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Multi-century periods since fire in an intact woodland landscape favour bird species declining in an adjacent agricultural region

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ABSTRACT

Habitat modification by fire and habitat loss via anthropogenic vegetation clearance and fragmentation both impact animal populations. Yet, there has been limited investigation as to whether animals that decline under one of these types of habitat change also decline under the other, and how their cumulative impacts affect the status of species and communities. Using a ~400-year chronosequence in the world's largest extant temperate woodland in south-western Australia, we examine how time since fire affects bird community richness, reporting rates and composition, and whether taxa grouped on the basis of responses to vegetation clearance and fragmentation in an adjoining agricultural landscape are associated with either recently-burnt or long-unburnt woodlands. Consistent with substantial changes in vegetation composition and structure after fire in obligate-seeder eucalypt woodlands, woodland bird communities were strongly affected by fire. Species richness and total reporting rates increased with time since fire, and community composition changed across the entire multi-century span of the chronosequence. Woodland birds most negatively impacted by vegetation clearance and fragmentation were strongly associated with long-unburnt woodlands. In a regional south-western Australian context, where extensive vegetation clearance has substantially reduced the range and populations of many woodland bird species, the ability of remaining unfragmented woodlands to support populations of these species will be strongly contingent on appropriate fire management. Specifically, as stand-replacement fires have affected 25–30% of extant woodland over recent decades, management to limit the extent of fire in remaining long-unburnt woodlands would appear a priority for conservation of woodland bird diversity.

1. Introduction

Fire is a recurrent disturbance in seasonally dry biomes worldwide (Archibald et al., 2013) and has played a role in shaping biome distribution, function and composition for millions of years (Pausas and Keeley, 2009). An understanding of how biota respond to fire is crucial for managing fire for biodiversity conservation (Driscoll et al., 2010), as recent alterations to fire regimes via changing land management (Pausas and Keeley, 2009) have contributed to many fauna declines. These include fauna species declining due to fire suppression (e.g. in pine-oak forests, Rose and Simons, 2016) or, perhaps more commonly, due to high incidence of fire and associated lack of time for development of hollows or other habitat resources (Woinarski and Recher, 1997; Clarke, 2008; Croft et al., 2016; e.g. in fynbos, Chalmandrier

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et al., 2013; mallee woodlands, Taylor et al., 2012). While the immediate effects of fires on fauna can be significant, it is often fire-associated changes to vegetation that ultimately drives the response of animals (Fox, 1982). Anthropogenic changes to habitats, particularly vegetation clearance and fragmentation, have also widely contributed to fauna declines (Andrén, 1994; Saunders, 1989). The extent to which biota is jointly susceptible to habitat modification through inappropriate fire regimes, and habitat loss via vegetation clearance and fragmentation, is poorly understood.

Temperate woodlands are one of the most imperilled biomes both globally and within Australia (Yates and Hobbs, 1997; Hoekstra et al., 2005; Prober et al., 2017). The temperate eucalypt woodlands across much of the intermediate rainfall zone (250–1200 mm) of southern Australia have been extensively cleared and modified for agricultural activities since European colonisation (Prober et al., 2017). In many districts native vegetation cover is < 10%, with remaining woodland remnants subsequently exposed to a range of associated processes that can lead to further vegetation degradation (Yates and Hobbs, 1997; Prober and Smith, 2009; Prober et al., 2017). Mirroring the changes to vegetation, many Australian temperate woodland bird species have become threatened through substantial and ongoing population declines, range contractions or local extinctions (Robinson and Traill, 1996; Saunders, 1989; Saunders and Ingram, 1995; Ford et al., 2001; Ford, 2011). Postulated causes of temperate woodland bird declines are many and interacting, but primarily are thought to be loss of habitat, the isolation and edge effects of fragmentation, and fragmentation-linked habitat degradation and its interaction with predation, competitive interactions, and food resources, all modulated through climatic cycles such as droughts (Ford et al., 2001; Ford, 2011; Stevens and Watson, 2013). Having avoided the extensive land transformation affecting other Australian temperate eucalypt woodlands, the Great Western Woodlands (GWW; the world's largest extant temperate woodland; Watson et al., 2008) of south-western Australia is considered to have a largely intact temperate woodland bird community. Specifically, the GWW supports populations of a range of species that have declined in woodlands of the adjoining south-western Australian wheatbelt and in eastern Australia, and is sufficiently large and intact enough to allow mobile bird species to track resources at a landscape scale (Recher, 2008; Fox et al., 2016). However, multiple, large (> 100,000 ha) wildfires have collectively burnt a substantial proportion of total woodland area in the GWW in recent decades (McCaw et al., 2014; Gosper et al., 2018), hence any fire regime-related decrease in the capacity of the GWW to support woodland birds is likely to have regional and national implications for woodland bird conservation.

Fire is regarded as a relatively minor contributor to declines in Australian temperate woodland birds, and is typically referred to in general terms regarding possible impacts of specific fire events or “inappropriate fire regimes” on the persistence of populations isolated by fragmentation (Ford et al., 2001; Ford, 2011; Watson, 2011). Yet fire modifies the availability of habitat resources used by woodland birds, such as vegetation structure and composition (Gosper et al., 2013a, 2013b; Croft et al., 2016), and this modification applies irrespective of the level of fragmentation. Furthermore, the apparent low threat of fire to temperate woodland bird communities contrasts with the postulated impact of fire on some individual woodland bird species (e.g. Luck, 2002), and bird abundance and composition in other Australian temperate and semi-arid vegetation (*Acacia* shrublands, Davis et al., 2016; mallee eucalypt shrublands, Taylor et al., 2012), and in temperate woodlands, forests and shrublands globally (Herrando and Brotons, 2002; Chalmandrier et al., 2013).

