

Large unburnt areas, not small unburnt patches, are needed to conserve avian diversity in fire-prone landscapes

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Summary

1. Mitigating the impacts of large-scale fires on biodiversity is becoming increasingly important as their frequency increases. In response, fire managers have engaged with the concept that retaining small unburnt residual areas of vegetation within extensively burnt landscapes may facilitate biodiversity conservation. However, it remains uncertain how the size and isolation of these unburnt residuals influence faunal distributions, persistence and recovery following fire.
2. We used a replicated observation study to test bird responses to the size and isolation of unburnt residuals in a mallee woodland area recently burnt by a 28 000 ha wildfire in southern Australia. The scale of our study provided a rare opportunity to consider the responses of large mobile organisms to fire-induced habitat fragmentation. Within five replicated spatial blocks, we crossed two levels of isolation with large (5–7 ha) and small (1–3 ha) unburnt patches and matrix sites burnt 5 years previously. We compared these site types to six continuous (non-fragmented) unburnt sites. We surveyed each site on eight occasions.
3. Most birds occurred more frequently in unburnt habitat beyond the extent of the fire. Bird responses to the availability and spatial distribution of unburnt remnants within the fire were largely influenced by their ability to use the recently burnt matrix. Occurrence of five species was higher in unburnt residuals when more of the landscape within 500 m was burnt.
4. A fire refuge effect may be likely for two competitive species that occurred more frequently in unburnt residuals than in the burnt matrix or continuous unburnt habitat. For the weebill, recolonization following fire was likely to occur gradually over time from *ex situ* sources.
5. *Synthesis and applications.* To maintain avian diversity in fire-prone landscapes, our results suggest a need to shift management focus from creating networks of small unburnt patches towards preserving large, intact areas of habitat. However, five species common to the burnt matrix preferentially selected residual patches when unburnt resources were locally scarce. Therefore, to benefit birds, land managers should limit the extent of applied burns and use narrow burns. When planning large burns, practitioners should consider that a number of species will remain absent from the landscape for several decades.

Key-words: disturbance, fragmentation, island biogeography theory, isolation, matrix, mosaics, patchiness, recolonization, refuges

Introduction

The frequency of large unplanned fires has increased globally in recent decades (Bowman *et al.* 2009). In response,

management agencies are exploring new strategies for mitigating the potentially detrimental effects of these fires on both property and biodiversity (Bradstock *et al.* 2005; Driscoll *et al.* 2010b). Among these new strategies, and as part of the wider ‘mosaic burning paradigm’ (Clarke 2008), is the concept that small unburnt patches of vegetation may enhance biodiversity retention in extensively

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burnt landscapes (Letnic & Dickman 2005). For example, the availability of unburnt patches has been linked to the retention of birds and small mammals following large fires in Australia (Lindenmayer *et al.* 2008; Pereoglou *et al.* 2011) and South Africa (Yarnell *et al.* 2008). These studies conclude that species survival after fire is linked to the availability of complex, unburnt, habitat structures within small patches. However, it remains uncertain how the spatial arrangement of unburnt remnants within extensively burnt landscapes will influence species' distribution, persistence and recovery (Bradstock 2008; Clarke 2008; Driscoll *et al.* 2010b).

The influence of the spatial arrangement of unburnt vegetation patches on faunal distributions in recently burnt landscapes has largely been overlooked (Bradstock *et al.* 2005; Clarke 2008). Simple post-fire landscape patterns comprising two predominant fire age classes may exhibit similar patch–matrix dynamics to traditional fragmented systems (Fahrig 1998; Driscoll & Henderson 2008). In these systems, the size, shape, isolation and arrangement of remnant patches strongly influence the survival of indigenous fauna (Turner 1989; Fahrig 2003). In particular, these spatial variables have been found to limit dispersal between populations (Tischendorf, Bender & Fahrig 2003; Heinz *et al.* 2005), increase competition (Fischer & Lindenmayer 2007), predation (Small & Hunter 1988; Henrik 1992) and alter breeding dynamics (Fahrig 1998). Therefore, understanding whether fire-induced intraserve fragmentation will produce similarly severe outcomes to traditional fragmented systems for fauna is necessary to manage biodiversity assets successfully within fire-prone reserves.

Two mechanisms of faunal persistence within extensively burnt landscapes have been proposed. First, species are thought to either perish or flee during a fire, to then repopulate suitable habitat patches from *ex situ* sources (Watson *et al.* 2012). Secondly, unburnt remnants embedded within the extent of a large burnt area may provide sufficient resources to support viable populations of species *in situ* until the surrounding habitat has reached a sufficient state of recovery for subsequent recolonization (Mackey *et al.* 2002; Turner, Romme & Tinker 2003). However, when applying these concepts to a scenario of intraserve fragmentation, considering the degree to which species use the matrix becomes relevant (Driscoll 2005; Driscoll *et al.* 2013).

