

# Landscape-scale effects of fire on bird assemblages: does pyrodiversity beget biodiversity?

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## ABSTRACT

**Aim** A common strategy for conserving biodiversity in fire-prone environments is to maintain a diversity of post-fire age classes at the landscape scale, under the assumption that ‘pyrodiversity begets biodiversity’. Another strategy is to maintain extensive areas of a particular seral state regarded as vital for the persistence of threatened species, under the assumption that this will also cater for the habitat needs of other species. We investigated the likely effects of these strategies on bird assemblages in tree mallee vegetation, characterized by multi-stemmed *Eucalyptus* species, where both strategies are currently employed.

**Location** The semi-arid Murray Mallee region of south-eastern Australia.

**Methods** We systematically surveyed birds in 26 landscapes (each 4-km diameter), selected to represent gradients in the diversity of fire age classes and the proportion of older vegetation (> 35 years since fire). Additional variables were measured to represent underlying vegetation- or fire-mediated properties of the landscape, as well as its biogeographic context. We used an information-theoretic approach to investigate the relationships between these predictor variables and the species richness of birds (total species, threatened species and rare species).

**Results** Species richness of birds was not strongly associated with fire-mediated heterogeneity. Species richness was associated with increasing amounts of older vegetation in landscapes, but not with the proportion of recently burned vegetation in landscapes.

**Main conclusions** The preference of many mallee birds for older vegetation highlights the risk of a blanket application of the ‘pyrodiversity begets biodiversity’ paradigm. If application of this paradigm involved converting large areas from long unburned to recently burned vegetation to increase fire-mediated heterogeneity in tree mallee landscapes, our findings suggest that this could threaten birds. This research highlights the value of adopting a landscape-scale perspective when evaluating the utility of fire-management strategies intended to benefit biodiversity.

## Keywords

Conservation, disturbance, fire management, heterogeneity, mallee, semi-arid.

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## INTRODUCTION

Globally, fire is an important disturbance process in many environments where it affects the distribution and structure of vegetation (Whelan, 1995; Bond & Keeley, 2005; Bowman *et al.*, 2009). Fire allows species with differing habitat require-

ments to occur, by creating a range of resources variously distributed through space and time (Sousa, 1985; Brawn *et al.*, 2001; Turner *et al.*, 2003). Some have argued that anthropogenic activities have reduced the capacity for ‘natural’ fire regimes to provide the variation in resources necessary to maintain biodiversity (Gill *et al.*, 2002; Dellasala *et al.*, 2004;

Noss *et al.*, 2006). Although altered fire regimes has been highlighted as a threatening process for more than 50 species of terrestrial birds in Australia, second only to habitat clearing and fragmentation (Garnett & Crowley, 2000), little is known about the particular temporal and spatial patterns of disturbance by fire that maintain or threaten diversity.

To counter threats to biodiversity loss, fire-management strategies intended to benefit biota, such as prescribed burning or fire suppression, have been recommended (e.g. Biggs & Potgieter, 1999; Fuhlendorf *et al.*, 2006; Thomas *et al.*, 2006a). However, determining the value of such strategies to biodiversity often is constrained by limited information regarding how animals respond to fire in both time and space (Parr & Chown, 2003; Saab & Powell, 2005; Clarke, 2008; Driscoll *et al.*, 2010). Moreover, most research has been conducted at a 'site' (local) scale, and so the response of biota to fire-mediated spatial properties of landscapes (e.g. their size, shape, age structure and configuration of patches) is virtually unknown (Bradstock *et al.*, 2005; Driscoll *et al.*, 2010).

A common approach for conserving animal diversity in fire-prone environments is to maintain a mosaic of patches of different post-fire age classes in the landscape, under the assumption that 'pyrodiversity begets biodiversity' (Parr & Andersen, 2006). Such a strategy is ecologically appealing as species diversity is often positively associated with landscape heterogeneity (Huston, 1994; Aauri & de Lucio, 2001; Williams *et al.*, 2002; Tews *et al.*, 2004). Furthermore, findings from site-scale studies suggest that different species are associated with particular seral states (Fox, 1982; Hutto, 1995; Kotliar *et al.*, 2002; Saab & Powell, 2005). Thus, multiple seral states in the landscape might be expected to support greater species diversity. Indeed, there is widespread support for the concept of fire-mediated heterogeneity in many regions (see references in Parr & Andersen, 2006). However, in the absence of empirical data on the relationship between biota and different levels or patterns of heterogeneity, 'creating heterogeneity' can be used to justify almost any prescribed-burning strategy, as new fire events almost inevitably create heterogeneity in the landscape (Clarke, 2008). Imposing novel disturbance regimes with unknown ecological ramifications has the potential to threaten biodiversity. Hence, there is an urgent need to examine the effect of fire-mediated heterogeneity on animal diversity in fire-prone environments (Bradstock *et al.*, 2005; Driscoll *et al.*, 2010).

In semi-arid mallee shrublands of the Murray Mallee region of south-eastern Australia, two major objectives of fire management are (1) to use prescribed burning to maintain a diversity of patches of differing fire age classes, and (2) to maintain large areas of older vegetation (e.g. Department of Environment and Heritage, 2008; Department of Sustainability and Environment, 2008). The requirement for large areas of older vegetation stems from the perception that a group of threatened bird species rely on this element for their persistence (Meredith, 1982; Woinarski, 1989; Benshemesh, 1990; Bradstock & Cohn, 2002; Clarke *et al.*, 2005). Indeed, inappropriate fire management (i.e. too-frequent fire) is

considered a major threatening process to the persistence of a number of bird species characteristic of mallee ecosystems (Woinarski & Recher, 1997).

The primary aim of this study was to examine the likely impact of these two dominant fire-management strategies on the mallee avifauna. We investigated the widely held, but rarely tested, assumption that 'pyrodiversity begets biodiversity'. We also examined the alternative management strategy that greater proportions of older vegetation in the landscape will have a positive effect on species richness and diversity. We adopted a whole-of-landscape approach in which both the response variable (bird species richness) and predictor variables (fire-mediated spatial elements of landscapes) were sampled at the scale of the 'whole' landscape (*sensu* Bennett *et al.*, 2006). Such an approach is useful as it allows landscape-scale inference of the effects of fire on biota at a spatial resolution directly amenable to management actions by land managers.