There has been limited research on the response of Australian temperate woodland birds to fire (Burbidge, 2003). Turner (1992) found relatively rapid (8 years) post-fire recovery of a woodland bird community, while Recher and Davis (2013) found substantially lower richness and abundance and distinct composition of birds using woodlands recently-burnt (2–5 year old) compared to woodlands burnt longer ago. These contrasting responses occurred in woodlands where, respectively, the dominant eucalypts either resprouted or were killed (obligate-seeders) by fires. Recent syntheses of eucalypt woodland vegetation dynamics after disturbance (Prober et al., 2017; Gosper et al., 2018) have recognised that woodlands dominated by resprouter eucalypts are functionally distinct from those dominated by obligate-seeders, indicating that a more nuanced assessment of the effect of fire on woodland bird communities may be informative. One plausible mechanism which could account for differences in the response of birds to fire between resprouter-dominated and obligate-seeder-dominated eucalypt woodlands is the typically more rapid recovery of vegetation biomass after fire in the former (Bellingham and Sparrow, 2000).

Studying the response of biota to fire is inherently challenging where fires are rare and fire-return intervals are long. Some forests, woodlands and shrublands have fire intervals regularly exceeding a century (Clarke et al., 2010; Lowe et al., 2012), including the eucalypt woodlands of the GWW (O'Donnell et al., 2011; Gosper et al., 2013c). In these situations, longitudinal studies after fire events are not feasible for informing current fire management. Chronosequence studies present an opportunity to observe responses over long time-frames, but require robust means to estimate the time since fire of long-unburnt vegetation in the absence of long-term fire records (Driscoll et al., 2010). In recent years, innovative methods for ageing long-unburnt vegetation have opened up the possibility of investigating relatively long-term fire responses (Clarke et al., 2010; Gosper et al., 2013c), however, few studies have examined changes over a time period of > 100 years (but see Lowe et al., 2012).

Using the obligate-seeder *Eucalyptus salubris* (gimlet) woodland chronosequence of Gosper et al. (2013a, 2013b) in the GWW, we examined the response of birds to time since fire. This chronosequence is unique in terms of its length, conservatively spanning a ~400 year period post-fire. We asked the following questions, as a basis for assessing the implications for woodland bird conservation of the extent and spatial pattern of recent fires in the GWW:

i) Do bird community richness, reporting rates, abundance and composition change with time since fire and, if so, over what time frame?
ii) How do groups of species, defined by their response to habitat loss and fragmentation in the adjoining south-western Australian wheatbelt, respond to time since fire? Of particular interest from a conservation perspective is whether birds that have declined in the wheatbelt are strongly associated with either recently-burnt or long-unburnt woodlands.

2. Materials and methods

2.1. Survey sites

Bird surveys were conducted at 56 sites near the western edge of the GWW, between Karroun Hill (30°14′S, 118°30′E) and Parker Range (31°47′S, 119°37′E). All survey sites were in patches of relatively uniform woodland at least 2 ha in area and had a dominant overstorey of *E. salubris*, sometimes in association with other *Eucalyptus* species. Survey sites were a subset of those of Gosper et al. (2013a, 2013b), with sites sampled listed in Appendix S1. Time since fire, ranging from 6 to ~400 years, was estimated through a combination of Landsat imagery analysis, growth ring counts and growth ring-size relationships (Gosper et al., 2013c – with the values used here based on their more conservative model 2). Information on aspects of the fire regime other than time since fire (e.g. intensity, fire patch size) was not available, and neither was comprehensive historical information on other forms of disturbance.

Table 1

Bird habitat and status groups and the number of species per group. See methods for more information on how habitat and status categories were defined. Non-woodland species were aggregated across all status categories, as were woodland species in non-declining (no change, lesser wheatbelt increasers, major wheatbelt increasers) status categories. The group classification of each species is contained in Appendix S2.

Habitat	Status				
	Major wheatbelt decliners	Lesser wheatbelt decliners	No change	Lesser wheatbelt increasers	Major wheatbelt increasers
Woodland	16	29	[————	————19————	————]
Non-woodland	[————	————	————7————	————	————]

2.2. Bird surveys

Bird surveys used the 2 ha–20 min survey method recording the number of different individuals of each species (Fox et al., 2016). Six surveys were conducted at each site in autumn and spring 2013, totalling 12 surveys per site (except two sites surveyed six times, which were excluded from richness and reporting rate analyses) by a single experienced birdwatcher. The order and time of surveys at each site was varied to prevent sampling bias. All bird species recorded, their scientific names and the taxonomy used, are contained in Appendix S2.

2.3. Woodland bird habitat and status groups

To examine how groups of species, defined by their response to anthropogenic vegetation clearance and fragmentation, respond to fire, we delineated bird habitat and status groups. This classification was based on combinations of published descriptions of habitat preference and changes in status (Table 1), noting that other approaches to classify species as 'woodland birds' and 'declining' are possible and may have some bearing on the results obtained (Fraser et al., 2015). For all species recorded, we used the 'Habitat' information from Saunders and Ingram (1995) (their Table 1) to divide species into two habitat categories: those that these authors regard as typically associated with woodlands (woodland birds), and those that are not (non-woodland birds i.e. mallee, shrubland and/or heath species). Specifically, this assessment makes no distinction on the relative importance of woodlands to a species relative to other habitat types (ie. a woodland species for the purposes of our study may also be typical of other habitats additional to woodlands). We combined the change assessments from Saunders (1989) and Saunders and Ingram (1995) from the south-western Australian wheatbelt to define five status categories: (i) major wheatbelt decliners (assessed as declining in both studies); (ii) lesser wheatbelt decliners (assessed as declining in one study, and no change in the other); (iii) no change (no change in both); (iv) lesser wheatbelt increasers (no change and increase); and (v) major wheatbelt increasers (increasers in both). To increase sample sizes in analyses, and bearing in mind the aims of our study, we aggregated some habitat and status combinations (Table 1).