Patch use may be determined by the ability of a species to survive and disperse through the recently burnt, interpatch matrix (Stevens & Tello 2011). Therefore, the relative isolation of an unburnt patch from other fragmented or continuous unburnt landscape elements may determine community composition (Watson *et al.* 2012). However, matrix hospitability may be enhanced by resources within the matrix, increasing a species' dispersal potential. Furthermore, some species may benefit from fine-scale habitat and resource heterogeneity (Stuart-Smith, Adams & Larsen 2002; Stevens & Tello

2011). For example, at an edge between recently burnt and unburnt mallee woodland habitat in south-east Australia, Luck, Possingham & Paton (1999) observed an increase in the abundance of white-eared honeyeater *Lichenostomus leucotis*, which they attributed to the availability of both a dense canopy for foraging in unburnt vegetation and a dense scrub layer for nesting available in areas regenerating after fire.

Recent efforts to examine the impacts of fire mosaic spatial components on species distributions have focused on comparing relative degrees of 'pyrodiversity' between landscapes (Kelly *et al.* 2012; Taylor *et al.* 2012). These studies compared landscapes with varying proportions of different time-since-fire vegetation to determine how the variety and extent of fire age classes affects community composition. They concluded that reptile richness was highest with a coarse mosaic of mid-successional vegetation, but that the richness of other taxa including birds was dependent on the preservation of large areas of old intact vegetation. However, to the best of our collective knowledge, no previous studies have examined the spatial consequences of the size and isolation of individual fire mosaic elements (Swengel & Swengel 2007; Clarke 2008; Hylander & Johnson 2010). This may be related to the dearth of sufficiently replicated, natural, post-fire study systems (Driscoll *et al.* 2010b).

To investigate the spatial components of a fire mosaic adequately, sites must share the same fire history (Gill 1977), be sufficiently replicated throughout the landscape (Mantgem, Schwartz & Keifer 2001), be of similar vegetation type (Bradstock *et al.* 2005) and be potentially available to the same species pool (Driscoll & Henderson 2008). This situation arose in a 28 154 ha fire mosaic at Pinkawillie Conservation Park, South Australia, which provided an ideal study system for examining the effects of unburnt residual size and isolation on bird distribution. In this study, we asked how is bird species occurrence influenced by the size and isolation of unburnt remnants, and how does individual bird occurrence differ between continuous unburnt, burnt and unburnt residual landscape elements? By quantifying bird occurrence in different landscape elements, we were able to provide a context within which to interpret species responses to unburnt residual patch size and isolation.

Materials and methods

STUDY SYSTEM

We conducted field observations in mallee woodland at Pinkawillie Conservation Park (*c.* 1500 km²), on the Eyre Peninsula, South Australia (mean annual rainfall: 346 mm, Australian Bureau of Meteorology). Pinkawillie Conservation Park is dominated by two notable topographic features: nonlinear parabolic sand dunes and the depressions between dunes, characterized by firm clay soils, known as swales (Matthew,

Carpenter & Croft 1996). In December 2005, an unplanned fire burnt 28 154 ha of the park and created many small unburnt residuals within its extent. Two other major fires had previously burnt the park: 826 ha in 2001 and 14 505 ha in 1986 (Fig. 1). We studied three landscape elements: unburnt residual patches within the 2005 fire area ('unburnt residuals'), unburnt habitat outside the 2005 fire area ('continuous unburnt') and areas burnt in the 2005 fire ('burnt matrix'). Fire history records over the past 40 years (DENR, 2011) indicated that all 'unburnt residual' and 'continuous unburnt' sites were previously burnt in the 1986 fires.

In topographically dynamic temperate forest ecosystems, the retention of unburnt residuals following extensive fire events is attributed to local variation in topography, wetness and vegetation (Mackey *et al.* 2002). However, in semi-arid mallee woodland, where topographic relief is relatively shallow, fire patterns are largely driven by the discontinuous nature of fuels and weather conditions during each fire event (Bradstock *et al.* 2002). Weather-driven fire patterns are less predictable and are more likely to produce ephemeral fire residuals which may not persist through multiple fire events (Bessie & Johnson 1995). Nonetheless, to control for underlying vegetation age between landscape elements and ensure that fire residuals were as far as possible representative of vegetation that was burnt in 2005, we excluded residuals that were also unburnt in the previous large fire in 1986 (Luck, Possingham & Paton 1999). In addition, to establish whether unburnt patches were physically representative of the broader landscape or determined by their unique local context, we examined the difference in mean site topographic wetness index between landscape elements using an ANOVA. The topographic wetness index is a relative measure of the long-term soil moisture availability of a given site in the landscape (Kopecký & Čížková 2010). Site level measures of topographic wetness index were generated from a digital elevation model derived from shuttle radar topography mission data (Gallant & Read 2009). We found no significant difference in topographic wetness between landscape elements (d.f. = 34, $F = 0.018$, $P = 0.983$). This implies that the probability of an area being retained as an unburnt residual was unlikely to be related to differences in topography between sites.

