levels of planned burning by fire management agencies aimed at reducing the risk of wildfires may pose a threat to lyrebird populations. It may be important for management agencies to modify their approach to planned burns in areas where lyrebirds are present. Planned burns in these areas should aim for a low-intensity fire that does not enter fire-sensitive gullies and does not trigger large-scale, dense seedling germination that would negatively affect lyrebird numbers. Effective management to remove and minimise threats to lyrebird populations, including predation from introduced species and large intense fire, may be pivotal for the preservation of this species and its habitat in the future.

Acknowledgements

The authors thank George Kanjere and Jack Nugent for outstanding assistance in the field, and Angie Haslem for statistical assistance. Further thanks to Jon Gwilt and Parks Victoria Kinglake office staff for providing access to sites. This project was a part of the collaborative Faunal Refuges project between Deakin University and La Trobe University, and was funded by the Department of Sustainability and Environment (DSE) and conducted under DSE permit number 10005533.

References

Abbott, I. (1984). Changes in the abundance and activity of certain soil and litter fauna in the Jarrah forest of Western Australia after a moderate intensity fire. *Australian Journal of Soil Research* **22**, 463–469. doi:10.1071/SR9840463

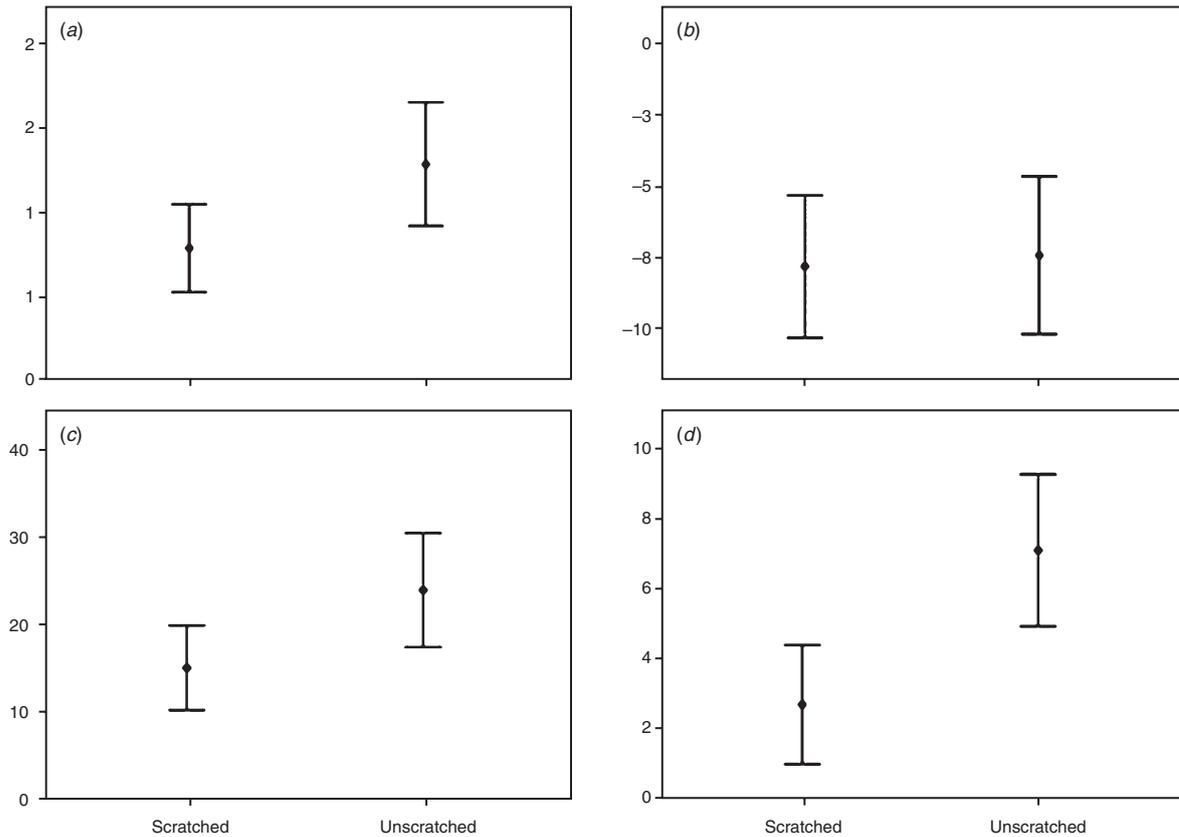
- Adamson, D., Selkirk, P., and Mitchell, P. (1983). 'The Role of Fire and Lyrebirds in the Sandstone Landscape of the Sydney Basin: Aspects of Australian Sandstone Landscapes.' (Eds R. Young and G. Nanson.) pp. 81–93. (Australian and New Zealand Geomorphology Group: Sydney.)
- Agee, J. K., Bahro, B., Finney, M. A., Omi, P. N., Sapsis, D. B., and Skinner, C. N. (2000). The use of shaded fuelbreaks in landscape fire management. *Forest Ecology and Management* **127**, 55–66. doi:10.1016/S0378-1127(99)00116-4
- Alexander, M. E., and Cruz, M. G. (2012). Interdependencies between flame length and fireline intensity in predicting crown fire initiation and crown scorchheight. *International Journal of Wildland Fire* **21**, 95–113. doi:10.1071/WF11001
- Archibald, S., Lehmann, C. E., Gomez-Dans, J. L., and Bradstock, R. A. (2013). Defining pyromes and global syndromes of fire regimes. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 6442–6447. doi:10.1073/pnas.1211466110
- Ashton, D. H. (1975). Studies of litter in *Eucalyptus regnans* forests. *Australian Journal of Botany* **23**, 413–433. doi:10.1071/BT9750413
- Ashton, D. (1976). The development of even-aged stands of *Eucalyptus regnans* (F.Muell.) in central Victoria. *Australian Journal of Botany* **24**, 397–414. doi:10.1071/BT9760397