2.4. Statistical analyses

For all analyses, with the exceptions of permuted species accumulation curves and species estimators, time since fire was treated as a continuous variable. In these two analyses relying on aggregation across sites within time since fire classes, sites were grouped following Gosper et al. (2013a, 2013b): 'young', 15 sites 6–21 years since fire; 'intermediate', 16 sites 38–130 years; and 'mature', 25 sites 150–~400 years. These classes correspond to breaks in the distribution of fire ages available and, as these classes have significant differences in vegetation composition and structure (Gosper et al., 2013a, 2013b), the classes represent differences in habitat features putatively important to birds.

We explored the contribution of time since fire, relative to that of a range of other predictors representing other forms of disturbance, differences in climate, and differences in landscape context (Table 2a), on patterns of bird occurrence using Hierarchical Partitioning (Chevan and Sutherland, 1991). Using the hier.part package (Walsh and Mac Nally, 2013) in R v.3.4.0 (https://www.r-project.org/), the proportion of variation in total species richness and aggregated reporting rate solely correlated with individual predictors was tested using a Poisson and Gaussian distribution respectively, and the r^2 goodness of fit measure.

Using *PRIMER* and *PERMANOVA* software (Version 6.1.11, PRIMER-E, Plymouth, UK), *DIVERSE* and *Species-Accum Plot* were used to calculate measures and indices of richness and diversity, using untransformed abundance data, either on each survey site (cumulative site richness, measuring alpha diversity; and Pielou's evenness, expressing how evenly individuals are distributed among species) and/or across time since fire classes (measuring beta and gamma diversity via permuted species accumulation curves using *UGE*, and Chao1 and Chao2 estimators of the total species pool, based on the occurrence of singleton individuals and samples respectively). Reporting rates (number of samples when a species was present divided by the number of samples per site) were also calculated, and aggregated at the whole community or status group level by summing the reporting rates of all relevant species. Relationships between site richness, Pielou's evenness and aggregated reporting rates, and richness and reporting rates of habitat and status groups, with time since fire (square-root transformed to reduce the leverage of one particularly long-unburnt site) were tested with regression models. Simple models (linear, quadratic, power or inverse, and exponential) were created from forms available within the polynomial standard curves regression module of Sigmaplot 10.0 (Systat Software Inc. 2006, Chicago, IL, USA), reflecting a variety of linear, non-linear and non-monotonic shifts in various habitat variables putatively of relevance for birds (Gosper et al., 2013a, 2013b). Models were selected on the basis of minimising AICc, with the performance of alternative models for each dependent variable contained in Appendix S3.

Analyses on multivariate community composition in *PRIMER* and *PERMANOVA* were conducted on both overall species reporting rates, and total species abundance ($\log_{10} + 1$ transformed) aggregated across all surveys per site. As results were similar, only reporting rate analyses are presented here. Bray-Curtis dissimilarity was calculated for use in principal coordinates analysis, with vectors produced representing the relationships between individual bird species and status and habitat groups and the ordination axes. The effects of time since fire (square-root transformed) and location on the composition of the bird community was tested with distance-based linear modelling, using the adjusted r^2 selection criterion. Canonical analysis of principal coordinates (*CAP*) was used to find the axis through the multivariate bird reporting rate data that best predicted differences in the single gradient of time since fire, allowing an assessment of the timeframe of post-fire changes in bird community composition.

3. Results

3.1. Richness and diversity

A total of 71 bird species were recorded across the 56 survey sites (Appendix S2). Mean cumulative species richness per site was 17.6 (± 0.17SE), with a range from 8 to 29 species. Mean aggregated

Table 2
Effect of time since fire, relative to other predictors, on bird richness, reporting rates and composition in *Eucalyptus salubris* woodlands.
Data sources: A, Gosper et al., 2013a; B, Gosper et al., 2013b; C, Gosper et al., 2015.

(a) Hierarchical Partitioning analysis of species richness and aggregated reporting rates, with predictors grouped into disturbance, landscape context and climate subsets.

Predictor	Data source	Species richness *I*[a]	Aggregated reporting rate *I*[a]
Disturbance			
Time since fire (years)	A, B	15.1[*]	18.3[*]
Distance to town (km)	C	10.7	7.0
Distance to mine feature (km)	C	12.8[*]	9.6
Landscape context[b]			
Distance to cleared landscape (km)		4.7	3.4
Minimum linear distance to woodland edge (km)		3.1	5.0
Maximum linear distance to woodland edge (km)		2.4	3.9
Climate			
Mean annual rainfall (mm)	C	5.0	9.2
Winter (May–October) rainfall (%)	C	3.3	7.8
Altitude (m ASL)	C	5.6	3.4
Mean maximum January temperature (°C)	C	13.3[*]	14.5[*]
Mean minimum July temperature (°C)	C	12.4[*]	4.9
Northing/100000		11.5[*]	12.6[*]

(b) Distance-based linear model (*DISTLM*) testing the effects of time since fire (in years) and location on bird community composition.

Variable	SS	Pseudo-F	P	r^2	Cumulative r^2	Cumulative Adj. r^2	df
Marginal tests							
Location[d]	7154	4.93	0.001	0.08			54
Time since fire[c]	8470	5.94	0.001	0.10			54
Sequential tests							
Location[d]	7154	4.93	0.001	0.08	0.08	0.07	54
Time since fire[c]	6005	4.40	0.001	0.07	0.15	0.12	53

SS = sum of squares.

[a] *I* = % independent explanatory power.

[b] Measured in ArcGIS (https://www.arcgis.com/) using the vegetation type and extant extent spatial layers as in Fig. 4.

[c] Square-root transformed.

[d] Northing/100000.

[*] Significant *Z*-scores (Z ≥ 1.65).

abundance per site was 110 (± 8.8SE) individuals, with a range of 33 to 451 individuals.

Time since fire had a significant effect on bird species richness and aggregated reporting rate, and contributed the greatest independent explanatory power among all tested predictors (Table 2a). Cumulative site species richness and aggregated site reporting rates both increased linearly with time since fire (Fig. 1a,b). There was no significant relationship between Pielou's evenness and time since fire.