STUDY DESIGN

We established five replicate blocks. Within each block, we identified six sites: two in the recently burnt matrix, plus two pairs of large and small unburnt residuals (Fig. 2). One of each pair was more isolated than the other. Small patches were classified as <3 ha and large patches >5 ha in size. Isolation was measured as the proportion of total burnt vegetation within each buffer. We measured isolation at two scales, first with a buffer radius of 500 m, then with a radius of 5 km. The use of two scales enabled the effects of both localized and landscape-scale isolation to be quantified. Patches were selected based on size, accessibility and to ensure equal representation of dune and swale vegetation communities. In addition to the five blocks, we established six continuous unburnt sites adjacent to the 2005 fire. These sites spanned a similar area to the blocks (*c.* 20 km) and were fixed to 3 ha in area. All continuous unburnt sites were more than 1 km from the 2005 fire to avoid possible edge effects (Luck, Possingham & Paton 1999).

BIRD SURVEY DESIGN

We used the timed active-search method to survey birds (Bibby 2004). We recorded all birds observed by sight or heard within a 30-min period, excluding those observed flying overhead. This method enabled bird responses to be quantified at the whole patch scale and reduced the likelihood that a species was present within a patch but not recorded (Brown 1988). As the largest sites (12 ha) could be completely searched in 30 min, it was thought that any variation in sampling effort associated with patch size would be negligible (MacNally & Horrocks 2002). A 3 ha search area was used at burnt matrix and continuous unburnt sites as it was representative of mean unburnt patch size.

We conducted surveys between 28th September and 17th November 2010 to coincide with peak breeding season, when birds are most detectable (Simpson & Day 2004). We completed surveys between 06:00 and 12:00 (Australian Standard Daylight Saving Time) and did not survey on days of heavy rain or strong wind. One observer surveyed each site eight

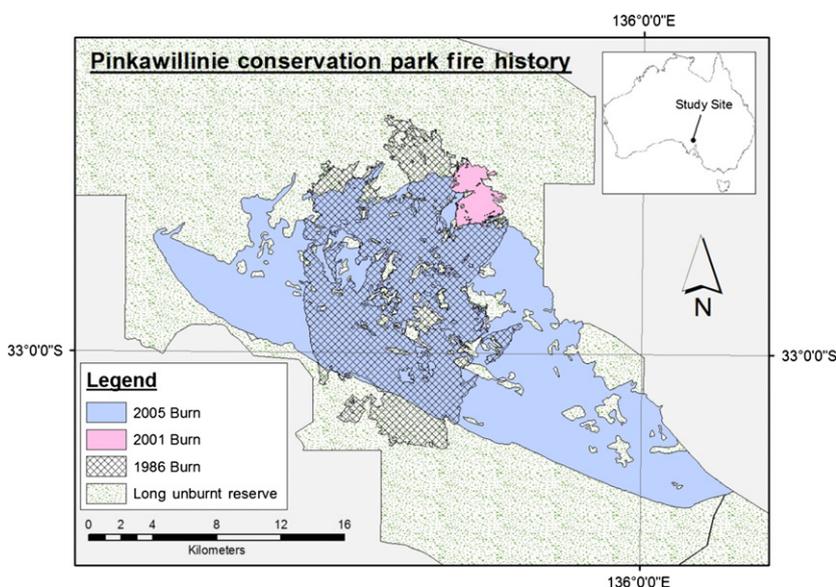


Fig. 1. Pinkawillinie Conservation Park fire history map with four burn categories. We classed long unburnt reserves as areas unburnt on record prior to 1986.

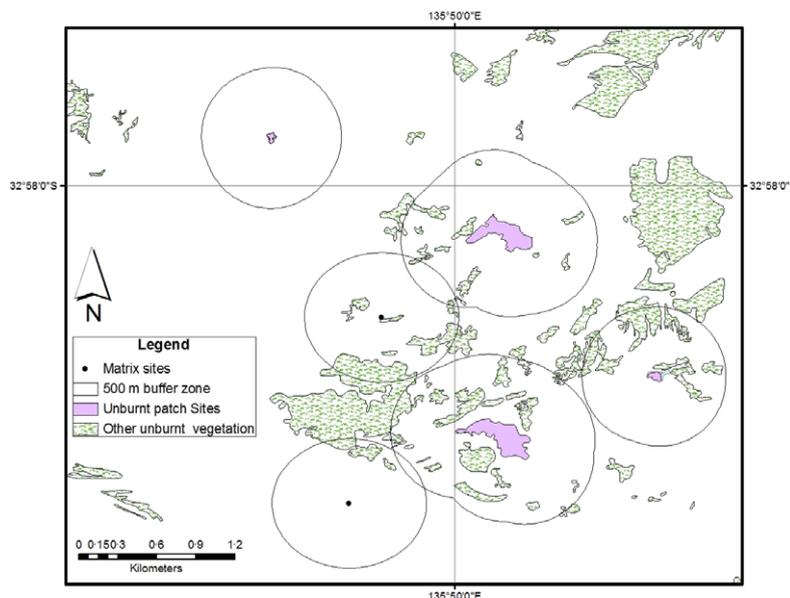


Fig. 2. An illustration of patch size and isolation site types within one spatial block. The six site types were divided as follows: one larger (5–7 ha) patch at higher isolation, one larger patch at lower isolation, one smaller patch (<3 ha) at higher isolation, one smaller patch at lower isolation, one matrix site at higher isolation and one matrix site at lower isolation.

times, on eight different mornings, each separated by at least 1 week. The timing of site surveys was varied upon each revisit, reducing possible sampling time bias. The number of repeat surveys in which a species was recorded was used in our analysis (i.e. a count of occurrence, with eight the maximum possible value).

