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Do bird communities differ with post-fire age in Banksia woodlands of south-western Australia?

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Running head: Bird responses to fire in *Banksia* woodlands

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Abstract. Prescribed fire is a widespread management practice in fire-prone ecosystems that can have significant effects on fauna. To inform the development of appropriate prescribed burning regimes, we explored bird responses to time since fire in threatened *Banksia* woodlands in south-western Australia. We used area searches to estimate bird densities on 20 plots ranging from 1 to 26 years post-fire. Fire had no significant effect on the overall bird community nor any foraging guilds and there was no clear post-fire succession. Of the 26 frequently occurring species analysed, only two showed responses to fire with Yellow-rumped Thornbills more abundant in early and late post-fire sites and Scarlet Robins being more abundant in either early, or early and late post-fire habitats. Our study suggested that bird communities in *Banksia* woodlands are relatively adaptable to a range of prescribed burning regimes. However, due to late successional reptiles, Carnaby's Black-Cockatoo and mammals in *Banksia* woodlands, we recommend prescribed burning regimes that reduce early and increases late successional habitat. *Phytophthora* dieback, urbanisation and associated habitat fragmentation and a drying climate may have important synergistic effects and the role of these in structuring bird communities needs to be further considered in developing appropriate fire regimes.

Brief summary: We explored bird responses to fire in threatened *Banksia* woodlands in south-western Australia and found post-fire age had little or no effect on the overall bird community. Two species responded to post-fire age but were most abundant early post-fire suggesting the bird community is adaptable to a range of prescribed burning regimes.

Keywords: succession, thornbill, robin, foraging guild, prescribed burning, fragmentation, nectarivores, insectivore

Introduction

In ecosystems where fire is a natural disturbance, fire is known to fundamentally influence faunal communities and the communities we observe in present-day ecosystems have often been shaped through co-evolution with fire over a long period (e.g. Taylor et al., 2013; Greene et al., 2016; Driessen & Kirkpatrick, 2017). Many aspects of fire (e.g. intensity, seasonality and frequency) influence faunal communities but one of the most important is inter-fire interval with faunal communities changing as the structure and floristics of the vegetation undergoes post-fire succession (e.g. Moreira et al., 2003; Valentine et al., 2012; Doherty et al., 2015; Jacobsen et al., 2020). However, how fauna respond to post-fire vegetation succession remains poorly understood in many ecosystems yet is critical if faunal communities are to be effectively managed and conserved. Furthermore, the importance of this knowledge for conservation will likely increase into the future as many regions of the globe become hotter and drier which will fundamentally change fire behaviour and frequency (Fernandez-Anez et al., 2021; Gannon & Steinberg, 2021).

Prescribed fire is a widespread management practice in fire-prone ecosystems, particularly in ecosystems close to cities and towns (Florec et al., 2020; Hunter & Robles, 2020). While the primary purpose of prescribed burning is to prevent, or reduce, the frequency and intensity of wildfires, it is also often used to manage and conserve biodiversity (Radford et al., 2020; Rainsford et al., 2021). Inappropriate fire regimes are considered to be the primary threat to many threatened fauna (Woinarski, 1999; Geyle et al., 2021a; Geyle et al., 2021b), yet the majority of fires in many ecosystems are prescribed burns (e.g. Mulqueeny et al., 2010; Plucinski, 2014). Therefore, understanding how faunal communities respond to post-fire succession after prescribed burns is likely to be important for their conservation (e.g. Eales et al., 2018; dos Anjos et al., 2021; Mason & Lashley, 2021).

Banksia woodlands are a threatened ecological community found in parts of southern Australia but which form an extensive and dominant vegetation type on the west coast of south-western Australia, where the canopy is dominated by Slender-leaved Banskia *Banksia attenuata*, Holly-leaved Banksia *B. ilicifolia*, Firewood Banksia *B. menziesii* and Acorn Banksia *B. prionotes* (Ritchie et al., 2021). Fires are a natural disturbance in *Banksia* woodlands with evidence of their occurrence dating back ~2.5 million years and evidence of indigenous burning dating back 30 000 years (Ritchie et al., 2021). However, due to their proximity to urban centres, the majority of *Banksia* woodlands are now burnt by prescribed burns (Plucinski, 2014; Ritchie et al., 2021), which aim to both protect urban areas and infrastructure and break-up landscape continuity by creating a mix of different post-fire age classes (Wilson et al., 2014). Although prescribed burns aim for an inter-fire interval of 8–12 years, the frequency of arson and accidental ignitions means that ~60% of *Banksia* woodlands near Perth are ≤6 years post-fire and very little is >21 years post-fire (Wilson et al., 2014). This heavily skewed fire age class distribution could have negative consequences for faunal communities if there are species adapted to older fire age classes. Studies on reptiles have shown that some species are only found in unburnt areas or are most abundant in older fire age classes (Valentine et al., 2012; Davis & Doherty, 2015), while food resources for the threatened Carnaby's Black-Cockatoo (*Zanda* *latirostris*) also peak in older fire age classes (Valentine et al., 2014). These studies indicate that *Banksia* woodland may support bird species adapted to older fire age classes but the responses of bird to post-fire succession in *Banksia* woodlands remains essentially unknown.