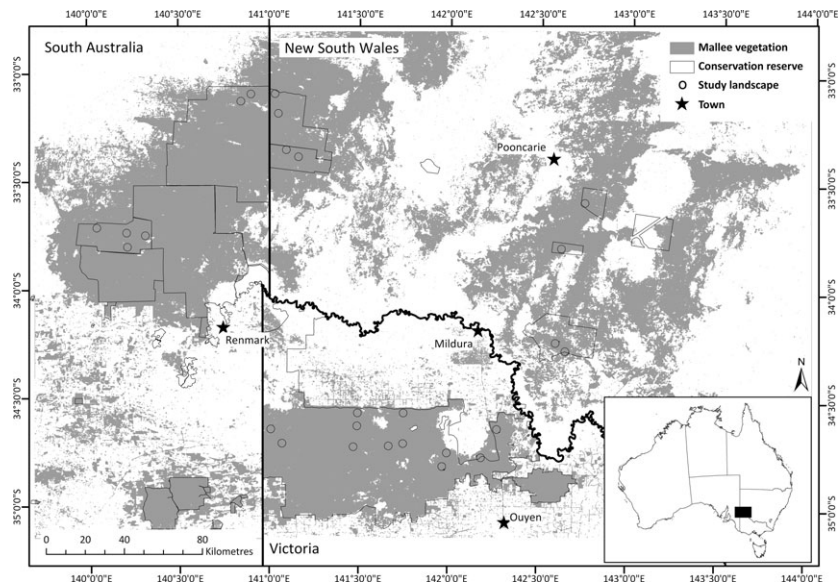
## METHODS

### Study area

The study was undertaken in the Murray Mallee region of south-eastern Australia (Fig. 1), an area of 104,000 km<sup>2</sup> within three state jurisdictions (Victoria, New South Wales, South Australia). The region experiences a semi-arid climate (Parsons, 1994), with mean annual rainfall ranging between 220 and 330 mm (data sourced from the Australian Bureau of Meteorology). The study region is characterized by a dune-swale system with limited topographic variation (Bradstock & Cohn, 2002). Native vegetation is dominated by 'tree mallee' vegetation (Fig. 1), characterized by multi-stemmed *Eucalyptus* species occurring as low shrubby trees (Parsons, 1994; Bradstock & Cohn, 2002). We previously developed a GIS layer of the spatial distribution of distinct types of tree mallee vegetation (Haslem *et al.*, 2010). The dominant vegetation types are 'triodia mallee' and 'chenopod mallee'. Triodia mallee is characterized by an understorey of the hummock grass *Triodia scariosa*, and both *Eucalyptus socialis* and *E. dumosa* generally are abundant in the canopy. Chenopod mallee is dominated by the canopy species, *E. gracilis* and *E. oleosa*, with a variable understorey of shrubs and/or chenopod species.

### Fire mapping

Landsat imagery was used to map the fire history of the study area between 1972 and 2007. Individual fires were located, and their fire boundaries (including unburned internal patches) were digitized by examining a chronosequence of 15 satellite images with resolutions of 25 m<sup>2</sup> (1989–2007) and 50 m<sup>2</sup> (1972–1988) in ENVI 4.2. Digitized images were then exported to ArcVIEW 9.2 for data checking and to add attributes. A precise fire year was assigned to fire patches with reference to management reports and personnel from natural resource management agencies. Satellite imagery was incomplete prior



**Figure 1** Location of 26 (4-km diameter) study landscapes (open circles) in the Murray Mallee region of south-eastern Australia.

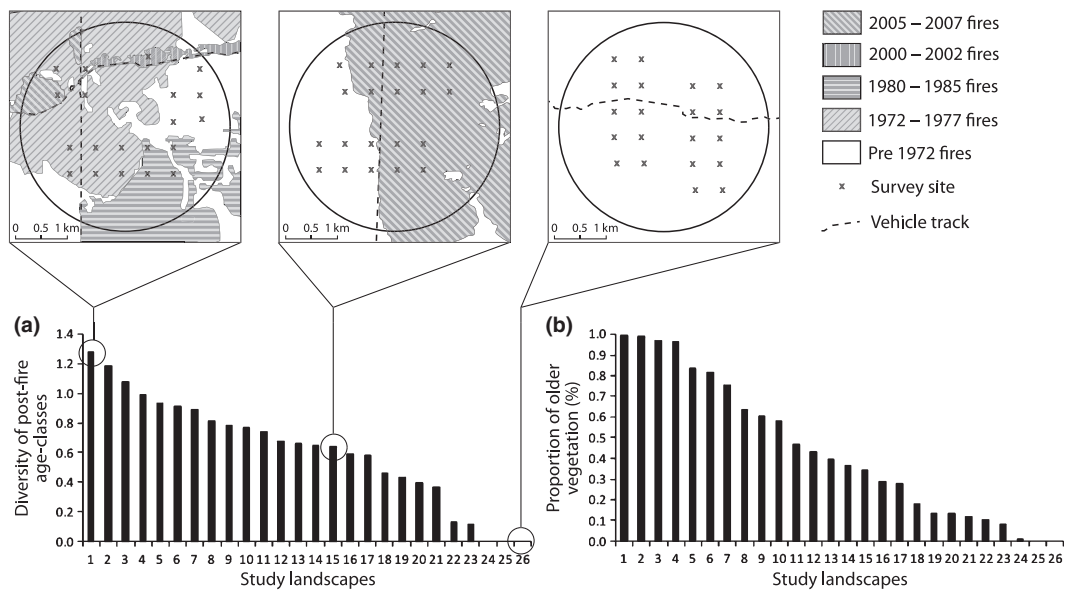
to 1972. Thus, areas burned before 1972 collectively represent ‘older’ vegetation (> 35 years since fire). We used this fire history map of the study region to select study landscapes.

**Study design**

Twenty-eight study landscapes were selected, each 4-km diameter circles (c. 12.5 km<sup>2</sup>). This size was chosen because it captured the variation in key landscape properties examined, at a scale commensurate with fire management and likely to be ecologically meaningful for avifaunal populations. Prior to analyses, two landscapes were excluded because they were dominated by a different vegetation type (Haslem *et al.*, 2010);

hence, only 26 landscapes were considered in this study (Fig. 1). Landscapes were selected along two gradients: first, the variation in fire-mediated heterogeneity (Fig. 2a), determined using Shannon’s diversity index (Magurran, 2004); and second, variation in the proportional extent of older vegetation (> 35 years since fire) (Fig. 2b). Landscapes were situated at least 2 km apart. *Triodia mallee* and chenopod mallee vegetation accounted for 71.4% and 27.5% of the total area within landscapes, respectively.