VEGETATION SURVEY DESIGN

To assess vegetation structure, we established six vegetation survey transects at each site, stratified into three transects per dune and three transects per swale. Each transect was 50 m in length and 4 m in width. On dunes, we placed transects parallel with topography, with the centre transect on the dune crest. The same approach was repeated for swales, with the centre transect placed at the lowest point. We spaced all transects within each topographic element 20 m apart.

To remove excessive colinearity in the data, we examined the correlation coefficients between the vegetation variables. Variables which returned correlation coefficients <0.7 were included in the final vegetation analyses. These were number of trees flowering, number of trees, number of tree seedlings, number of dead trees, maximum shrub height, mean canopy height, sparse litter and canopy cover. We excluded *Spinifex Triodia* sp. cover, dense litter cover, shrub cover, number of shrubs, number of flowering trees and shrubs and mean shrub height. For cases where multiple variables shared a correlation coefficient >0.7, we included the variable with the fewest >0.7 correlations.

SPATIAL ANALYSIS

We calculated patch area and isolation for each of the 36 survey patches using the projected GDA 1994 MGA zone 53, coordinate system in ArcMap 9.3.1 (Environmental Systems Research Institute, Redlands, CA, USA). The distance to nearest continuous unfragmented habitat element shared a correlation coefficient of 0.815 with the buffer measure at 5 km. We chose to use the 5-km measure as it considered total amount of available unburnt habitat within the buffer area.

STATISTICAL ANALYSES

Bird detectability

Accounting for bird detection is desirable in ecological studies as bird detectability may vary in different habitats (Diefenbach *et al.* 2003). However, adjusting occupancy models for non-detection can be as misleading as ignoring non-detection completely (Welsh, Lindenmayer & Donnelly 2013). The high mobility of many species in our study and their presence within the interpatch matrix violated a key assumption of the single season occupancy model that populations are closed between repeat surveys (MacKenzie *et al.* 2002). However, covariates of detection probability can be effectively controlled with study design (Banks-Leite *et al.* 2014). Watson *et al.* (2012) examined bird detectability in mallee woodland landscapes similar to those in our study, which presented different degrees of 'pyrodiversity'. Using distance sampling, they found that bird detection probabilities did not decrease in areas of higher vegetation density at sites between 1 and 147 years post-fire (Watson *et al.* 2012). Therefore, it is unlikely that differences in vegetation density between sites influenced bird detection in our study. However, to avoid interpreting bird responses that may be strongly influenced by detectability, we did not include rare species. Specifically, we excluded 28 species which each had fewer than five total occurrences across all sites, equal to the number of site type replications in our models.

Spatial effects

We tested the influence of patch size and isolation on the probability of bird occurrence using a binomial generalized linear model (GLM) with a logit link function (McCulloch & Neuhaus 2001). We fitted area, isolation measured within a 500-m buffer, isolation measured within a 5-km buffer, site type (patch = 1, matrix = 0), block and the first two components of the vegetation PCA as fixed effects. Block was fitted as a fixed effect in the model because there were too few blocks to fit it as a random effect (Lin 1997). We repeated the model fitting species richness as

the response variable. Continuous unburnt sites were excluded from this spatial analysis because there was no logical way to add each to a block given that they were located beyond the extent of the 2005 fire (Appendix S1) and lacked size and isolation covariates.

Landscape element

We tested differences in bird occurrence between landscape elements (unburnt residual, burnt matrix and continuous unburnt) using a binomial generalized linear model (GLM) with a logit link function. We used total number of repeat surveys in which a species was present at a site as our response variable. We fitted landscape element and log survey area as fixed effects. We repeated the model fitting species richness as the response variable. We used a Wald's test to determine the significance of landscape element in the model. For models where the Wald's test returned a significant result, we plotted the predicted probability of bird occurrence across landscape elements. We included the 'Firth Correction' in our model to bring the P -value away from infinity in cases of complete separation. We conducted this analysis using the package 'logistf' (Heinze & Schemper 2002) in the R statistical environment (R Development Core Team, 2008).

Vegetation

We compared vegetation structure between sites using a principal components analysis (PCA) to determine the extent to which unburnt patch sites were representative of continuous unburnt landscape elements (McKenzie *et al.* 2004). The first two components of our PCA accounted for 77% of the total variation in vegetation structure between sites. We plotted the similarity in vegetation structure between sites using the first two components of the PCA as axes.