To address this lack of knowledge, we investigated the responses of birds in *Banksia* woodlands to post-fire succession. Knowledge of bird responses to fire are critical to the development of prescribed burning regimes that contribute to the maintenance and conservation of biodiversity because birds are known to display a wide range of responses to fire and many species are adapted to long unburnt seral stages (Taylor et al., 2012; Davis et al., 2016; Connell et al., 2017). Furthermore, birds are critical for a range of ecosystem services, such as pollination (Frick et al., 2014), and utilise a wide range of resources so can act as indicators of likely broader ecosystems impacts of fire. We explored how birds respond to post-fire succession in *Banksia* woodlands by asking the following questions: (1) How does the overall bird community respond to fire?; (2) Is there clear post-fire succession?; (3) How do individual species respond to fire?; and (4) Are there early, mid or late successional species? We used the answers from these questions to recommend an optimal prescribed burning regime for birds in *Banksia* woodlands.

Methods

Study area

The study was conducted in an extensive contiguous area of *Banksia* woodlands to the north of Perth, Western Australia. All sites were located on the Bassendean Dune System to reduce variation of floristic communities. The canopies of woodlands on this dune system are dominated by *Banksia menziesii* and *B*. *attenuata* with Bull Banksia *B*. *grandis* present in lower abundance and *B*. *ilicifolia* occurring low in the landscape and Swamp Banksia *B*. *littoralis* in valley bottoms with impeded drainage. Flowering seasons encompass the whole year with individual species flowering either throughout the whole year (*B. ilicfolia*) or Feb-Oct (*B. menziesii)*, Sep/Oct-Feb (*B. attenuata, B. grandis*) and Feb-Aug (*B. prionotes*). *Banksia* woodlands support an open but highly speciose understorey with species from the families Proteaceae, Myrtaceae, Fabaceae, Dilleneaceae, Asteraceae, Epacridaceae, Restionaceae, Cyperaceae and Orchidaceae predominating. The climate of the area is Mediterranean with cool, wet winters and hot, dry summers. The closest four weather stations are Wanneroo, Pearce, Gingin Airport and Woodridge Estate and, across these stations, annual rainfall in the study area was 687.9 mm with ~80% falling between May and September inclusive. Temperatures in the hottest and coldest months across Pearce and Gingin Airport were daily maxima of 33.3 and 18.1°C in January and July respectively and daily minima of 17.3 and 7.4°C in February and July respectively.

The study area has been subject to prescribed burns for several decades, and wildfires for a longer period, and currently ~60% of the area is ≤6 years post-fire and less than 10% is ≥21 years post-fire (Wilson et al., 2014). From 1970–2009, 78% of remnant vegetation was burnt 1 to 3 times, with 22% burnt between 4 and 9 times (plus 7% of remnant vegetation had an unknown fire history). The average number of times an area was burnt was 3.13 (Wilson et al., 2014).

Experimental design

To explore how bird communities varied with post-fire age, we took a chronosequence approach. We surveyed birds at 20 sites of varying post-fire ages to explore post-fire succession in bird communities. These sites were spread over an area of approximately 40 x 10 km and included post-fire ages from 1 year to 26 years with post-fire ages interspersed as much as possible (Fig. 1). Sites were dispersed as much as practicable to minimise the movement of birds between sites with the average minimum distance between sites being 886 m. Sites were likely historically burnt by a mixture of prescribed and wildfires but information on the nature of the fire was not recorded at the time of the study.

Bird surveys

Birds were surveyed using the national standard prescribed by Birdlife Australia and utilised in the Atlas of Australian Birds (Barrett et al., 2003) and after Loyn (1986). This involved conducting 2-ha area searches over a 200 x 100 m area and counting all birds seen or heard within the 2-ha survey plot over a 20 min period. The edges of the 2-ha survey plot were marked with flagging tape to ensure that surveyors were able to accurately determine whether birds were inside or outside the survey plot and also covered the entire plot. Surveys were conducted within 5 hours of sunrise on days with light winds and no rain. The order in which sites were surveyed each morning were randomised with respect to post-fire ages. Bird surveys were conducted using the same team of experienced observers to minimise bias. All surveys occurred between March and December 2008. Each site was surveyed 16 times (except for one 8-year old site surveyed 12 times) with sites surveyed 3 times in March to April, 4 times in May to June and July to August, twice in September to October and 3 times in November to December (except the 8-year old site which was surveyed once in March to April and twice in May to June). Area searches have been shown to be robust to changes in vegetation density (Craig & Roberts, 2001) which, combined with the open nature of *Banksia* woodland vegetation, means that they provided comparable density estimates across a range of fire ages. Birds names and taxonomy follow IOC World Bird List Version 11.2 (Gill et al., 2021).