When sites were grouped in categorical age classes, species accumulated more slowly, relative to the number of sites sampled, in young (i.e. recently-burnt) woodlands than in intermediate-age or mature (long-unburnt) woodlands (Fig. 2). There was also evidence of a smaller total species pool using young woodlands (species estimators Chao1 = 64.6 ± 15SD; Chao2 = 64.1 ± 11SD), compared to mature woodlands (Chao1 = 68.6 ± 4.2; Chao2 = 75.3 ± 7.6), with the pool of species using intermediate-aged woodlands being more variable (Chao1 = 63.3 ± 5.2; Chao2 = 105 ± 31) depending on the estimator used. The overall species pool estimated from all sites was 83.3 (± 13, Chao1) and 73.7 (± 2.6, Chao2).

3.2. Community composition

Ordination showed time since fire affected bird community composition (Fig. 3a), with the two best principal coordinates analysis axes broadly separating sites of younger time since fire from older ones. Of the bird species with the strongest correlation with the ordination axes, the non-woodland White-fronted Honeyeater was orientated in a direction perpendicular to the axis (*PCO1*) which primarily separated sites by time since fire. Among the remaining species, all typical of woodlands, none were clearly associated with recently-burnt woodlands. A range of major wheatbelt decliners (e.g. Rufous Treecreeper, Dusky Woodswallow), lesser wheatbelt decliners (e.g. Striated Pardalote, Chestnut-rumped Thornbill), and wheatbelt no change/increasers (Willie Wagtail) were associated with mature woodlands.

Both location and time since fire had highly significant effects on bird community composition in distance-based linear modelling, both singly and in combination (Table 2b). Time since fire had the stronger effect, and including both in the model explained 15% of the variation in bird community composition. A single axis through the multivariate bird community with strong correlation with site time since fire was found in canonical analysis of principal coordinates (Fig. 3b). Mature woodlands were generally clearly separated along this axis, but there was much more overlap in community composition between young and intermediate-aged woodlands. Importantly, separation of long-unburnt woodlands along this axis remained apparent well beyond 200 years since fire, indicating that the composition of the woodland bird community continues to change as woodlands mature even after multi-century periods since fire.

3.3. Response of habitat and status groups

The species richness of birds in *E. salubris* woodlands increased with time since fire (Fig. 1a), with mature woodlands typically supporting five to ten more species than recently-burnt woodlands. This pattern of change was not uniform across bird species grouped by habitat and susceptibility to habitat loss and fragmentation. With greater time since fire both woodland bird species that are major wheatbelt decliners and wheatbelt no change/increasers increased in richness, at a similar overall rate of about three species per group across the span of the chronosequence (Fig. 1a). In contrast, there was no significant