Results

To quantify the effects of unburnt patch size and relative isolation from other landscape elements on bird species' distributions, we collected 5897 records of 71 species at our 36 study sites. Patch size ranged from 1 to 12 ha. When measured at 500 m, isolation (percentage area burnt) ranged from 35% to 70.9%. When measured at 5 km, isolation ranged from 60.6% to 96.7%.

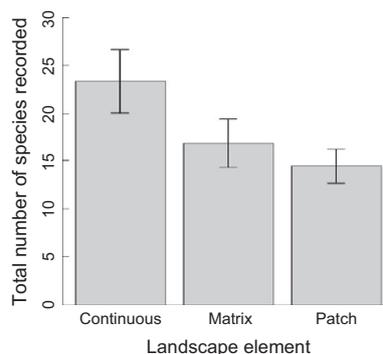
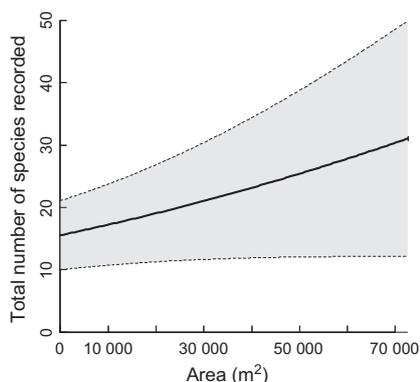


Fig. 3. Results of generalize linear models demonstrating the relationship between species richness and unburnt residual area (left) and between Landscape Elements (right). The shaded area on plot and bars on the histogram represent 95% confidence intervals.

HOW IS BIRD SPECIES OCCURRENCE INFLUENCED BY THE SIZE AND ISOLATION OF UNBURNT REMNANTS?

Bird species richness was significantly greater in larger patches ($t = 2.76$, $P = 0.011$, Fig. 3). We found fifteen significant responses to patch size and isolation at the local and landscape scale (Fig. 4). Four species occurred more often in larger patches (Fig. 4a): weebill *Smicrornis brevirostris* ($Z = 2.07$, $P = 0.038$), grey currawong *Strepera versicolour* ($Z = 3.36$, $P < 0.001$), inland thornbill *Acanthiza apicalis* ($Z = 2.97$, $P = 0.002$) and golden whistler *Pachycephala pectoralis* ($Z = 2.08$, $P = 0.038$). The southern scrub robin *Drymodes brunneopygia* occurred less often in larger patches ($Z = -2.54$, $P = 0.011$). At sites with high isolation, measured with a 500-m buffer, five species had a higher probability of occurrence (Fig. 4b): weebill ($Z = 2.08$, $P = 0.038$), spiny-cheeked honeyeater *Acanthagenys rufogularis* ($Z = 2.41$, $P = 0.016$), white-browed babbler *Pomatostomus superciliosus* ($Z = 2.35$, $P = 0.019$), crested bellbird *Oreoica gutturalis* ($Z = 2.61$, $P = 0.009$) and Richard's pipit *Anthus australis* ($Z = 2.65$, $P = 0.008$). Weebill also occurred less often at sites that were more isolated ($Z = -2.44$, $P = 0.015$), when measured with a 5-km buffer. Conversely, the occurrence of four species was higher at sites that were more isolated when measured with a 5-km buffer (Fig. 4c): blue-breasted fairy-wren *Malurus pulcherrimus* ($Z = 1.99$, $P = 0.047$), southern scrub robin ($Z = 2.93$, $P = 0.003$), chestnut quail-thrush *Cinlosoma castanotus* ($Z = 2.06$, $P = 0.039$) and Richard's pipit ($Z = 1.98$, $P = 0.047$). The occurrence of three species was significantly related to vegetation principal component 2 (Appendix S2): spiny-cheeked honeyeater ($Z = -2.19$, $P = 0.0283$), weebill ($Z = -2.42$, $P = 0.016$) and the yellow-throated miner *Manorina flavigula* ($Z = 2.67$, $P = 0.008$).

HOW DID BIRD OCCURRENCE DIFFER BETWEEN LANDSCAPE ELEMENTS?

Bird species richness was significantly greater in unburnt continuous landscape elements ($t = -3.38$, $P = 0.02$, Fig. 3). The occurrence of 21 species was influenced by landscape element (Fig. 5). Most of these (11 species)