Statistical analysis

We analysed birds at the community, guild and species level. For guilds, we assigned birds to one of six foraging guilds (insectivore, nectarivores, carnivore, omnivore, granivore and insectivore/herbivore: Table 2) based on Craig and Roberts (2005) and Davis et al. (2014). To visually identify whether there was directional post-fire succession we first created a between-site resemblance matrix using the Bray-Curtis similarity measure. To do this we used abundance data pooled across all surveys. We then visually represented succession in a Bray-Curtis space using a Principal Coordinates Analysis (PCO). This analysis was done on the whole bird community and each of the six guilds separately. We also supported this analysis statistically by conducting a permutational multivariate analysis of variance (PERMANOVA) between young (1 – 8 years post-fire), intermediate (9 – 15 years post-fire) and old (18 – 26 years post-fire) post-fire ages for the overall bird community and the six guild communities separately.

We then explored the relationship between post-fire age and birds at the community, guild and species level. We posed three general *a priori* hypotheses (linear, threshold and quadratic) to examine relationships with post-fire age and included an intercept-only model. We then ran each of these four models against two community metrics (overall bird density [sum of the density of each species at a site] and species richness [number of species at each site]), density of each guild separately and each species separately and ranked each model using AIC_c. We calculated the weight of each model and considered all models $<\Delta 2$ AIC_c of the best model to be plausible models. We ran all plausible linear, threshold and quadratic models in a general linear model to determine whether they explained a significant amount of the variation in the dependent variable. The threshold model was calculated using $\ln(x+1)$. Thresholds were not identified to a specific value but indicated, if significant, that the response of the species to fire either declined initially and then remained relatively constant at a low level or increased initially and then remaining relatively constant at a high level. For individual species, we only analysed those 26 species where $\geq$12 individuals were recorded. All analyses were conducted using Primer 6 + PERMANOVA (Primer-E, 2008) and R 3.5.2 (R Development Core Team, 2013).

Results

We recorded 3574 individuals of 51 species of which the most frequently recorded species were Brown Honeyeater (*Lichmera indistincta*: 915 individuals), Splendid Fairywren (*Malurus splendens*: 463), Western Thornbill (*Acanthiza inornata*: 390), New Holland Honeyeater (*Phylidonyris novaehollandiae*: 377), Western Spinebill (*Acanthorhynchus superciliosus*: 314), Western Wattlebird (*Anthochaera lunulata*: 197), Red Wattlebird (*Anthochaera carunculata*: 148), Silvereye (*Zosterops lateralis*: 94), Rufous Whistler (*Pachycephala rufiventris*: 80) and Scarlet Robin (*Petroica boodang*: 70). The mean number of species recorded per site was 17.55 with a range of 10-23. The highest number of species was recorded in the 1-year site, followed by the 26-year site then 4, 23 and 25 were all equal, followed by the 3 and 7-year sites (Table 1).

How does the overall bird community respond to fire and is there clear post-fire succession?

Neither the whole bird community nor any of the guilds showed any clear post-fire succession in community composition, even though the first two axes of the PCO explained 60.7% of the variation in the overall bird community (Fig. 2). Overall community composition was more strongly influenced by sites supporting large numbers of nectarivores rather than post fire age (Fig. 3), but insectivores, granivores and omnivores also showed no clear succession in relation to post-fire age even though the first two axes of the PCOs explained 85.1, 52.1, 81.0 and 56.5% of the variation in those guilds respectively (Fig. 3). Although there were too few carnivores and insectivore/herbivores to be certain of post-fire successional patterns for these guilds, there was no indication of any directional succession. The lack of directional post-fire succession was confirmed by the lack of difference between young, intermediate and old post-fire ages with respect to the overall bird community (Pseudo-$F_{2,17}$ = 1.05, P = 0.404), nectarivores (Pseudo-$F_{2,17}$ = 0.75, P = 0.603), insectivores (Pseudo-$F_{2,17}$ = 1.37, P = 0.178), granivores (Pseudo-$F_{2,12}$ = 1.55, P = 0.201), omnivores (Pseudo-$F_{2,15}$ = 1.00, P = 0.466), carnivores (Pseudo-$F_{2,6}$ = 0.29, P = 0.907) or insectivore/herbivores (Pseudo-$F_{2,4}$ = 1.49, P = 0.494).

This lack of directional post-fire succession at the community and guild level was supported by univariate analyses. The best-supported relationship between post-fire age and overall bird density was the intercept-only model and, although the linear and threshold models were plausible, neither explained a significant amount of variation in overall bird density (Table 2). The best-supported relationship between post-fire age and species richness was quadratic but it did not explain a significant amount of variation in species richness and the intercept-only model was almost as plausible (Table 2). Among guilds, the intercept-only model was the only plausible model for omnivores and insectivore/herbivores. For carnivores, nectarivores and granivores the best-supported model was the intercept-only model, with the linear model being marginally plausible for carnivores, the linear and threshold models being plausible for nectarivores and the linear and quadratic models being plausible for granivores. For insectivores, the best supported model was the linear model but the intercept-only model was also plausible (Table 2). None of the models for any of the six guilds explained a significant amount of variation in guild density.

How do individual species respond to fire and are there early, mid or late successional species?