Bird surveys were conducted at 20 sites within each study landscape. The number and locations of sites were assigned proportional to the area of the study landscape covered by each fire age-class. For example, an element comprising 40% of a



**Figure 2** Depiction of (a) the diversity of post-fire age classes (Shannon’s diversity index) and (b) the proportion of older vegetation (i.e. > 35 years since fire) in the 26 study landscapes. Examples of three study landscapes with differing diversities of fire age classes are shown.

landscape was allocated eight of the 20 sites. We did not sample elements that represented < 1.5% of the area of a landscape. In general, sites were positioned > 500 m from their nearest neighbour and > 100 m from fire-scar boundaries. At least four sites were assigned to each quadrant of a landscape to ensure adequate spatial representation of sampling in landscapes. Sites within age classes were allocated between different features of the landscape (e.g. dune crests, slopes, swales and flats) to account for topographic variation.

### Predictor variables

Landscape variables were calculated using FRAGSTATS version 3.3 (McGarigal *et al.*, 2002) from vegetation and fire mapping data. Three variables described the *extent* of elements within landscapes (Table 1): (1) the proportion of older vegetation (ExtOld); (2) the proportion of recently burned vegetation (< 10 years since fire: ExtNew) and (3) the proportion of triodia mallee vegetation (ExtTMV). The degree of fire-mediated heterogeneity in landscapes (Table 1: HetFire) was characterized by the number of fire age classes and their proportional area, using Shannon's diversity index (Magurran, 2004). Fire age classes that comprised < 1.5% of the landscape were excluded. We also examined predictor variables characterized by fire-age contrasts (edge 'contrast' variables generated by FRAGSTATS) for which we allocated different contrast values to different fire ages. In each case, the contrast variable was positively correlated with the proportional extent of recently burned vegetation (Pearson correlation coefficients:  $r = 0.81$  and  $0.76$ , respectively) and so, to avoid collinearity, these were not included in analyses.

The biogeographic context of landscapes was also included, by using variables to represent 'northing' and 'easting' of each landscape (Table 1). Pearson correlation coefficients between final predictor variables were < 0.5.

### Bird data

Four rounds of bird surveys were conducted during the austral spring and autumn of 2006/2007 and 2007/2008. Surveys commenced within 15 min of sunrise on days without strong wind or persistent rain. RST and SJW conducted all sampling. A single landscape was surveyed each day. All sites were

surveyed twice by each observer, and the order of surveys was varied to ensure that every site was surveyed twice during early morning. At each site, we undertook 5-min point counts during which birds within a 60-m radius were recorded. Distance estimates from the census point to the first position of detection of each individual (visual or aural) were recorded to allow analysis of detectability. Distance estimates were measured by a rangefinder (Opti-logic Laser Rangefinder-600 yd) where possible. Birds flying above the canopy (e.g. raptors) and nocturnal species were excluded from analyses.

Upon completion of 5-min surveys, four threatened species [Mallee emu-wren (*Stipiturus mallee*), striated grasswren (*Amytornis striatus*), black-eared miner (*Manorina melanotis*) and red-lored whistler (*Pachycephala rufogularis*)] were targeted with a standardized call playback of their vocalizations. An individual detected using playback was recorded as present at that site. During surveys, yellow-throated miners (*Manorina flavigula*) were intermingled with groups of black-eared miners and/or hybrids of the two species. To eliminate potential misclassification errors, they were recorded as a single species complex in all surveys.

The detectability of birds can vary by species and vegetation type, resulting in potential bias in count data. To investigate the possibility of detection bias, we used the distance estimates of species to model the variation in species' detectability by using multiple-covariate distance sampling (Buckland *et al.*, 2004) in DISTANCE version 5.2 (Thomas *et al.*, 2006b). Vegetation density was included as a covariate in the model. Species with too few records to model individually were grouped with similar species, and a common detection function was generated (following Allredge *et al.*, 2007). Most species (and species groups) exhibited high probabilities of detection within 60-m radius point surveys, with the lowest probability of detection calculated for the group comprising splendid (*Malurus splendens*) and variegated fairy-wrens (*M. lamberti*) ( $P = 0.44$ , 95% CI 0.29–0.66,  $n = 67$ ). Detection probabilities of species were not significantly biased by vegetation density. Therefore, adjusting species abundance for detectability to estimate species richness of birds was not considered necessary.

Bird species richness metrics for total species, threatened species and rare species were calculated for each landscape. A species contributed to the species richness of a landscape if it

Variable	Abbreviation	Description
Older vegetation	ExtOld	Proportion of landscape > 35 years since fire
Recently burned vegetation	ExtNew	Proportion of landscape < 10 years since fire
Triodia mallee vegetation	ExtTMV	Proportion of triodia mallee vegetation in a landscape
Fire-mediated heterogeneity	HetFire	Diversity of post-fire age classes in a landscape calculated using Shannon's diversity index
Northing	North	Northing coordinate at centre of landscape
Easting	East	Easting coordinate at centre of landscape

**Table 1** Summary of predictor variables used in analyses.

was detected during bird surveys or standardized call playback (for the four target species only). Threatened species were classified from listings compiled by federal and state natural resource management agencies (see Table S1 in Supporting Information). Rare species were defined as those recorded in six or fewer landscapes and were also distinguished by their rarity within the study area; each detected at < 2.5% of sites.

### Statistical analyses

We modelled relationships between the richness of each response group and the six predictor variables (Table 1) using generalized linear models (GLMs) with a Gaussian distribution. For all analyses, each landscape was treated as a single sampling unit.

Preliminary univariate analyses were undertaken to investigate possible non-linear relationships between response and predictor variables using GLMs. Models represented by untransformed and second-order polynomial terms were compared; the polynomial term was retained where it was significant ( $P < 0.05$ ), and support for the polynomial model was substantially higher than for an untransformed model [Akaike's information criterion (AIC) difference > 2: Burnham & Anderson, 2002]. Predictor variables were standardized (mean 0, standard deviation 1) to enable a direct comparison of regression parameters (Quinn & Keough, 2002).

Response variables were tested for spatial autocorrelation using Moran's  $I$  test statistic calculated using the `SPDEPACKAGE` v.0.4 in R (R Development Core Team, 2010). We tested for autocorrelation in the residuals of each response variable, calculated from the 'global model' (i.e. model with all six predictor variables included) within nearest neighbour (landscape) groups ranging from the two nearest landscapes, up to the 10 nearest landscapes (i.e. nine separate groups tested for each response variable). All landscape pairs at distances < 50 km were examined.