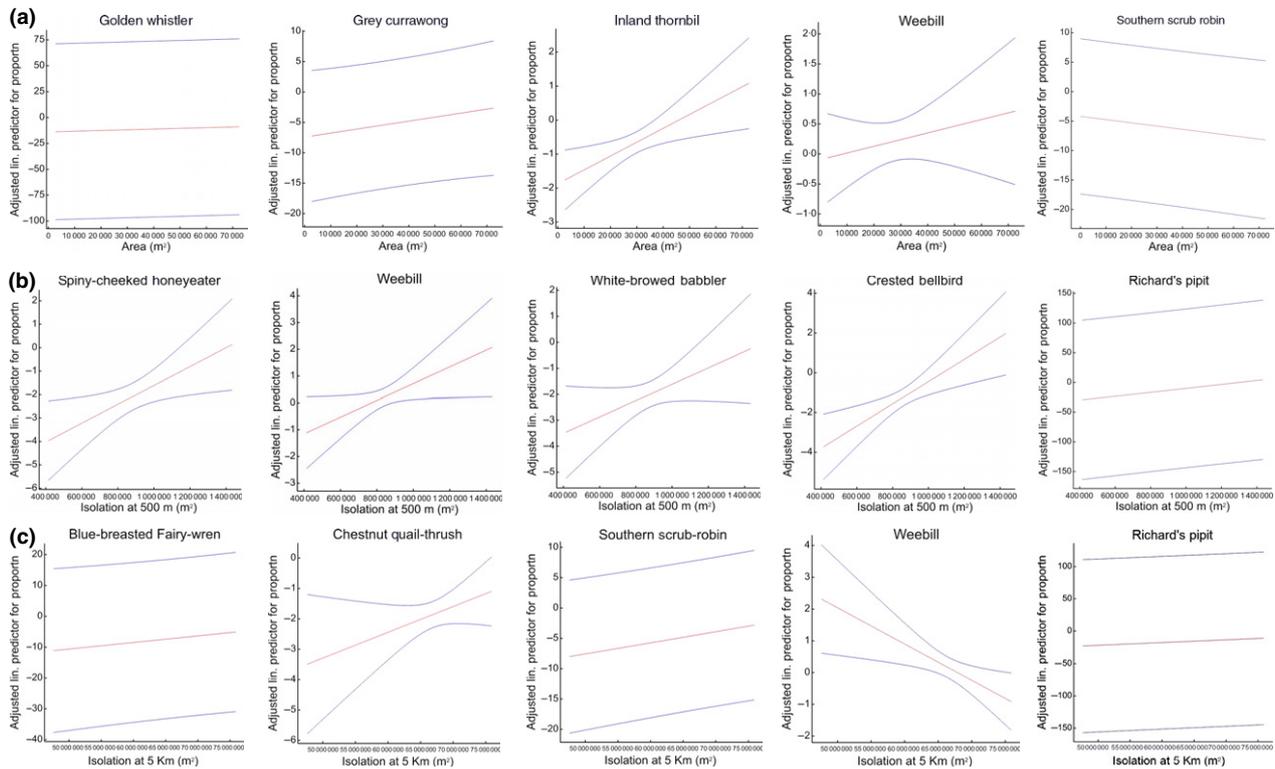


Fig. 4. Significant bird responses to Area (a), Isolation at 500 m (b) and Isolation at 5 Km (c) plotted on the linear predictor scale with 95% confidence intervals.

occurred more often in continuous unburnt vegetation. Five species occurred more frequently in the burnt matrix. Two species occurred more frequently in unburnt residuals. Three species occurred equally in all landscape elements. A further 22 species had no significant relationship with landscape element.

The occurrence of three species was significantly related to vegetation principal component 2: spiny-cheeked honeyeater ($Z = -2.19$, $P = 0.0283$), weebill ($Z = -2.42$, $P = 0.016$) and the yellow-throated miner ($Z = 2.67$, $P = 0.008$). We found that unburnt residuals and unburnt continuous elements shared a similar range of vegetation structures (Appendix S2).

Discussion

Fire management planning for biodiversity conservation often assumes that species will benefit from fine-scale, post-fire landscape patterns (Bradstock *et al.* 2005; Clarke 2008; Driscoll *et al.* 2010b). However, there have been very few examples in post-fire landscapes to support this (Driscoll *et al.* 2010a). Our results indicate that species responses to the availability and spatial distribution of unburnt remnants are influenced by the extent to which species were able to use the matrix. Many species were able to persist within the burnt landscape regardless of the presence and distribution of unburnt residuals. However, small unburnt residuals may potentially act as fire

refuges for two species. Our results also suggest that post-fire recolonization can occur from *ex situ* sources beyond the area of the fire. We recommend that when considering landscape patterns for conserving birds in fire-prone woodland ecosystems, practitioners should aim to protect large areas of intact unburnt vegetation. To facilitate rapid rates of post-fire recolonization, practitioners should seek to minimize the extent of large homogeneously burnt areas, such as by burning narrow strips.

ARE UNBURNT RESIDUALS IMPORTANT FOR BIRD CONSERVATION WITHIN EXTENSIVELY BURNT LANDSCAPES?