Of the 26 species analysed individually, the intercept-only model was the best-supported model for 18 species with it being the only plausible model for 12 of those species (Table 2). The remaining six species had either linear, threshold or quadratic models also being plausible but none of those models explained a significant of variation in the species' density (Table 2). For Red-capped Parrots (*Purpureicephalus spurius*), Singing Honeyeaters (*Gavicalis virescens*) and Western Gerygones (*Gerygone fusca*), the linear model was the best-supported model, with intercept-only and threshold models also plausible, although none of the models explained a significant amount of variation in the density of those three species. For Splendid Fairywrens, the threshold model was best-supported but the intercept-only model was almost as plausible, with the linear also plausible, but none explained a significant amount of variation in Splendid Fairywren density. For Western Thornbills and Australian Ringnecks (*Barnadius zonarius*), the quadratic model was the best-supported model with the intercept-only and linear models also being plausible, although none of the models explained a significant amount of variation in the density of those two species. For all of these 24 species, the intercept-only model was a plausible model.

For Yellow-rumped Thornbills (*Acanthiza chrysorrhoa*), the best-supported model was the quadratic model and it explained a significant amount of variation in Yellow-rumped Thornbill density, suggesting a trough-shaped relationship with post-fire age with densities highest in young and old post-fire ages (Fig. 4). The threshold model was also plausible but it did not explain a significant amount of the variation in Yellow-rumped Thornbill density. For Scarlet Robins, the threshold model was the best-supported model with the linear and quadratic models also being plausible. The threshold and linear models supported a decreasing density of Scarlet Robins with increasing post-fire age while the quadratic model indicated a trough-shaped relationship with densities highest in young and old post-fire ages. All three models explained a significant amount of variation in Scarlet Robin density (Fig. 4).

Discussion

Our study showed that birds in *Banksia* woodlands show relatively subdued responses to post-fire succession and there was no evidence that any species was restricted to long unburnt sites. Neither the overall bird community nor any of the foraging guilds showed any directional response to post-fire succession with bird communities varying greatly between individual sites of similar post-fire age and density and species richness remaining fairly consistent as vegetation matured post-fire. Furthermore, only 2 of the 26 species analysed showed a response to post-fire succession and both of these species were most abundant in young post-fire sites with a smaller increase in old post-fire sites as well.

How does the overall bird community respond to fire and is there clear post-fire succession?

The lack of a directional response to post-fire succession by the bird community and guilds is in contrast to many Australian ecosystems (e.g. Clarke et al., 2005; Parsons & Gosper, 2011; Connell et al., 2017). Notably, however, Loyn and McNabb (2015) and Kuchinke et al. (2020) both reported minimal effects of prescribed fire on bird communities in forest and woodlands in Victoria, while Kuchinke et al. (2020) recorded a relatively quick recovery of the bird community within two years of a prescribed fire.

The apparent level of resilience of the bird community in our study may reflect the low intensity of prescribed burns in *Banksia* woodlands and the consequent rapid recovery of vegetation structure post-fire. In *Banksia* woodlands, many plants recover within 2 years of fire (Hobbs & Atkins, 1990) and the primary canopy species resprout rapidly from epicormic buds (Baird, 1984; Bell et al., 1992) so changes to vegetation structure are relatively short-lived. Post-fire succession of vegetation mainly involves changes to the ground layer, with litter depth increasing and bare ground decreasing with time since fire (Valentine et al., 2012).

However, few species in *Banksia* woodlands forage primarily on the ground (Comer & Wooller, 2002) so these changes may have little effect on the overall bird community. Furthermore, forest and woodlands in south-western Western Australia support a relatively generalist avifauna, due to past habitat contractions and lack of refugia (Wykes, 1985), and birds display relatively subdued and transient responses to fire in a range of south-western ecosystems (Christensen & Abbott, 1989). These responses are likely to be even less marked with low intensity fires typical of prescribed burns and understorey insectivores have been shown to survive these low intensity burns in south-western karri (*Eucalyptus diversicolor*) forests (Wooller & Brooker, 1980).

The lack of a response in foraging guilds indicates that low intensity prescribed fire generally has small and transient effects on a range of food resources in *Banksia* woodlands, such as insects, nectar and seeds as well as the availability of other resources such as shelter and foraging substrates. Although studies on fire effects on invertebrates in *Banksia* woodlands are few, they have shown that invertebrate abundance generally declines for a short period post-fire but rapidly recovers while some groups, such as ants, increase in abundance in the early post-fire years (Bamford, 1992). Similarly, many *Banksia* woodland plant species flower and set seed in the first few years post-fire (Baird, 1984; Cowling et al., 1987; Hobbs & Atkins, 1990; Bowen & Pate, 2004) so the availability of nectar and seeds is likely to return rapidly post-fire. Overall, our study indicates that the effect of low intensity prescribed burns on food resources for many birds in *Banksia* woodlands are transient and these food resources recover rapidly post-fire.

How do individual species respond to fire and are there early, mid or late successional species?