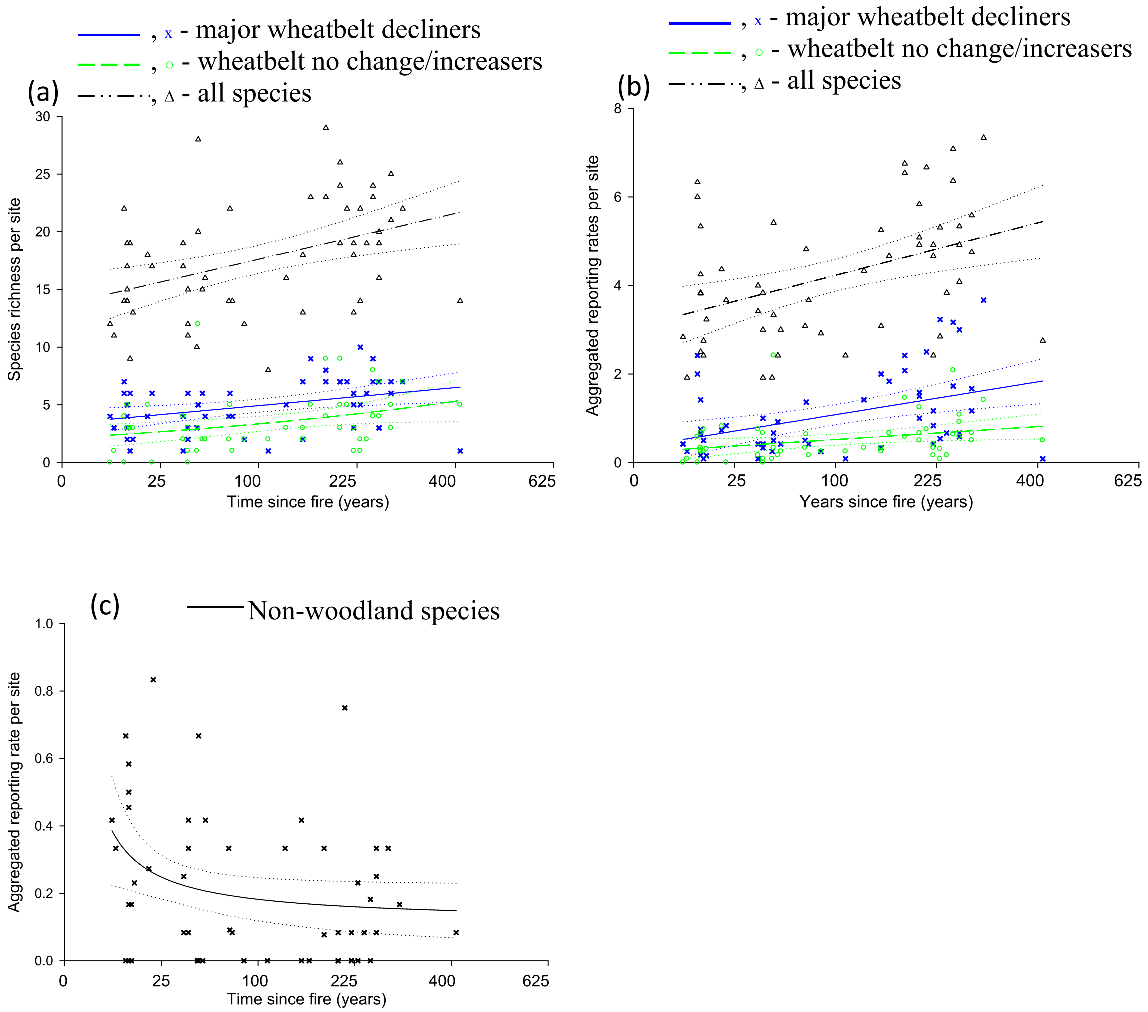

Fig. 1. Relationships between time since fire (square-root transformed) in *Eucalyptus salubris* woodlands and (a) cumulative species richness per site of all birds, woodland birds that are major wheatbelt decliners, and woodland birds that are wheatbelt no-change/increasers; (b) aggregated reporting rates per site of all birds, woodland birds that are major wheatbelt decliners and woodland birds that are wheatbelt no-change/increasers; (c) aggregated reporting rates per site of non-woodland species. Dotted lines show 95% confidence bands. All relationships were significant, $P \le 0.026$; model details, summary statistics and alternative models tested are shown in Appendix S3.

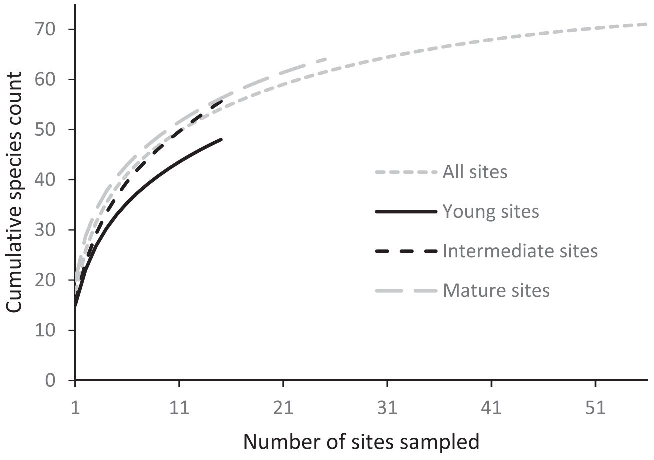

Fig. 2. Permuted species accumulation curves for birds in *Eucalyptus salubris* woodlands, for all sites sampled, and with sites divided into young (< 21 years since fire), intermediate (38–130 years), and mature (150–~400 years) time-since-fire classes.

relationship between richness of woodland birds that are wheatbelt lesser decliners and non-woodland birds with time since fire. Results for aggregated reporting rates were broadly similar, with both woodland birds that are major wheatbelt decliners and no change/increasers again having greater reporting rates in woodlands with longer times since fire, and these changes driving the overall pattern of increasing total reporting rates with time since fire (Fig. 1b). Significantly, the relationship between reporting rates of woodland birds that are major wheatbelt decliners and time since fire had a greater slope than that for no change/increasers, indicating that major decliners are more strongly associated with long-unburnt woodlands and that major decliners are the greatest contributor to the linearly increasing all-species pattern. Non-woodland bird reporting rates declined with time since fire (Fig. 1c), which was largely driven by the occurrence of the most-frequently recorded species of this habitat and status group, the White-fronted Honeyeater (Fig. 3a). There was no evidence for a change with time since fire in the reporting rates of woodland birds that are lesser wheatbelt decliners. Among all habitat and status groups, there were some member species that responded either in a different fashion to that of the aggregated group response, and/or seemingly not to time since fire at all (Appendix S2).