We investigated the influence of predictor variables on response variables using an information-theoretic approach (Burnham & Anderson, 2002). For each response variable, we compared the level of support of all subsets of models ( $n = 63$ ) using AIC, corrected for small sample size ( $AIC_c$ ). Models were ranked using Akaike weights ( $w_i$ ), which indicate the relative likelihood that a given model is the 'best' (most parsimonious) of all models considered (Burnham & Anderson, 2002). Akaike weights are based on the fit of the model to the data, penalized for the increasing number of parameters (complexity) in the model (Burnham & Anderson, 2002). When no single best model ( $w_i > 0.9$ ) was identified (as was the case for all response variables in this study), we derived model-averaged parameter coefficients and standard errors for each predictor variable. Important predictor variables were identified as those for which the 95% confidence intervals of model-averaged coefficients did not include zero (Burnham & Anderson, 2002). The relative importance of predictor variables was also assessed by summing  $w_i$  for all models in which a predictor variable occurred: the larger the summed  $w_i$ , the more important that

predictor variable was relative to others (Burnham & Anderson, 2002).

We used  $r^2$  values from the model-averaged models to indicate model fit for each response variable, which were calculated using the sums of squares values and applying model-averaged coefficients (Quinn & Keough, 2002).

Cross-validation was used to assess the predictive performance of the global model for each response variable (Pearce & Ferrier, 2000). Study landscapes were divided randomly into seven groups (five groups of four and two groups of three). For each group, we fitted a model to the data from the other six groups, until all landscapes had predictions derived from independent data. The mean correlation (and standard error) between observed and predicted values was determined by averaging across all seven groups. We used the median of three cross-validated trials to evaluate models.

Calculation of  $w_i$  using  $AIC_c$ , model-averaged parameter estimates and cross-validation was undertaken using source code (M. Scroggie, unpublished data; Elith *et al.*, 2008) in R (R Development Core Team, 2010).

## RESULTS

In total, 64 species of birds were recorded during surveys across 26 landscapes, including 20 threatened species and 24 rare species (see Table S2). Mean species richness recorded in landscapes was 30.3 (range, 24–40, SD = 3.8). Fewer threatened and rare species were recorded in landscapes, with mean richness values of 8.1 (range, 5–13, SD = 1.9) and 2.9 (range, 0–7, SD = 1.7), respectively.

### Model evaluation

Model fit, indicated by model-averaged  $r^2$ , was high for total (0.67), threatened (0.52) and rare species richness (0.57), respectively (Table 2). A mean cross-validation correlation of  $\geq 0.70$  for total species richness suggests that this model has a high level of predictive accuracy (Table 2). The models for the richness of threatened and rare species exhibited a moderate to high predictive performance, with mean cross-validation correlations of 0.54 and 0.42, respectively (Table 2). No effects of spatial autocorrelation were detected for response variables.

### Fire-mediated spatial properties

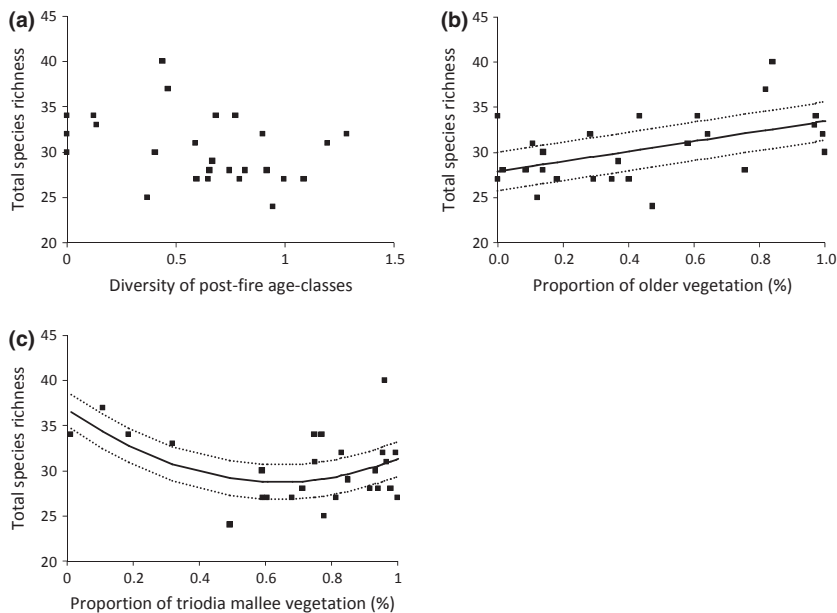
Model-averaging analyses indicated that fire-mediated heterogeneity in landscapes was not an influential factor for any of the three species richness response variables considered (Table 2, Fig. 3a), as indicated by the low summed  $w_i$  values for fire-mediated heterogeneity, relative to other predictor variables (Fig. 4a–c).

Total and rare species richness was strongly influenced by the amount of older vegetation in landscapes (Table 2, Fig. 3b). In all cases, response variables were positively associated with landscapes with more of this element. The

**Table 2** Summary of model-averaged parameter coefficients and standard errors (SE) for predictor variables for each of the richness response groups.

Species richness	Intercept	ExtOld	ExtNew	ExtTMV	ExtTMV2	HetFire	North	East	$r^2$	CroVal
Total	28.94 (0.98)	<b>1.38 (0.62)</b>	0.02 (0.36)	1.56 (0.96)	<b>1.47 (0.59)</b>	-0.05 (0.33)	-1.26 (0.71)	-0.98 (0.76)	0.67	0.75 (0.07)
Threatened	8.12 (0.3)	0.35 (0.34)	-0.27 (0.33)	0.64 (0.39)		0.02 (0.16)	-0.41 (0.38)	<b>-1.26 (0.48)</b>	0.52	0.54 (0.17)
Rare	2.34 (0.43)	<b>0.84 (0.27)</b>	-0.003 (0.15)	0.37 (0.36)	<b>0.6 (0.26)</b>	0.04 (0.18)	-0.03 (0.14)	0.01 (0.12)	0.57	0.42 (0.23)

Bold type indicates predictor variables for which the 95% confidence interval of the model-averaged coefficients did not include zero. Model-evaluation statistics include model-averaged  $r^2$  and mean cross-validation correlation values (CroVal) with standard errors in parentheses. ExtTMV was the only variable with a second-order polynomial term for total and rare species richness.



**Figure 3** Examples of relationships between total species richness in landscapes and (a) the diversity of post-fire age classes, (b) the proportion of older vegetation (> 35 years since fire) and (c) the proportion of triodia mallee vegetation. Predicted trends and 95% confidence intervals (broken lines) are depicted for important predictor variables (i.e. those for which the 95% confidence intervals of model-averaged coefficients did not include zero). Squares represent raw data.

importance of older vegetation to response variables investigated was also indicated by larger values of summed  $w_i$  (Fig. 4a,c).