- Ashton, D., and Bassett, O. (1997). The effects of foraging by the superb Lyrebird (*Menura novae hollandiae*) in *Eucalyptus regnans* forests at Beenak, Victoria. *Australian Journal of Ecology* **22**, 383–394. doi:10.1111/j.1442-9993.1997.tb00688.x
- Bond, W. J., and Keeley, J. E. (2005). Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution* **20**, 387–394. doi:10.1016/j.tree.2005.04.025
- Bradstock, R. A. (2008). Effects of large fires on biodiversity in south-eastern Australia: disaster or template for diversity? *International Journal of Wildland Fire* **17**, 809–822. doi:10.1071/WF07153
- Bureau of Meteorology (2012). 'Climate Data Online.' Available at <http://www.bom.gov.au/climate/data> [verified 10 April 2012].
- Byram, G. M. (1959). Combustion of forest fuels. In 'Forest Fire: Control and Use'. (Ed. K. P. Davis.) pp. 61–84. (McGraw-Hill: New York.)
- Carvalho, K. S., Alencar, A., Balch, J., and Moutinho, P. (2012). Leafcutter ant nests inhibit low-intensity fire spread in the understory of transitional forests at the Amazon's forest–savanna boundary. *Psyche (Cambridge, Massachusetts)* **2012**, 1–7. doi:10.1155/2012/780713
- Collins, L., Bradstock, R. A., Tasker, E. M., and Whelan, R. J. (2012). Can gullies preserve complex forest structure in frequently burnt landscapes? *Biological Conservation* **153**, 177–186. doi:10.1016/j.biocon.2012.04.021
- Cruz, M. G., Sullivan, A. L., Gould, J. S., Sims, N. C., Bannister, A. J., Hollis, J. J., and Hurley, R. J. (2012). Anatomy of a catastrophic wildfire: the Black Saturday Kilmore East fire in Victoria, Australia. *Forest Ecology and Management* **284**, 269–285. doi:10.1016/j.foreco.2012.02.035
- Dickinson, K. J. M., and Kirkpatrick, J. B. (1985). The flammability and energy content of some important plant species and fuel components in the forests of southeastern Tasmania. *Journal of Biogeography* **12**, 121–134. doi:10.2307/2844836
- Fuhlendorff, S. D., Engle, D. M., Kerby, J., and Hamilton, R. (2009). Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. *Conservation Biology* **23**, 588–598. doi:10.1111/j.1523-1739.2008.01139.x
- Gill, A. (1981). Adaptive responses of Australian vascular plant species to fires. In 'Fire and the Australian Biota'. (Eds A. M. Gill, R. H. Groves and I. R. Noble.) pp. 243–272. (Australian Academy of Science: Canberra.)
- Gill, A. M., and Catling, P. C. (2002). Fire regimes and biodiversity of forested landscapes of southern Australia. In 'Flammable Australia: the Fire Regimes and Biodiversity of a Continent'. (Ed. R. A. Bradstock, J. E. Williams and M. A. Gill.) pp. 351–369. (Cambridge University Press: Cambridge, UK.)