The role that unburnt residual patches will have in the post-fire ecology of birds within extensively burnt landscapes is dependent on the extent to which birds can use the matrix. Our results indicate that for many species, the burnt matrix is not a 'sea' of inhospitable habitat between high-quality habitat islands (Driscoll 2005). When formulating fire management plans, land managers should consider that the recently burnt matrix will become hospitable for a wide range of bird species within 5 years of a fire. It is possible that some of these species are able to exploit the dense structure of regenerating *Eucalyptus spp.* for shelter (Noble 2001; Clarke *et al.* 2010). At 5 years after fire, many grasses and small shrubs had recovered sufficiently to flower and set

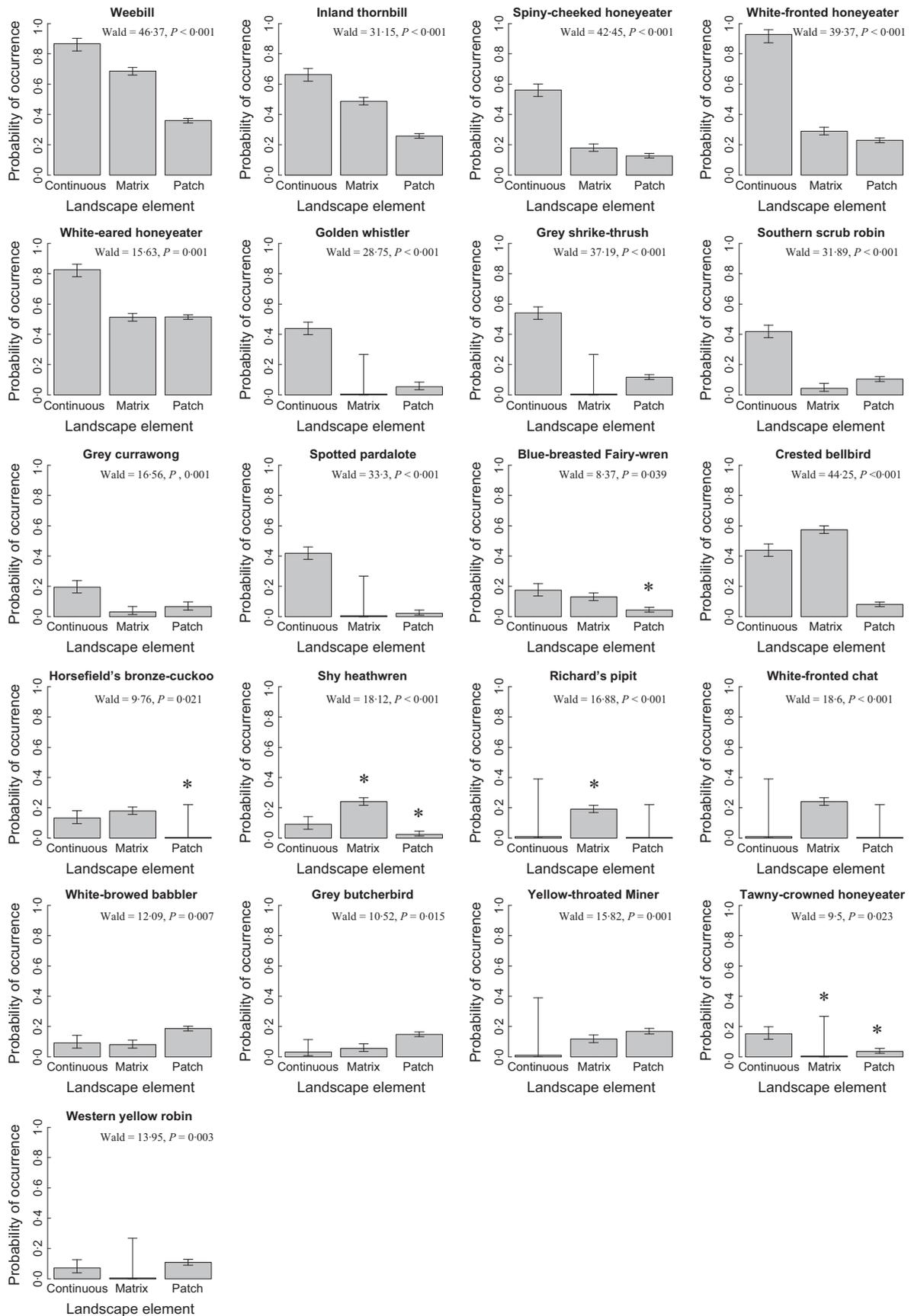


Fig. 5. Probability of bird occurrence in each landscape element. Error bars indicate 95% confidence intervals. Asterisks denote significant responses where all responses are not significant.

seed, providing potential food sources for nectivorous and granivorous bird species (Noble 1989). The abundance of invertebrates at all times after fire appears to be sufficient to support insectivorous bird species (Teasdale *et al.* 2013).

As rudimentary canopy cover in mallee woodland is not generally restored until at least 15 years after fire (Enright *et al.* 2012), two native species common to open agricultural landscapes, the white-fronted chat and Richard's pipit, were able to colonize the burnt matrix from surrounding farmland. While these species are both common in Australia, in other countries, similar kinds of open-country specialists are threatened by agricultural intensification (Turner & Romme 1994). Open-country species may become more reliant on recently burnt reserves as agricultural practices intensify (Brotons, Herrando & Pons 2008). However, as the majority of species native to the reserve occurred more often in continuous unburnt habitat elements, the application of fire as a tool for increasing avian diversity in the short term cannot be justified.