No species richness groups were strongly associated with the amount of recently burned vegetation in landscapes (Table 2). This element also ranked poorly in summed  $w_i$  for all response variables (Fig. 4a–c).

### Vegetation type

Model-averaging analyses identified significant second-order polynomial relationships between total and rare species richness and the amount of triodia mallee in landscapes, which indicated that these response variables were higher in landscapes with less of this vegetation type (and therefore, more chenopod mallee: Table 2, Fig. 3c). The importance of vegetation type for mallee avifauna was also indicated by its high ranking in summed  $w_i$  of all response variables (Fig. 4a–c).

### Biogeographic context

Model-averaging analyses indicated that threatened species richness was strongly associated with landscapes located in the

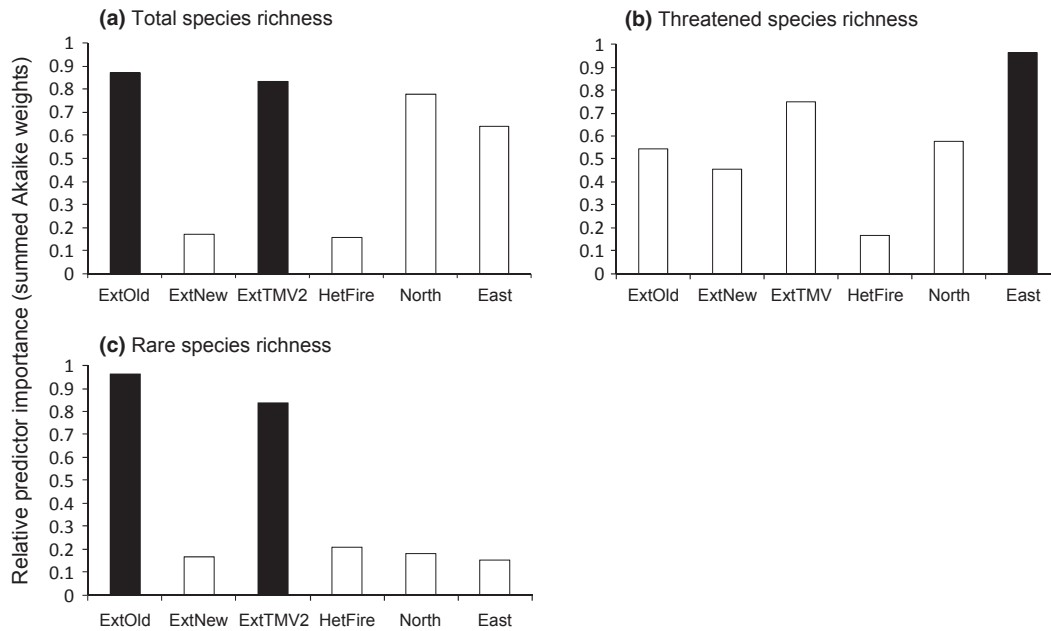
western portion of the study area (Table 2). Summed  $w_i$  provided confirmation of this result, with the east–west biogeographic gradient ranking first for this response variable (Fig. 4c). In contrast, the north–south biogeographic gradient was not important for any response variable (Table 2).

## DISCUSSION

To our knowledge, this study is the first to specifically investigate the relative effects of fire-mediated spatial properties on bird assemblages at the scale of the ‘whole landscape’. An understanding of animal responses to whole landscapes is critically important if one is to understand the ecological value of their differing spatial properties (Wiens, 1994; Fahrig, 2003; Bennett *et al.*, 2006).

### Fire-mediated spatial properties

Increased fire-mediated heterogeneity in study landscapes (12.5 km<sup>2</sup>) was not associated with increased richness of birds. This result is contrary to: (1) the general notion that increased heterogeneity of landscape elements will promote faunal diversity (Huston, 1994; Tews *et al.*, 2004), (2) major paradigms underpinning fire ecology and management (Brockett



**Figure 4** Summary of the relative importance of predictor variables affecting the richness of bird species [(a) total species richness, (b) threatened species richness, (c) rare species richness] in study landscapes according to the summed Akaike weights of each predictor variable. Filled columns indicate predictor variables for which the 95% confidence interval of the model-averaged coefficients did not include zero.

*et al.*, 2001; Parr & Andersen, 2006) and (3) fire-management strategies in the study region (e.g. Department of Sustainability and Environment, 2008). Our findings also differ from studies in other fire-prone environments (e.g. see reviews by Smith, 2000; Kotliar *et al.*, 2002; Saab & Powell, 2005) that suggest that a range of seral states is required to maintain avifaunal assemblages. However, as these studies do not directly consider the effects of spatial properties on bird assemblages at a landscape scale (i.e. most were conducted at the site scale), the capacity for comparison between our research and these studies is limited.

Why did fire-mediated heterogeneity have no effect on mallee bird assemblages? One explanation may be that birds do not perceive heterogeneity as we measured it as ecologically meaningful (i.e. diversity of different post-fire age classes in a 12.5-km<sup>2</sup> landscape). Heterogeneity may be more appropriately defined as the diversity of different 'seral states' (as opposed to fire age classes) in a landscape, where a seral state is defined by habitat resources identified as important to fauna that are present within specific periods after fire (e.g. Fox, 1982). Under such circumstances, different fire age classes may comprise a single seral state. However, our measure of heterogeneity remains important as it provides a direct assessment of management strategies in the study region (e.g. Department of Environment and Heritage, 2008; Department of Sustainability and Environment, 2008) and other fire-prone environments (Parr & Andersen, 2006). In this context, the finding that an increased diversity of fire age classes in the landscape did not enhance the richness of birds suggests that current fire management for avifaunal conservation may require substantial refinement.

Our analyses identified no strong associations between the richness of bird species and the extent of recently burned vegetation in landscapes. The fire-mediated heterogeneity concept depends on the existence of different species that require different fire age classes to persist (Bradstock *et al.*, 2005; Parr & Andersen, 2006). Consequently, the lack of a strong positive response to recently burned vegetation by any of the response groups investigated may explain the negligible effect of fire-mediated heterogeneity. Indeed, related work investigating the responses of individual species of bird to fire-mediated spatial properties of landscapes (R. Taylor, unpublished data) did not identify any species that depend on recently burned vegetation in mallee shrublands. These findings contrast with avifaunal assemblages in other fire-prone regions (Herrando *et al.*, 2002; Kotliar *et al.*, 2002; Hutto *et al.*, 2008), where early seral-stage specialists represent key components of the avifauna. In these regions, early seral-stage specialists are thought to rely on the predictable occurrence of ephemeral resources in recently burned vegetation (e.g. Hutto *et al.*, 2008). Our findings suggest no similar provision of reliable ephemeral resources is available for birds in semi-arid mallee ecosystems.