- González, G., and Seastedt, T. R. (2001). Soil fauna and plant litter decomposition in tropical and subalpine forests. *Ecology* **82**, 955–964. doi:10.1890/0012-9658(2001)082[0955:SFAPLD]2.0.CO;2
- Gould, J. S., McCaw, W. L., Cheney, N. P., Ellis, P. F., Knight, I. K., and Sullivan, A. L. (2007). 'Project Vesta – Fire in Dry Eucalypt Forest: Fuel Structure, Fuel Dynamics and Fire Behaviour.' (CSIRO and Department of Environment and Conservation: Perth.)
- Howard, T. (1973). Studies in the ecology of *Nothofagus Cunninghamii* Oerst. II. Phenology. *Australian Journal of Botany* **21**, 67–78. doi:10.1071/BT9730067
- Kirkpatrick, J., Marsden-Smedley, J., and Leonard, S. (2011). Influence of grazing and vegetation type on post-fire flammability. *Journal of Applied Ecology* **48**, 642–649. doi:10.1111/j.1365-2664.2011.01962.x
- Lawton, J. (1994). What do species do in ecosystems? *Oikos* **71**, 367–374. doi:10.2307/3545824
- Leonard, S., Kirkpatrick, J., and Marsden-Smedley, J. (2010). Variation in the effects of vertebrate grazing on fire potential between grassland structural types. *Journal of Applied Ecology* **47**, 876–883. doi:10.1111/j.1365-2664.2010.01840.x
- Leonard, S. W. J., Bennett, A. F., and Clarke, M. F. (2014). Determinants of the occurrence of unburnt forest patches: potential biotic refuges within a large, intense wildfire in south-eastern Australia. *Forest Ecology and Management* **314**, 85–93. doi:10.1016/j.foreco.2013.11.036
- Lill, A. (1980). Reproductive success and nest predation in the superb lyrebird, *Menura superba*. *Australian Wildlife Research* **7**, 271–280. doi:10.1071/WR9800271
- Loynd, R. H. (1985). Bird populations in successional forests of mountain ash *Eucalyptus regnans* in central Victoria. *Emu* **85**, 213–230. doi:10.1071/MU9850213
- Loynd, R. H., Cameron, D. G., Traill, B. J., Sloan, J. F., Malone, B. S., Schulz, M., Earl, G. E., and Triggs, B. E. (1992). Flora and fauna of the Cooagalah Forest Block, East Gippsland, Victoria. Ecological Survey Report No. 20. Department of Conservation and Environment, Melbourne.
- McNaughton, S. (1992). The propagation of disturbance in savannas through food webs. *Journal of Vegetation Science* **3**, 301–314. doi:10.2307/3235755
- Mikami, O. K., Katsuno, Y., Yamashita, D. M., Noske, R., and Eguchi, K. (2010). Bowers of the great bowerbird (*Chlamydera nuchalis*) remained unburned after fire: is this an adaptation to fire? *Journal of Ethology* **28**, 15–20. doi:10.1007/s10164-009-0149-9
- Mooney, C. (2010). 'Fuelbreak Effectiveness in Canada's Boreal Forests: a Synthesis of Current Knowledge.' (FPInnovations: Vancouver, Canada.)
- Nader, G., Henkin, Z., Smith, E., Ingram, R., and Narvaez, N. (2007). Planned herbivory in the management of wildfire fuels. *Rangelands* **29**, 18–24. doi:10.2111/1551-501X(2007)29[18:PHITMO]2.0.CO;2
- Neumann, F., and Tolhurst, K. (1991). Effects of fuel reduction burning on epigeal arthropods and earthworms in dry sclerophyll eucalypt forest of west-central Victoria. *Australian Journal of Ecology* **16**, 315–330. doi:10.1111/j.1442-9993.1991.tb01060.x
- Noble, I. R., Bary, G. A. V., and Gill, A. M. (1980). McArthur's fire-danger meters expressed as equations. *Australian Journal of Ecology* **5**, 201–203. doi:10.1111/j.1442-9993.1980.tb01243.x
- O'Donnell, A. J., Boer, M. M., McCaw, W. L., and Grierson, P. F. (2011). Vegetation and landscape connectivity control wildfire intervals in unmanaged semi-arid shrublands and woodlands in Australia. *Journal of Biogeography* **38**, 112–124. doi:10.1111/j.1365-2699.2010.02381.x
- Quinn, G. P., and Keough, M. J. (2002). 'Experimental Design and Data Analysis for Biologists.' (Cambridge University Press: Cambridge, UK.)
- R Core Development Team (2013). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at <http://www.R-project.org/> [verified 29 August 2014].
- Recher, H., Lunney, D., and Posamentier, H. (1975). A grand natural experiment: the Nadgee wildfire. *Australian Natural History* **18**, 150–163.