Our study showed that few bird species displayed marked responses to fire and that no species appeared to be restricted to mid or late post-fire ages. This in marked contrast to many other Australian ecosystems that support late successional species that require long unburnt vegetation for persistence (e.g. Smith, 1985; Clarke et al., 2005; Parsons & Gosper, 2011; Verdon et al., 2019). One explanation could be that those species have already disappeared from the study system; or occur in low numbers and hence were not included in our analyses. Alternatively, species in our study could be utilising all of the habitat and require all of the habitat post-fire ages to fulfill their resource needs. Only two species in *Banksia* woodlands showed a clear response to fire with Yellow-rumped Thornbills being an early and late successional species, being most abundant in early and late post-fire ages (particularly the former) and being scarce or absent in intermediate fire ages.

Scarlet Robins were either an early successional species, declining in abundance with increasing post-fire age, or preferring both early and late post-fire ages like the thornbill.

Yellow-rumped Thornbills have been shown to be most abundant in young post-fire ages (Brooker, 1998) and this likely relates to their preference for habitats with an open ground layer and the fact that they forage primarily on the ground, often on the bare ground between litter (Ford et al., 1986; Recher & Davis Jr, 1998). This decrease in bare ground with increasing post-fire age likely explains why this species is most abundant in early post-fire ages. However, this species also increases slightly in older post-fire ages and this likely relates to the decrease in litter cover and increase in bare ground in older (>20 years) post-fire ages. The fact that Yellow-rumped Thornbill also forage regularly above ground on trunks, branches and foliage (Ford et al., 1986; Recher & Davis Jr, 1997) possibly also explains their increase in older post-fire ages, as vegetation cover remains relatively high (Valentine et al., 2012). The preference of Scarlet Robins for young post-fire ages has been found in other studies (Reilly, 1991; Loyn, 1997; Brooker, 1998) and likely relates to preference of this species for habitats with an open ground layer, a sparse shrub-and-sapling layer and a lot of bare ground (Robinson, 1992; Recher & Davis Jr, 1998; Recher et al., 2002; Holmes, 2013). As bare ground decreases in *Banksia* woodlands with increasing time post-fire, this likely explains the preference of this species for young past-fire ages and decline with increasing post-fire age. However, there was some evidence that the species increases slightly in older post-fire ages and, like Yellow-rumped Thornbills, this probably results from the decrease in litter cover and increase in bare ground in sites >20 years post-fire (Valentine et al., 2012). There was also weak evidence of a fire response in six species (Australian Ringneck, Red-capped Parrot, Singing Honeyeater, Splendid Fairywren, Western Gerygone and Western Thornbill). However, in five of these species (all except Splendid Fairywren), the response was driven by highest numbers of individuals as a single site (Figure S1: or two sites for Australian Ringneck) and, as the null model was almost as plausible as the linear, threshold or quadratic models, we consider it most likely the possible relationship is spurious. The was weak evidence that Splendid Fairywrens increased in abundance post-fire, however this species was abundant in young post-fire ages, and the null model was equally as plausible as the threshold model. This indicates any fire response is weak and that the species would be resilient to a wide range of prescribed burning regimes. We would encourage further research to better elucidate fire responses in these six species.

What would be the optimal prescribed burning regime for birds in Banksia *woodlands?*

The results of our study can potentially help inform what would be an optimal prescribed burning regime to maintain biodiversity in *Banksia* woodlands. Our results indicate that the bird community is likely to be relatively adaptable to a wide range of prescribed burning regimes. The only species that responded to post-fire vegetation succession were most abundant in young post-fire ages and no species was most abundant in older, or even intermediate, post-fire ages. This suggests that the current skew towards *Banksia* woodlands in early (≤6 years) post-fire stages should not have significant negative effects on the current bird community (though acknowledging that some species preferring late post-fire ages may already have been lost from the system). However, before we use our study to recommend an optimal prescribed burning regime, we need to appreciate the limitations of our study and also consider the requirements of other fauna in *Banksia* woodlands.

One of the limitations of our study is that many bird species are highly mobile and able to exploit resources in post-fire seral stages even if they do not provide all the resources they require (Taylor et al., 2012; Berry et al., 2015). As burn patches in our study area average 212 ha for prescribed burns and 383 ha for wildfires (Wilson et al., 2014), it is possible that birds in young post-fire sites were reliant on surrounding older post-fire patches for resources unavailable in younger sites. However, we believe that most birds in young post-fire stages were able to survive in those patches for two reasons. Firstly, several sedentary species with small home ranges, such as Splendid Fairywren, Western Thornbill, Rufous Whistler and Grey Fantail, showed no significant response to fire and were common in both young and old post-fire ages. Secondly, previous studies have shown that the recovery post-fire in the availability of insects, flowers and seeds is rapid in *Banksia* woodlands (Baird, 1984; Hobbs & Atkins, 1990; Bamford, 1992) so these resources are likely to be able to support bird populations in young post-fire stages.