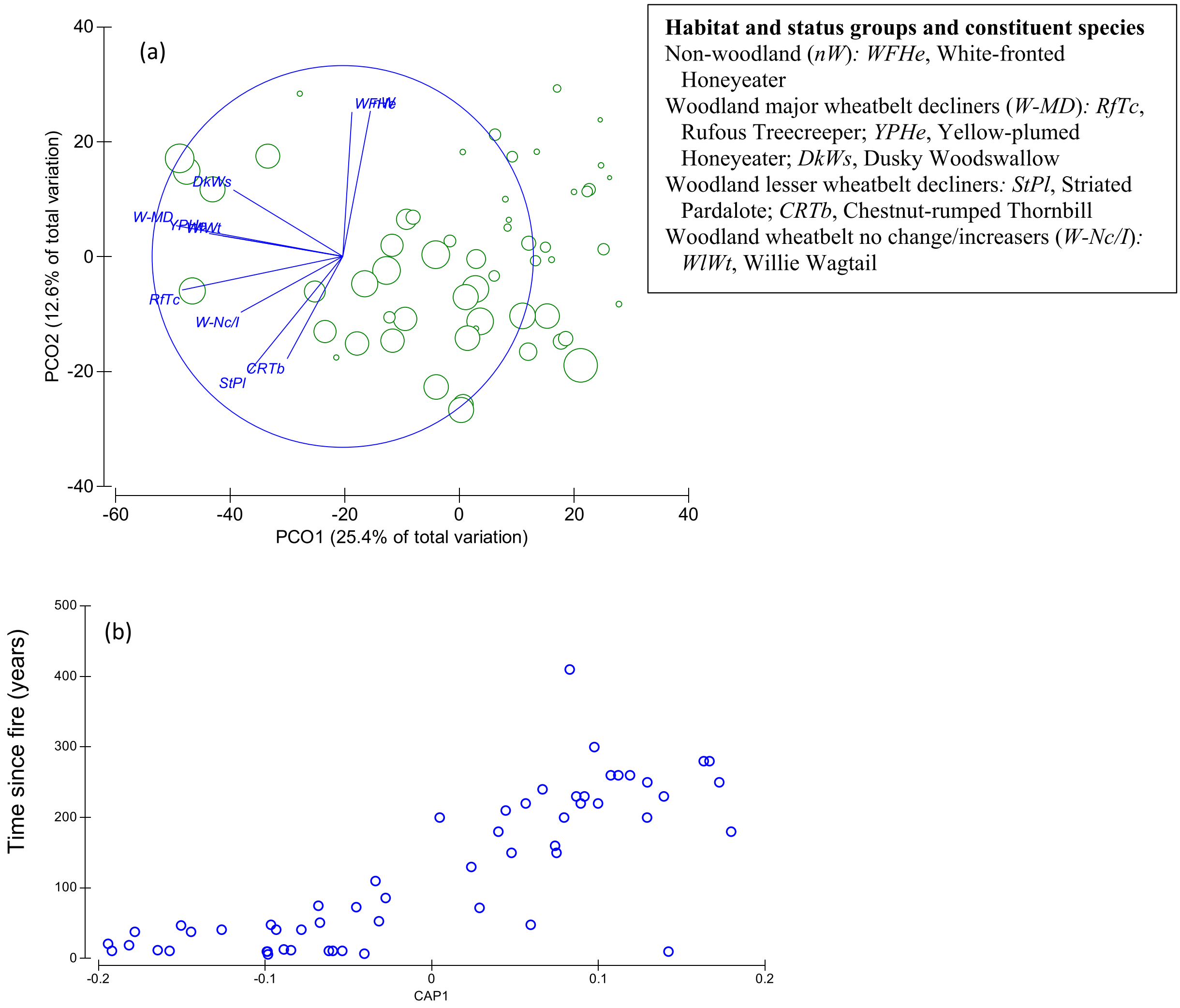

Fig. 3. Effect of time since fire on bird community composition of *Eucalyptus salubris* woodlands: (a) principal coordinates analysis (*PCO*) of sites by species reporting rates. Bubble size shows site time since fire, with a range of 6 (smallest bubble) to ~400 (largest bubble) years. Vectors, with surrounding circle for scale and orientation, are species and status and habitat groups with Spearman correlations > 0.6 (see key; noting that there is overlap in the placement in ordination space of ***nW*** and ***WFHe***, and *YPHe* and *WlWt*, respectively); (b) Canonical analysis of principal coordinates (*CAP*) relating multivariate bird community composition based on reporting rates to the time since fire gradient. $m = 16$; squared canonical correlation = 0.66; permutation test trace statistic $P = 0.001$.

4. Discussion

4.1. Changes in bird occurrence with time since fire

Time since fire clearly had a major influence on the birds of obligate-seeder *E. salubris* woodlands, at the level of individual species, habitat and status groups, and the whole bird community. The effect of time since fire, which we interpret as encompassing both post-fire successional changes in vegetation (Gosper et al., 2013a, 2013b) and the passage of time allowing for post-fire recolonization, was stronger than the effect of a range of other predictors representing other disturbances, climate variation and landscape context in an unfragmented landscape.

Richness and reporting rates of birds increased with greater time since fire (Fig. 1), indicating that the alpha diversity of long-unburnt woodlands is greater than recently-burnt woodlands. Species accumulation curves (Fig. 2) and species estimators for long-unburnt woodlands were also greater than recently-burnt woodlands, indicating greater species turnover between sites and a larger regional species pool using long-unburnt woodlands (beta and gamma diversity). These site and regional effects (alpha-, beta- and gamma-diversity) on birds are reflected in the spread of long-unburnt sites in ordination, indicating that long-unburnt sites encompass a range of variability in bird composition associated with time since fire and/or can develop along alternative trajectories. In contrast, recently-burnt woodlands had lower overall bird richness and abundance and, as recent fires have created large amounts of regenerating woodland (Fig. 4), there would appear to be limited value for woodland bird conservation in using prescribed fire to create recently-burnt woodlands, even in landscapes with seemingly uniform expanses of mature woodlands.

Similar to a previous study in obligate-seeder eucalypt woodlands (Recher and Davis, 2013), and other dry to semi-arid Australian vegetation types (Taylor et al., 2012; Davis et al., 2016), our results emphasise the role of time since fire in influencing bird communities and the importance of long-unburnt vegetation for bird conservation. The relatively rapid recovery of woodland birds within 10 years after fire in an eastern Australian woodland (Turner, 1992), in contrast to the pattern observed here, may reflect (combined with differences in rainfall) the relatively rapid recovery of above-ground vegetation structure arising via epicormically resprouting eucalypts, compared to the obligate-seeder *E. salubris* (Woinarski and Recher, 1997; Bellingham and Sparrow, 2000; noting obligate-seeder *Callitris* co-dominated Turner's study area).