- Robinson, F., and Frith, H. (1981). The superb lyrebird (*Menura novaehollandiae*) at Tidbinbilla, ACT. *Emu* **81**, 145–157. doi:10.1071/MU9810145
- Robinson, N. M., Leonard, S. W. J., Ritchie, E. G., Bassett, M., Chia, E. K., Buckingham, S., Gibb, H., Bennett, A. F., and Clarke, M. F. (2013). Refuges for fauna in fire-prone landscapes: their ecological function and importance. *Journal of Applied Ecology* doi:10.1111/1365-2664.12153
- Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., and Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature* **413**, 591–596. doi:10.1038/35098000
- Sibley, C. G. (1974). The relationships of the lyrebirds. *Emu* **74**, 65–79. doi:10.1071/MU974065
- Soulé, M. E., Mackey, B. G., Recher, H. F., Williams, J. E., Woinarski, J. C. Z., Driscoll, D., Dennison, W. C., and Jones, M. E. (2004). The role of connectivity in Australian conservation. *Pacific Conservation Biology* **10**, 266–279.
- Springett, J. (1979). The effects of a single hot summer fire on soil fauna and on litter decomposition in jarrah (*Eucalyptus marginata*) forest in Western Australia. *Australian Journal of Ecology* **4**, 279–291. doi:10.1111/j.1442-9993.1979.tb01219.x
- SPSS Statistics (2009). 'SPSS. Release 18 for Windows.' (SPSS Inc.: Chicago, IL.)
- Stone, L., and Berman, T. (1993). Positive feedback in aquatic ecosystems: the case of the microbial loop. *Bulletin of Mathematical Biology* **55**, 919–936. doi:10.1007/BF02460692
- Sutherland, E. F., and Dickman, C. R. (1999). Mechanisms of recovery after fire by rodents in the Australian environment: a review. *Wildlife Research* **26**, 405–419. doi:10.1071/WR97045
- Teague, B., McLeod, R., and Pascoe, P. (2010). 2009 Victorian Bushfires Royal Commission: Final Report. Parliament of Victoria. Government Printer for the State of Victoria, Melbourne.
- Van Langevelde, F., Van De Vijver, C. D. A. M., Kumar, L., Van de Koppel, J., De Ridder, N., van Andel, J., Skidmore, A. K., Hearne, J. W., Stroosnijder, L., Bond, W. J., Prins, H. H., and Rietkerk, M. (2003). Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**, 337–350. doi:10.1890/0012-9658(2003)084[0337:EOFAHO]2.0.CO;2
- Walker, J. (1981). Fuel dynamics in Australian vegetation. In 'Fire and the Australian Biota'. (Ed. A. M. Gill, R. H. Groves and I. R. Noble.) pp. 101–127. (Australian Academy of Science: Canberra.)
- Whelan, R. J., and York, J. (1998). Post-fire germination of *Hakea sericea* and *Petrophile sessilis* after spring burning. *Australian Journal of Botany* **46**, 367–376. doi:10.1071/BT97075
- Woinarski, J., and Recher, H. (1997). Impact and response: a review of the effects of fire on the Australian avifauna. *Pacific Conservation Biology* **3**, 183–205.
- York, A. (1999). Long-term effects of frequent low-intensity burning on the abundance of litter-dwelling invertebrates in coastal blackbutt forests of southeastern Australia. *Journal of Insect Conservation* **3**, 191–199. doi:10.1023/A:1009643627781

Appendix 1. Weather variable inputs used in McArthur Mk5 Forest Fire Behaviour model

FFDI, forest fire danger index; KBDI, keetch bryam drought index; SDI, soil dryness index

FFDI	Air temperature (°C)	Relative humidity (%)	Wind speed at 10 m (km/h)	Amount of rain (mm)	No. of days since rain	KBDI or SDI
Extreme (91.9)	40	15	50	40	17	120
High (18)	33	35	20	40	17	120
Low to moderate (3.9)	25	65	10	40	17	120



Appendix 2. Comparison of seedling and ground fern characteristics between paired open and lyrebird-exclusion quadrats ($n = 18$). (a) The mean change in number of ground ferns. (b) The mean change in the number of seedlings. (c) The mean change in average height of ground ferns (cm). (d) The mean change in average height of seedlings (cm). Bars indicate one standard error.



Appendix 3. A single uprooted ground fern *Pteridium esculentum*, at a lyrebird scratch site, Black Range State Forest, February 2012. Scale bar = 20 cm.