In contrast, total and rare bird species richness was positively associated with the amount of older vegetation in landscapes. Interestingly, threatened species richness was not strongly associated with the amount of older vegetation in landscapes, a finding that contrasts with earlier research investigating several threatened birds that appear to exhibit strong preferences for this element (Meredith, 1982; Woinarski, 1989; Benshemesh, 1990; Clarke *et al.*, 2005). This finding suggests that at least for some threatened species, the amount

of older vegetation in the landscape is not a critical element for their persistence. Nevertheless, the positive influence of older vegetation on total and rare species richness suggests a strong preference for this element by the mallee avifauna generally and provides additional evidence for the lack of influence of fire-mediated heterogeneity. It is likely that within such older vegetation, species may show a range of affinities for different fire age classes, given that some fire-affected structural attributes that are likely to be important to species continue to change for at least 110 years following fire (Haslem *et al.*, 2011). A better understanding of species' associations with structural attributes of vegetation (and other habitat resources) that define seral states would lead to more effective faunal management in fire-prone environments.

Our inability to detect a relationship between fire-mediated heterogeneity and richness of bird species may also be an artefact of the fixed spatial scale at which we sampled landscapes. Responses of organisms to patterns and processes are scale-dependent (Levin, 1992). Thus, developing an understanding of the effects of landscape heterogeneity on biota requires that we record both the species of interest, and the landscape pattern, at a spatial scale relevant to species. Adopting a fixed sampling scale is unlikely to be appropriate for all species examined. Nevertheless, the sampling scale adopted was consistent with the scale of prescribed burning conducted in reserves. Our results suggest that manipulating fire to maximize landscape heterogeneity at this scale is unlikely to enhance species richness of birds in general, or of threatened or rare species of birds.

### Vegetation type

Unlike other landscape-scale studies (e.g. Pino *et al.*, 2000; Atauri & de Lucio, 2001), bird species richness was not positively associated with greater vegetation diversity (in this case: landscapes with similar amounts of *triodia* mallee and *chenopod* mallee). Instead, total and rare species richness was positively associated with landscapes with greater amounts of *chenopod* mallee. Differences in the proportional area of fire age classes between vegetation types in study landscapes may explain this result. Older vegetation was more common in *chenopod* mallee (recently burned = 7.3%, older = 66.7%) than *triodia* mallee (recently burned = 26.5%, older = 36.1%). Thus, the strong positive association between total and rare species richness and landscapes with older vegetation may explain the preference of these response variables for landscapes with more *chenopod* mallee. Ideally, future research in fire-prone environments should control for differences in the proportion of fire age classes when investigating the needs of bird assemblages for particular vegetation types from a landscape perspective.

### Biogeographic context

The richness of threatened birds was strongly influenced by the east–west biogeographic gradient across the study area, with

this response variable higher in more westerly landscapes. The size and position of conservation reserves within the Murray Mallee region may be driving this response. For example, the largest continuous block of mallee vegetation (c. 700,000 ha) in the Murray Mallee, the Bookmark Biosphere Reserve (Department of Environment and Heritage, 2008), is situated in the western portion of the study area. The size of the Bookmark Biosphere Reserve relative to even the most catastrophic wildfire events (e.g. > 100,000 ha wildfires) may be sufficient to protect populations of threatened species, which otherwise may become locally extinct in smaller reserves subject to large wildfires (e.g. Brown *et al.*, 2009). Effective fire management within the Bookmark Biosphere Reserve is likely to be critical for maintaining region-wide avian diversity.

### Study design considerations

We investigated responses of birds to fire-mediated landscape structure using a space-for-time substitution approach. Valid comparison of avian response groups between study landscapes under this approach requires several assumptions: (1) landscapes comprise similar pre-fire faunal compositions; (2) fire-induced patches of a similar age have experienced the same post-fire disturbance regimes (e.g. climate and grazing); and (3) these similarly aged patches should also have matching fire regimes (Gill, 1975), including shared characteristics of the most recent fire event (e.g. intensity, severity and season of fire) and the history of previous fires. While it is impossible to experimentally control all of these factors at the landscape scale using any other approach, it must be recognized that conformity to these assumptions is unlikely, and key findings in this study should be interpreted with caution.

We did not consider the influence on bird assemblages of differing configurations of fire-mediated patches in landscapes (e.g. size, shape and interspersed patches with differing fire histories, amount of ecotone habitat). Little quantitative data pertaining to such relationships exist from fire-affected environments. Despite this, at least one management strategy (Department of Sustainability and Environment, 2008) supports the creation of ecotone habitat in mallee ecosystems using prescribed burning to achieve an irregular spatial mix of recently burned and long-unburned patches. Hence, there remains an urgent need to determine the possible influence that differing fire-mediated configurations, and ecotone habitat, have on birds from a landscape perspective.

In this study, we infer the biodiversity value of landscapes for avifauna from the relative influence of predictor variables on the richness of species. However, important relationships between richness measures and predictor variables may not be detected if similar numbers of species exhibit positive and negative responses. Additionally, significant responses by a few species may be 'swamped' when the majority of species exhibit an opposing, or null, response. Nevertheless, species richness remains the most common measure of, and an important indicator of, biodiversity (Gaston, 2000; Myers *et al.*, 2000). Moreover, the use of species richness measures is important for



incorporating the needs of rarely recorded species, when total detections of these species are too few to allow meaningful species-specific analyses.

While birds comprise a key component of the biota of mallee ecosystems, developing effective fire-management strategies for the conservation of biodiversity also requires knowledge of how other organisms (e.g. mammals, reptiles, invertebrates and plants) respond to differing fire-mediated properties of landscapes. Studies of such taxa have been undertaken contemporaneously with this study and will provide a complementary perspective for determining management strategies appropriate for all biotic components of mallee ecosystems.