Another limitation of our study is that we were unable to assess the response to fire of rare species that are poorly sampled by plot-based studies (Craig & Roberts, 2005). However, often rare and threatened species are those that are late successional and require long unburnt vegetation (e.g. Clarke et al., 2005; Verdon et al., 2019) and food resources for the threatened Carnaby's Black-Cockatoo (*Zanda latirostris*) in *Banksia* woodlands were found to peak 20-25 years post-fire (Valentine et al., 2014). Hence, when making recommendation for prescribed burning regimes we need to acknowledge that our studies only assessed fire responses in the in 26 most common bird species and that rare bird species may have requirements for long unburnt vegetation.

A last limitation of our study is that it was conducted in continuous woodlands, yet much *Banksia* woodland remains as small, isolated remnants in urbanised landscapes close to Perth (Ritchie et al., 2021). These remnants support a suite of declining species, some of which require well-connected landscapes (Davis et al., 2013) even under appropriate fire regimes. Furthermore, these remnants often suffer from *Phytophthora*-dieback, which results in significant structural and floristic changes (Davis et al., 2014), and the synergistic effect of dieback and fire may increase local extinction rates of declining species. Hence, it is likely that appropriate prescribed burning regimes in these remnants, where declining species may be unable to recolonise due to their isolation from continuous woodlands, will be different from with those in the continuous woodlands examined in this study.

We also need to consider the post-fire responses of other fauna in formulating recommendations for prescribed burning regimes in *Banksia* woodlands. In the same study area, overall reptile abundance and abundance of the skink The Shrubland Morethia Skink *Morethia obscura* increased with time since last fire and four rarely recorded species (Southern Blind Snake *Anilios australis*, Southern Shovel-nosed Snake *Brachyurophis semifasciatus*, Yellow-faced Whipsnake *Demansia reticulata* and Black-striped Burrowing Snake *Neelaps calonotus*) were only recorded in long unburnt sites (>16 years) (Valentine et al., 2012). Similarly, Honey Possum (*Tarsipes rostratus*) abundance increased with time since fire and peaked 20 – 26 years post-fire (Wilson et al., 2014). These results indicate that some fauna in *Banksia* woodlands require long unburnt sites, which is unsurprising as many Australian ecosystems support species that require long unburnt vegetation for persistence (e.g. Smith et al., 2013; Taylor et al., 2013).

Consequently, we would recommend an ecological prescribed burning regime for *Banksia* woodlands that retains patches of long unburnt vegetation throughout the study area and aims to reduce the area currently in young post-fire ages. The exact area of each fire age would need to be determined by further study incorporating the specific ecological objectives. Retaining patches of long unburnt vegetation should facilitate the persistence of reptile and mammal species, and perhaps some rare bird species, that require long unburnt patches for their persistence whilst maintaining the diversity of species observed in this study. *Banksia* woodland fuels accumulate rapidly in the first four years post-fire, and at that age would support an intense and fast moving wildfire under extreme fire weather conditions, and fuel loads stabilise at 6 – 8 tonnes ha^{-1} at 6 years post-fire (Burrows & McCaw, 1990). Hence, the challenge will be in developing prescribed burning practices that will enable the implementation of an appropriate regime in such a fire prone ecosystem, particularly as the study area heads into a warmer, drier, more fire-prone future (Wilson et al., 2014). While we do not have the answers to this challenge, we would encourage land managers to explore options of burning some *Banksia* woodlands more frequently (<4 years) to create patchiness and break up fuel loads across the landscape to protect unburnt patches from wildfire (Ritchie et al., 2021). Exploring indigenous or cultural burning (e.g. Fletcher et al., 2021; McKemey et al., 2021), including possibly moving prescribed burns to cooler parts of the year, might be one way of achieving an appropriate regime although we caution that much remains to be understood about the cumulative effects of repeated fires on fauna (e.g. Reside et al., 2012; Gorissen et al., 2015; Ondei et al., 2021).

Conclusion

Our study found that post-fire age had a relatively small effect on structuring the bird community. Neither the overall bird community, community metrics nor guild abundance showed a significant relationship with post-fire age. Furthermore, only 2 of the 26 species analysed showed a relationship with post-fire age and these species displayed a troughed relationship being most abundant in young post-fire ages and then increasing slightly in old post-fire ages. Overall, these results indicate that the bird community would be adaptable to a wide range of prescribed burning regimes. However, we would recommend that a prescribed burning regime for *Banksia* woodlands that reduced the area of young post-fire ages and increased the areas of old post-fire ages because some reptiles and mammals in *Banksia* woodlands, and potentially some rare birds such as Carnaby's Black-Cockatoo, require long unburnt vegetation for persistence. Implementing a prescribed burning regime to achieve this is challenging, particularly into the future as woodlands become warmer, drier and more fire-prone due to climate change. However, developing prescribed burning regimes that facilitate the persistence of fauna under a range of climatic conditions are likely to be relevant to a range of Australian ecosystems outside *Banksia* woodlands.

Finally, it should be noted that a range of other factors are likely to be impacting the avifauna of *Banskia* woodlands, including a drying climate and the impacts of *Phytophthora* dieback on vegetation. Birds of small banksia woodland remnants in the urban matrix are also likely to be heavily affected by the changd permeability of the matrix which will favour some species and select against dispersal by others. These factors need to be considered as interacting and multiplicative affects when considering the impacts of fire on birds in these systems.