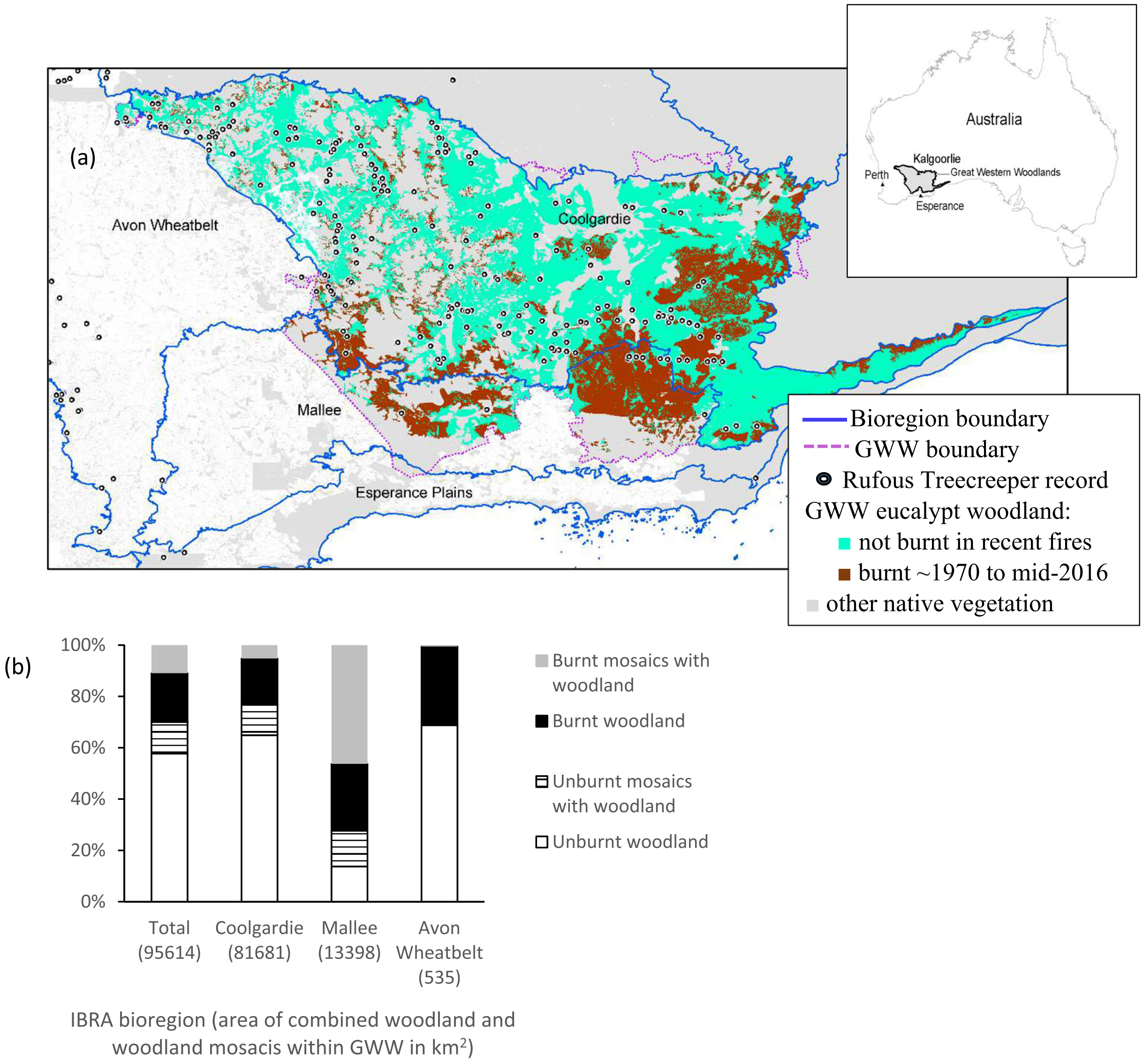

Fig. 4. Extent and spatial distribution of recent fires affecting eucalypt woodlands and woodland birds in the Great Western Woodlands (GWW):
(a) Spatial extent of temperate eucalypt woodlands and fires impacting woodlands in the GWW, derived from intersecting vegetation type and fire history spatial layers held in the Department of Biodiversity, Conservation and Attractions corporate database. Delineation of eucalypt woodlands follows Gosper et al. (2018). Other native vegetation shows the extent of loss of potential habitat in the adjoining Western Australian wheatbelt (in IBRA bioregions Avon Wheatbelt, Mallee and Esperance Plains) for major wheatbelt decliners, for example the Rufous Treecreeper (post-2010 records from the Atlas of Living Australia [https://www.ala.org.au/], extracted 25 August 2017).
(b) Proportion of woodland burnt over the period ~1970–2016 in the GWW, per IBRA bioregion, with vegetation units of mosaics including woodlands tallied separately. Total areas within the GWW: total = 156,530 km^2; Coolgardie bioregion = 129,105 km^2; Mallee bioregion = 26,132 km^2; Avon Wheatbelt bioregion = 1293 km^2.

4.2. Declining woodland birds and time since fire

Woodland birds that are major wheatbelt decliners (i.e. those bird species typically found in woodland habitats and having declined substantially in response to woodland clearance and fragmentation in the south-western Australian wheatbelt) were strongly associated with long-unburnt vegetation. This finding emphasizes the importance, previously largely overlooked, of appropriate fire management for woodland bird conservation in some regions. Obligate-seeder eucalypt woodlands have multi-century periods of recovery after stand-replacement fires (Gosper et al., 2013a, 2013b) which is reflected in the timescale of bird community change (Fig. 3b). Consequently, limiting the extent of fires in mature woodlands is important from the perspective of conservation of woodland birds that have declined in agricultural regions.

The scale of recent fires (post-~1970) in the GWW, which have burnt ~20,000–30,000 km^2 of woodlands (25–30% of total woodland area; depending on which vegetation units are classified as ‘woodland’; Fig. 4b), may have substantially reduced the available habitat for woodland bird species that are major wheatbelt decliners. However, the current absence of a comprehensive spatial representation of pre-1970 fires (and any fires pre-1940; O'Donnell et al., 2011; Gosper et al., 2016) hinders our ability to assess temporal changes in the extent of recently-burnt, compared to long-unburnt, woodland over an ecologically-relevant timescale. Consequently, whether the pattern of occurrence of recent fires is compatible with ongoing maintenance of extensive long-unburnt woodlands characterised by fire intervals frequently exceeding 300 years (O'Donnell et al., 2011; Gosper et al., 2013c), and that support woodland birds that have declined in agricultural regions, is yet to be fully resolved.

However, two factors are cause for concern. Firstly, fires in recent decades have been more extensive in the relatively wetter south of the GWW (Gosper et al., 2018; Fig. 4a), where ~70% of woodland vegetation has burnt post-~1970 in the Mallee IBRA bioregion, compared to 20–30% in the more northerly Coolgardie and Avon-Wheatbelt IBRA bioregions (Fig. 4b). The reasons for this disparity in fire activity have yet to be resolved, but may relate to quantitative (productivity) and qualitative (flammability) litter and understorey fuel differences (Bradstock, 2010; Gosper et al., 2018). Secondly, because of changes in the structure and distribution of fuels, regenerating woodlands may be more flammable than long-unburnt woodlands, possibly instigating a positive vegetation-flammability feedback (or fire trap) such that the probability of regenerating woodland remaining unburnt for the centuries necessary to develop the habitat features of long-unburnt woodland may be low (O'Donnell et al., 2011; Gosper et al., 2013b, 2018).