### Management implications

Our findings do not support the widely accepted notion that fire-mediated heterogeneity benefits biodiversity, suggesting that the use of prescribed burning to 'create' heterogeneity in the landscape may detrimentally affect components of the mallee avifauna. In contrast, management to protect older vegetation is supported. Indeed, protection of older vegetation may be essential if future climate changes result in increased fire frequency in mallee shrublands (Pitman *et al.*, 2007). Managing for extensive older vegetation also provides the flexibility to implement a range of management strategies in the future (Good, 1981). For example, in the event that 'obligate', early seral-state specialists are identified in mallee vegetation, and natural wildfires have not delivered sufficient areas of this element already; then, conversion of older vegetation to recently burned vegetation can be achieved quickly and easily. The opposite is not true.

While bird assemblages did not respond positively to fire-mediated heterogeneity at the spatial scale of the study landscapes (12.5 km<sup>2</sup>), the goal to manage for extensive areas of older vegetation does not obviate the need for a diversity of post-fire ages at larger (e.g. reserve or region) scales to ensure the progression of seral stages over time. The slow recovery of key structural attributes of vegetation in mallee ecosystems (e.g. at least 110 years: Haslem *et al.*, 2011) suggests that land managers can maintain a progression of seral stages while continuing to manage for large amounts of older vegetation (i.e. > 35 years since fire) in the landscape.

Contemporary understanding of animal–fire relationships has been derived primarily from site-scale studies, which typically investigate the influence of the characteristics of fire (e.g. time-since-fire, fire severity) and associated fire-affected structural attributes on animal distributions (Driscoll *et al.*, 2010). We consider that studies that compare 'whole' landscapes serve a vital function in ongoing fire ecology research and management by elucidating animal preferences for particular fire-mediated landscapes, usefully complementing site-based knowledge. Our study highlights the value of applying a landscape-scale approach to test fundamental assumptions that underpin ecological management of fire around the world.

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### REFERENCES

- Allredge, M.W., Pollock, K.H., Simons, T.R. & Shriner, S.A. (2007) Multiple-species analysis of point count data: a more parsimonious modelling framework. *Journal of Applied Ecology*, **44**, 281–290.
- Atauri, J.A. & de Lucio, J.V. (2001) The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. *Landscape Ecology*, **16**, 147–159.
- Bennett, A.F., Radford, J.Q. & Haslem, A. (2006) Properties of land mosaics: implications for nature conservation in agricultural environments. *Biological Conservation*, **133**, 250–264.
- Benshemesh, J. (1990) Management of the malleefowl with regard to fire. *The mallee lands: a conservation perspective* (ed. by J.C. Noble, P.J. Joss and G.K. Jones), pp. 206–211. CSIRO, Melbourne.
- Biggs, H.C. & Potgieter, A.L.F. (1999) Overview of the fire management policy of the Kruger National Park. *Koedoe*, **42**, 101–110.
- Bond, W.J. & Keeley, J.E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution*, **20**, 387–394.
- Bowman, D.M.J.S., Balch, J.K., Artaxo, P. *et al.* (2009) Fire in the earth system. *Science*, **324**, 481–484.
- Bradstock, R.A. & Cohn, J.S. (2002) Fire regimes and biodiversity in semi-arid mallee ecosystems. *Flammable Australia: the fire regimes and biodiversity of a continent* (ed. by R.A. Bradstock, J.E. Williams and M.A. Gill), pp. 238–258. Cambridge University Press, Cambridge.
- 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 Research*, **32**, 409–423.
- Brawn, J.D., Robinson, S.K. & Thompson, F.R. (2001) The role of disturbance in the ecology and conservation of birds. *Annual Review of Ecology, Evolution and Systematics*, **32**, 251–276.

- Brockett, B.H., Biggs, H.C. & van Wilgen, B.W. (2001) A patch mosaic burning system for conservation in southern African savannas. *International Journal of Wildland Fire*, **10**, 169–183.
- Brown, S., Clarke, M.F. & Clarke, R.H. (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*). *Biological Conservation*, **142**, 432–445.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (eds) (2004) *Advanced distance sampling: estimating abundance of biological populations*. Oxford University Press, New York.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodal inference: a practical information-theoretical approach*, 2nd edn. Springer-Verlag, New York.
- Clarke, M.F. (2008) Catering for the needs of fauna in fire management: science or just wishful thinking? *Wildlife Research*, **35**, 385–394.
- Clarke, R.H., Boulton, R.L. & Clarke, M.F. (2005) Estimating population size of the black-eared miner, with an assessment of landscape-scale habitat requirements. *Pacific Conservation Biology*, **11**, 174–188.
- Dellasala, D.A., Williams, J.E., Williams, C.D. & Franklin, J.F. (2004) Beyond smoke and mirrors: a synthesis of fire policy and science. *Conservation Biology*, **18**, 976–986.
- Department of Environment and Heritage. (2008) *Bookmark mallee fire management plan*. Department for Environment and Heritage, Adelaide.
- Department of Sustainability and Environment. (2008) *Mildura District fire protection plan*. Department of Sustainability and Environment, Melbourne.
- Driscoll, D.A., Lindenmayer, D.B., Bennett, A.F., Bode, M., Bradstock, R.A., Carey, G., Clarke, M.F., Dexter, N., Fensham, R., Friend, G.R., Gill, A.M., James, S., Kay, G., Keith, D.A., MacGregor, C., Russell-Smith, J., Salt, D., Watson, J., Williams, R.J. & York, A. (2010) Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation*, **143**, 1928–1939.
- Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, **77**, 802–813.
- Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics*, **34**, 487–515.
- Fox, B.J. (1982) Fire and mammalian secondary succession in an Australian coastal heath. *Ecology*, **63**, 1332–1341.
- Fuhlendorf, S.D., Harrell, W.C., Engle, D.M., Hamilton, R.G., Davis, D.A. & Leslie, D.M. (2006) Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecological Applications*, **16**, 1706–1716.
- Garnett, S.T. & Crowley, G.M. (2000) *The action plan for Australian birds 2000*. Natural Heritage Trust, Commonwealth of Australia, Canberra.
- Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.
- Gill, A.M. (1975) Fire and the Australian flora. *Australian Forestry*, **38**, 4–25.
- Gill, A.M., Bradstock, R.A. & Williams, J.E. (2002) Fire regimes and biodiversity: legacy and vision. *Flammable Australia: the fire regimes and biodiversity of a continent* (ed. by R.A. Bradstock, J.E. Williams and A.M. Gill), pp. 429–446. Cambridge University Press, Cambridge.
- Good, R. (1981) Adaptations of Australian plants to fires. *Bushfires: their effect on Australian life and landscape* (ed. by P. Stanbury), pp. 48–59. The Macleay Museum, Sydney.
- Haslem, A., Callister, K.E., Avitabile, S.C., Griffioen, P.A., Kelly, L.T., Nimmo, D.G., Spence-Bailey, L.M., Taylor, R.S., Watson, S.J., Brown, L., Bennett, A.F. & Clarke, M.F. (2010) A framework for mapping vegetation over broad spatial extents: a technique to aid land management across jurisdictional boundaries. *Landscape and Urban Planning*, **97**, 296–305.
- Haslem, A., Kelly, L.T., Nimmo, D.G., Watson, S.J., Kenny, S., Taylor, R.S., Avitabile, S.C., Callister, K.E., Spence-Bailey, L.M., Clarke, M.F. & Bennett, A.F. (2011) Habitat or fuel? Implications of long-term, post-fire dynamics in the development of key resources for fauna and fire. *Journal of Applied Ecology*, **48**, 247–256.
- Herrando, S., Brotons, L., Del Amo, R. & Llacuna, S. (2002) Bird community succession after fire in a dry Mediterranean shrubland. *Ardea*, **90**, 303–310.
- Huston, M.A. (1994) *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, Cambridge.
- Hutto, R.L. (1995) Composition of bird communities following stand-replacement fires in Northern Rocky Mountain (U.S.A.) conifer forests. *Conservation Biology*, **9**, 1041–1058.
- Hutto, R.L., Conway, C.J., Saab, V.A. & Walters, J.R. (2008) What constitutes a natural fire regime? Insights from the ecology and distribution of coniferous forest birds in North America. *Fire Ecology*, **4**, 115–132.
- Kotliar, N.B., Hejl, S.J., Hutto, R.L., Saab, V.A., Melcher, C.P. & McFadden, M.E. (2002) Effects of fire and post-fire salvage logging on avian communities in conifer-dominated forests of the western United States. *Studies in Avian Biology*, **25**, 49–64.
- Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943–1967.
- Magurran, A.E. (2004) *Measuring biological diversity*. Blackwell Science Ltd, Oxford.
- McGarigal, K., Cushman, S.A., Neel, M.C. & Ene, E. (2002) *FRAGSTATS: spatial pattern analysis program for categorical maps, version 3.3*. University of Massachusetts, Amherst. Available at: <http://www.umass.edu/landeco/research/fragstats/fragstats.html> (accessed 15 June 2009).
- Meredith, C.W. (1982) The research input to fire management in natural areas with particular reference to wildlife research in the semi-arid lands of Victoria and New South Wales. *Fire ecology in semi-arid lands* (ed. by A. Heislers, P. Lynch and B. Walters), pp. 1–10. CSIRO, Deniliquin, New South Wales.

- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.
- Noss, R.F., Franklin, J.F., Baker, W.J., Schoennagel, T. & Moyle, P.B. (2006) Managing fire-prone forests in the western United States. *Frontiers in Ecology and the Environment*, **4**, 481–487.
- Parr, C.L. & Andersen, A.N. (2006) Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. *Conservation Biology*, **20**, 1610–1619.
- Parr, C.L. & Chown, S.L. (2003) Burning issues for conservation: a critique of faunal fire research in southern Africa. *Austral Ecology*, **28**, 384–395.
- Parsons, R.F. (1994) Eucalyptus scrubs and shrublands. *Australian vegetation* (ed. by R.H. Groves), pp. 291–319. Cambridge University Press, Cambridge.
- Pearce, J. & Ferrier, S. (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling*, **133**, 225–245.
- Pino, J., Roda, F., Ribas, J. & Pons, X. (2000) Landscape structure and bird species richness: implications for conservation in rural areas between natural parks. *Landscape and Urban Planning*, **49**, 35–48.
- Pitman, A.J., Narisma, G.T. & McAneney, J. (2007) The impact of climate change on the risk of forest and grassland fires in Australia. *Climatic Change*, **84**, 383–401.
- Quinn, J.P. & Keough, M.J. (2002) *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge.
- R Development Core Team. (2010) *A language and environment for statistical computing*. Royal Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org>.
- Saab, V.A. & Powell, H.D.W. (2005) Fire and avian ecology in North America: process influencing pattern. *Studies in Avian Biology*, **30**, 1–13.
- Smith, J.K. (ed.) (2000) *Wildland fire in ecosystems: effects of fire on fauna*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- Sousa, W.P. (1985) The role of disturbance in natural communities. *Annual Review of Ecology, Evolution and Systematics*, **15**, 353–391.
- Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, **31**, 79–92.
- Thomas, J.W., Franklin, J.F., Gordon, J. & Johnson, K.N. (2006a) The Northwest Forest Plan: origins, components, implementation experience, and suggestions for change. *Conservation Biology*, **20**, 277–287.
- Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B. & Marques, T.A. (2006b) Distance 5.0 release 2. Research unit for wildlife population assessment, University of St. Andrews, UK. Available at: <http://www.ruwpa.st-and.ac.uk/distance/> (accessed 14 October 2008).
- Turner, M.G., Romme, W.H. & Tinker, D.B. (2003) Surprises and lessons from the 1988 Yellowstone fires. *Frontiers in Ecology and the Environment*, **1**, 351–358.
- Whelan, R.J. (1995) *The ecology of fire*. Cambridge University Press, Cambridge.
- Wiens, J.A. (1994) Habitat fragmentation: island v landscape perspectives on bird conservation. *Ibis*, **137**, S97–S104.
- Williams, S.E., Marsh, H. & Winter, J. (2002) Spatial scale, species diversity and habitat structure: small mammals in Australian tropical rainforest. *Ecology*, **83**, 1317–1329.
- Woinarski, J.C.Z. (1989) The vertebrate fauna of broombush *Melaleuca uncinata* vegetation in northwestern Victoria, with reference to effects of broombush harvesting. *Australian Wildlife Research*, **16**, 217–238.
- Woinarski, J.C.Z. & Recher, H.F. (1997) Impact and response: a review of the effects of fire on the Australian avifauna. *Pacific Conservation Biology*, **3**, 183–205.

## SUPPORTING INFORMATION

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

**Table S1** Twenty threatened species of bird recorded at sites in study landscapes in the Murray Mallee region of south-eastern Australia.

**Table S2** Sixty-four species of bird recorded at sites in study landscapes in the Murray Mallee region of south-eastern Australia.

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## BIOSKETCH

**Rick Taylor's** research interests include fire ecology, landscape ecology and vertebrate conservation and management. This work was undertaken while he was a member of the Mallee Fire and Biodiversity Project.

Author contributions: All authors contributed to the development of the study design and ideas presented in this work; R.S.T. analysed all data; R.S.T. and S.J.W. collected all bird data; R.S.T. and M.F.C. led the writing.

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