Conflicts of Interest

The authors declare no conflicts of interest.

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Data Availability Statement

Data from this study is available at ECU's Research Online publicly available repository https://ro.ecu.edu.au/datasets/

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Table 1. Mean number of bird species at each site. Site numbers reflect the number oo years since last fire. Site 8b was a duplicate site of the same fire age.

Site	Mean number of species
1	23
2	14
3	20
4	21
6	10
7	20
8	16
8b	15
9	23
10	14
11	18
12	17
13	12
14	18
15	13
18	15
22	18
23	21
25	21
26	22

Table 2. Results of modelling three responses to fire (linear, threshold and quadratic) and an intercept-only model for community metrics, abundance of each guild and abundance of the 26 most common species.

Guild membership for the 26 species in also shown (GRA = granivore, INS = insectivore, IN/HE = insectivore/herbivore, NEC = nectarivores and OMN = omnivore). For all plausible models (<$\Delta 2AIC_c$ of best model), the adjusted r^2 and probability of a general linear model are shown. Significant general linear models are shown in bold.

Variable	n	Guild	Form	Direction	ΔAIC_c	ω_i	Adj-r^2	P of $F_{2,17}$
Community metrics								
Overall density	3574		Intercept		0.00	0.511		
			Linear	Increased	1.47	0.244	0.01	0.282
			Threshold	Increased	1.97	0.191	-0.01	0.396
Species Richness	51		Threshold	Decreased	0.00	0.437	-0.05	0.806
			Intercept		0.39	0.360		
Guilds								
Nectarivores	2041		Intercept		0.00	0.451		
			Linear	Increased	0.87	0.292	0.04	0.194
			Threshold	Increased	1.76	0.187	-0.00	0.341
Insectivores	1356		Linear	Decreased	0.00	0.487	0.14	0.057
			Intercept		1.34	0.249		

Granivores	95		Intercept		0.00	0.351		
			Linear	Increased	0.25	0.311	0.07	0.135
			Quadratic	Peaked	0.91	0.223	0.13	0.117
Ominvores	47		Intercept		0.00	0.634		
Carnivores	17		Intercept		0.00	0.556		
			Linear	Increased	1.97	0.208	-0.01	0.395
Insectivore/Herbivore	18		Intercept		0.00	0.636		
Species								
Common Bronzewing	12	GRA	Intercept		0.00	0.519		
			Linear	Decreased	1.73	0.219	-0.00	0.333
Painted Buttonquail	17	IN/HE	Intercept		0.00	0.630		
Red-capped Parrot	38	GRA	Linear	Increased	0.00	0.399	0.11	0.081
			Intercept		0.68	0.284		
			Threshold	Increased	1.21	0.218	0.16	0.159
Australian Ringneck	44	GRA	Quadratic	Trough	0.00	0.436	0.20	0.058
			Intercept		0.76	0.299		
			Linear	Increased	1.70	0.187	0.04	0.203
Splendid Fairywren	463	INS	Threshold	Decreased	0.00	0.347	-0.05	0.810

			Intercept		0.04	0.340		
			Linear	Increased	1.15	0.195	0.04	0.225
Western Spinebill	314	NEC	Intercept		0.00	0.618		
Tawny-crowned Honeyeater	41	NEC	Intercept		0.00	0.591		
New Holland Honeyeater	377	NEC	Intercept		0.00	0.453		
			Linear		0.95	0.281	0.04	0.204
			Threshold		1.68	0.195	0.00	0.324
White-cheeked Honeyeater	49	NEC	Intercept		0.00	0.636		
Brown Honeyeater	915	NEC	Intercept		0.00	0.635		
Singing Honeyeater	17	INS	Linear	Increased	0.00	0.414	0.12	0.077
			Intercept		0.77	0.282		
			Threshold	Increased	1.67	0.180	0.04	0.198
Western Wattlebird	197	NEC	Intercept		0.00	0.569		
Red Wattlebird	148	NEC	Intercept		0.00	0.435		
			Linear	Increased	0.86	0.283	0.04	0.193
			Threshold	Increased	1.42	0.214	0.01	0.273
Western Gerygone	15	INS	Linear	Decreased	0.00	0.439	0.15	0.050
			Threshold	Decreased	1.02	0.263	0.11	0.087
			Intercept		1.58	0.200		

Western Thornbill	390	INS	Quadratic	Trough	0.00	0.438	0.20	0.058
			Intercept		0.75	0.301		
			Linear	Decreased	1.73	0.185	0.04	0.207
Yellow-rumped Thornbill	54	INS	**Quadratic**	**Trough**	**0.00**	**0.440**	**0.25**	**0.033**
			Threshold	Decreased	0.82	0.292	0.14	0.059
Dusky Woodswallow	30	INS	Intercept		0.00	0.617		
Varied Sittella	20	INS	Intercept		0.00	0.643		
Rufous Whistler	80	INS	Intercept		0.00	0.453		
			Threshold	Decreased	0.66	0.326	0.05	0.172
Grey Shrikethrush	15	OMN	Intercept		0.00	0.632		
Grey Fantail	38	INS	Intercept		0.00	0.398		
			Linear	Decreased	0.49	0.311	0.06	0.156
			Threshold	Decreased	1.12	0.227	0.03	0.226
Australian Raven	21	OMN	Intercept		0.00	0.632		
Hooded Robin	13	INS	Intercept		0.00	0.592		
Scarlet Robin	70	INS	**Threshold**	**Decreased**	**0.00**	**0.387**	**0.23**	**0.019**
			Linear	**Decreased**	**0.27**	**0.339**	**0.22**	**0.022**
			Quadratic	**Trough**	**1.26**	**0.206**	**0.26**	**0.031**
Tree Martin	23	INS	Intercept		0.00	0.618		