A precautionary and conservative approach would argue for fire being recognised as a threat to woodland birds in obligate-seeder woodlands. This is a consequence of the scale of recent fire-driven transformation of mature woodland, the timeframe required for habitat resources important for woodland birds to develop, and likely higher flammability of regenerating woodlands, notwithstanding the uncertainty of temporal trends in the extent of long-unburnt woodlands. Furthermore, the combination of fire-driven habitat change in the GWW with widely-recognised losses and fragmentation of woodland habitat in the adjoining wheatbelt (Saunders, 1989; Saunders and Ingram, 1995), suggests that the status of declining woodland birds in south-western Australia is likely to be poorer, and the distribution of currently suitable habitat more limited, than an assessment based solely on the extent of vegetation clearance. Importantly, the threats of habitat clearance and fire to woodland birds are cumulative, but affect portions of the landscape differently. Vegetation clearance and fragmentation effects are severe in the wheatbelt where fires are rare, but in the GWW, where vegetation clearance and fragmentation is low, fires are much more frequent and widespread (Prober and Smith, 2009; Parsons and Gosper, 2011). Consequently, many remnants of native vegetation in the wheatbelt are unlikely to function as refugia for fire-sensitive woodland birds due to the effects of habitat loss and fragmentation and, conversely, the ability of the GWW to function as a refuge for woodland bird species vulnerable to habitat clearance and fragmentation may have been compromised by extensive recent fires. As an example, Rufous Treecreepers are vulnerable to habitat loss and fragmentation and have disappeared from many woodland remnants, and some entire districts, in the wheatbelt (Saunders, 1989; Fig. 4a). Rufous Treecreepers are strongly associated with long-unburnt woodlands (Fig. 3a), and in presence-only species distribution modelling a high proportion of the surrounding landscape with no record of fire (at the scale of a 927 m pixel) was the strongest predictor of Rufous Treecreeper occurrence among a wide range of vegetation, productivity, climatic and disturbance variables (Fox et al., 2016). There have been few recent treecreeper records in parts of the GWW with extensive recent fires (Fig. 4a), possibly reflecting the fire-associated loss of important habitat features provided by large live trees (Luck, 2002).

Among other habitat and status groups, some showed significant responses to time since fire while others did not. In the case of woodland birds that are lesser wheatbelt decliners, logical explanations for absences of relationships with time since fire are not immediately apparent. While extant native vegetation is presumably important for these species, they appear more flexible in using woodlands of variable structure and composition spanning a range of times since fire. Increasing vegetation openness with longer time since fire (Gosper et al., 2013b, 2018) is a plausible explanation of the preference for long-unburnt woodland by a suite of woodland birds not impacted, or even benefiting, from vegetation clearance in the south-western Australian wheatbelt (wheatbelt no change/increasers, e.g. Willie Wagtail). The association of non-woodland birds with recently-burnt woodlands is consistent with these woodlands having low stature and dense low vegetation cover (Gosper et al., 2013b), somewhat similar to the nearby mallee and *Acacia* shrubland habitats often preferred by these species. Several of the non-woodland birds, such as White-fronted Honeyeater, Shy Heathwren and Southern Scrub Robin, have declined in the wheatbelt (Saunders and Ingram, 1995). Fire, therefore, is not uniformly disadvantageous for birds declining following land clearance and fragmentation. The effect of fire is likely mediated through changes in vegetation structure (Fox, 1982), such that it is birds that prefer open vegetation with large trees (i.e. typical woodland species) that are most detrimentally affected by fire in *E. salubris* woodlands.

4.3. *Management of infrequently-burnt ecosystems*

A new and innovative method allowing estimation of time since fire over multi-century timescales (Gosper et al., 2013c) has provided the basis for demonstrating that the composition of the woodland bird community continues to change beyond 200 years post-fire (Fig. 3b). Previous studies have suggested that obligate-seeder eucalypt woodlands may return to a mature state 100–200 years post-fire (Hopkins and Robinson, 1981; Recher and Davis, 2013), but our data strongly suggest this is a substantial underestimate, at least in terms of providing woodland bird habitat. Consistent with other studies in infrequently-burnt ecosystems (Clarke et al., 2010; Gosper et al., 2013a), solely using necessarily truncated time-since-fire distributions derived from remotely-sensed fire mapping (post-~1940 for the GWW; O'Donnell et al., 2011; Gosper et al., 2016) would not have allowed full appreciation of the multi-century time-frame of changes in the occurrence of bird species and community composition.

As far as we are aware, the length of our bird-time since fire chronosequence substantially exceeds that of other published studies, providing a benchmark for the lengths of time that bird communities can continue to change in response to vegetation development after fire. Notably, the time-since-fire effects on birds in *E. salubris* woodlands appear more pronounced than in boreal forests (Lowe et al., 2012), despite the similarity of vegetation dynamics being driven by stand-replacement disturbances and changes being assessed over a multi-century period in both cases.

5. Conclusions

Fires in obligate-seeder *E. salubris* woodlands substantially affect the bird community. Comprising the largest extant temperate woodland in the world, the GWW are globally important for the conservation of a range of temperate woodland birds that have declined following clearance and fragmentation of eucalypt woodlands elsewhere in Australia (Recher, 2008; Fox et al., 2016). Many of the same species susceptible to decline from habitat clearance and fragmentation following land transformation are, however, also negatively affected by habitat changes associated with burning obligate-seeder woodlands. The ability of the GWW to continue to support populations of declining woodland birds will, in large part, be dependent on appropriate fire management to maintain extensive stands of long-unburnt woodlands where they currently exist. The timescale of bird responses after fire demonstrates that contemporary fires will affect the bird community for centuries to come, highlighting the long-term consequences of contemporary fire management events and decisions. The importance of fire as a threat to individual woodland bird taxa and temperate woodland bird communities in obligate-seeder woodlands is worthy of greater conservation attention. As the effects of fire and anthropogenic habitat clearance and fragmentation were cumulative in our study, the combined effects of these two drivers of habitat change on biota should be considered in other fire-prone ecosystems.

Conflicts of interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data: sites sampled; species recorded and their habitat and status group classification; and alternative statistical models tested

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