Many fragmentation studies conclude that larger patch sizes are necessary to maintain species diversity and abundance in recently disturbed landscapes (Heinze & Schemper 2002; MacKenzie *et al.* 2002; Rota *et al.* 2011). We found higher species richness and occurrence of four species in larger patches. The grey currawong and golden whistler had a positive relationship with patch area and occurred more frequently in patches than the burnt matrix. These species may be able to capitalize on the additional resource opportunities presented by larger patches (MacArthur & Wilson 1967). For example, the grey currawong is an egg predator and may benefit from additional predation opportunities in larger patches (Gardner 1998). The golden whistler is a migratory species in Australia and its preference for larger patches may be attributed to its ability to disperse to areas where competition pressures may be lower (van Dongen & Yocom 2005).

DO UNBURNED RESIDUALS HAVE THE POTENTIAL TO ACT AS FIRE REFUGES?

It has been suggested that following a whole-reserve-scale fire, unburnt patches could act as fire refuges (Mackey *et al.* 2002), enabling survival *in situ*. Fire refuges could be essential for species which cannot survive in recently burnt vegetation (Royle 2006; Driscoll & Henderson 2008). Although we found evidence that two species occurred more often in unburnt residuals, these species were not absent from the burnt matrix and therefore not solely dependent on these areas for survival (Fig. 5). The positive responses to high local isolation (measured with a 500-m buffer) suggest that some birds are drawn to unburnt residuals when unburnt resources within the immediate landscape are scarce (Fig. 4). All but one of these species was equal or more abundant in the burnt

matrix, so they appear to not be dependent on unburnt residuals. Nevertheless, increased occurrence in patches when patches are rare in the landscape suggests that matrix-using birds benefit from using unburnt residuals (Kelly *et al.* 2012). A clearer fire refuge effect may be detected by repeating the study at a shorter interval than 5 years following fire. Fire refuges may be most important in providing shelter for birds during and immediately following a fire (Geluso & Bragg 1986).

We found that the carnivorous grey butcherbird and the territorial white-browed babbler were the most likely to benefit from the presence of unburnt residuals. The white-browed babbler is a colonial species, which has been observed to chase away competitors when food resources are limited (Cale 2002). The grey butcherbird aggressively excludes other species from their territories (Fulton 2008). It also may limit the establishment of other birds in unburnt patches through nest predation (Loyn 2002). The monopolization of small residuals by these competitive species may contribute to lower residual use by several other species.

While *in situ* fire refugia can be an important source of post-fire recolonization, we found that bird recolonization may also occur from unburnt edges. The weebill has limited movement and a small home range (Schodde & Mason 1999) and was recorded in the burnt matrix. It occurred less frequently at sites further away from unburnt edges (5-km buffer). We speculate that this species may gradually expand its range across the burnt landscape, possibly over several generations. Although the pattern of decreasing occurrence with increasing isolation may arise by gradual colonization or routine exploration during daily foraging, we suggest the former is more likely.

Isolating the pattern of gradual recolonization from a fire refuge dynamic could have been more successfully achieved by surveying within 1 year of the fire (Mackey *et al.* 2002). We employed a design which focused upon patch spatial attributes, controlling for temporal variation between site types. This did not allow us to investigate the potential for long-term fire refuges to maintain fire sensitive old-growth species in the landscape (Geluso & Bragg 1986). As a result, species intolerant to habitat younger than 25 years post-fire may have been absent from our study area (Price, Russell-Smith & Edwards 2003).

CONCLUSION

Existing fire management strategies for bird conservation require substantial refinement (Taylor *et al.* 2012). Our results suggest a shift in current fire management thinking (Bradstock *et al.* 2005) is needed, away from a focus on creating small, unburnt patches towards preserving large, intact, unburnt areas. Although small unburnt residuals may potentially act as fire refuges for some birds, we found that most species occurred more often in large areas of continuous habitat last burnt 25 years ago.

We found that larger patches (>3 ha) had greater bird occurrence rates. The range of residual patch sizes in this study (1–9 ha) appeared to be insufficient to detect ‘fire refuge’ effects. This highlights the need for targeting the preservation of larger areas of unburnt habitat.

Prescribed fire plans aimed at fuel reduction should consider that the retention of unburnt vegetation will increase landscape permeability and habitat quality for a range of bird species. Land managers also should consider taxa other than birds which may benefit from the retention of unburnt patches, such as small mammals (Yarnell *et al.* 2008; Pereoglou *et al.* 2011). Land managers should consider that following large homogeneous burns, a number of species may remain absent from the landscape for several generations.

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Data accessibility

Bird survey data and site locations: <http://dx.doi.org/10.4227/05/548541119D331>, url: <http://portal.aekos.org.au/dataset/171719> (Berry 2014).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. site locations.

Fig. S1. Satellite image displaying the distribution of sites and blocks at Pinkawillinie.

Appendix S2. differences in vegetation structure between sites and results of vegetation PCA.

Fig. S2. Ordination displaying similarity in vegetation structure between landscape elements.