Silvereye	94	INS	Intercept		0.00	0.491		
			Linear	Increased	1.47	0.236	0.01	0.281
			Threshold	Increased	1.57	0.233	0.01	0.302

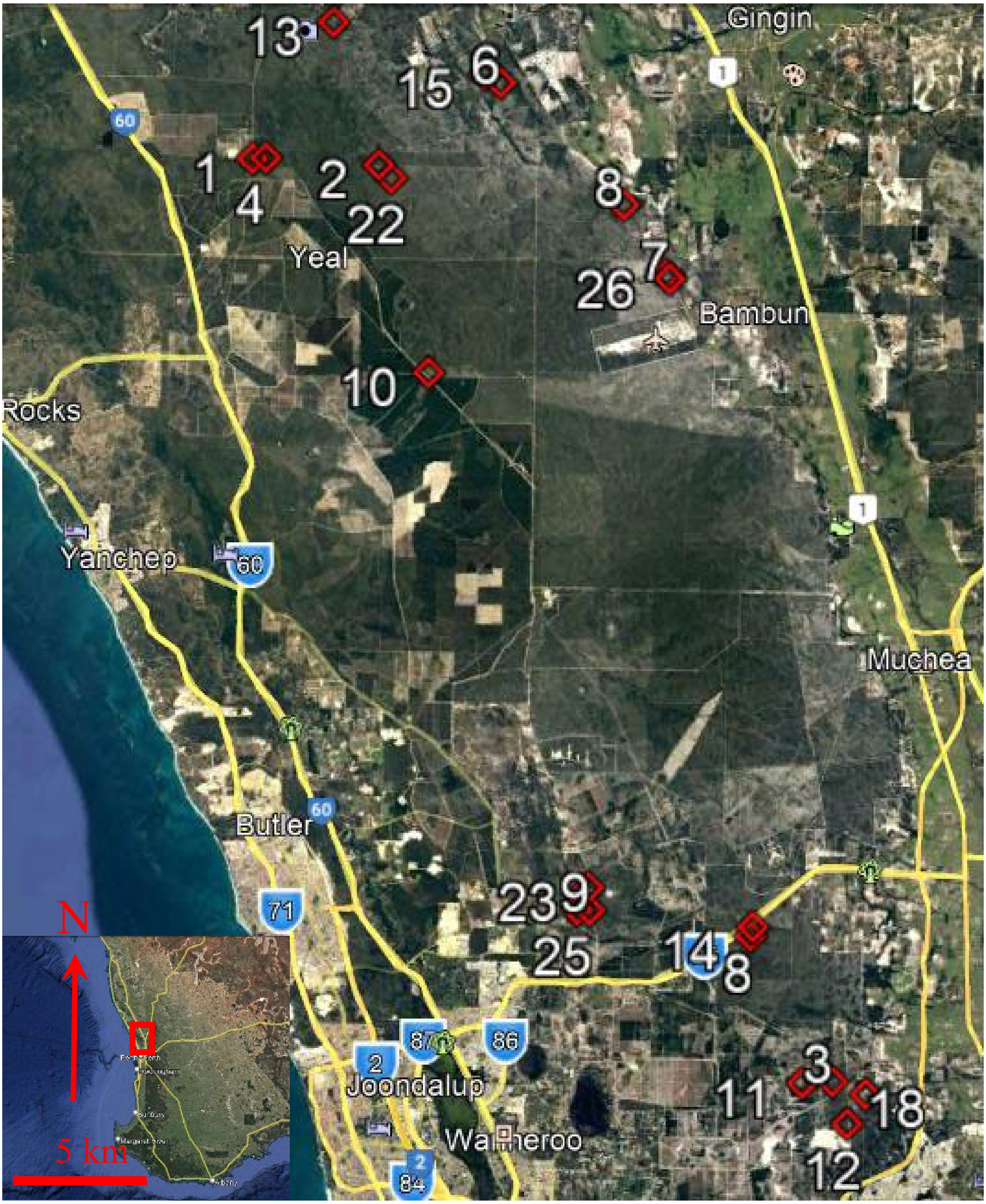


Fig. 1. Map showing the location of bird sampling locations as red diamonds and their post-fire age as white numbers. Also shown are major roads in yellow and surroundings towns and cities. Inset shows the location of the study area to the north of the major metropolitan area of Perth in south-west Western Australia (Imagery from Google Earth).

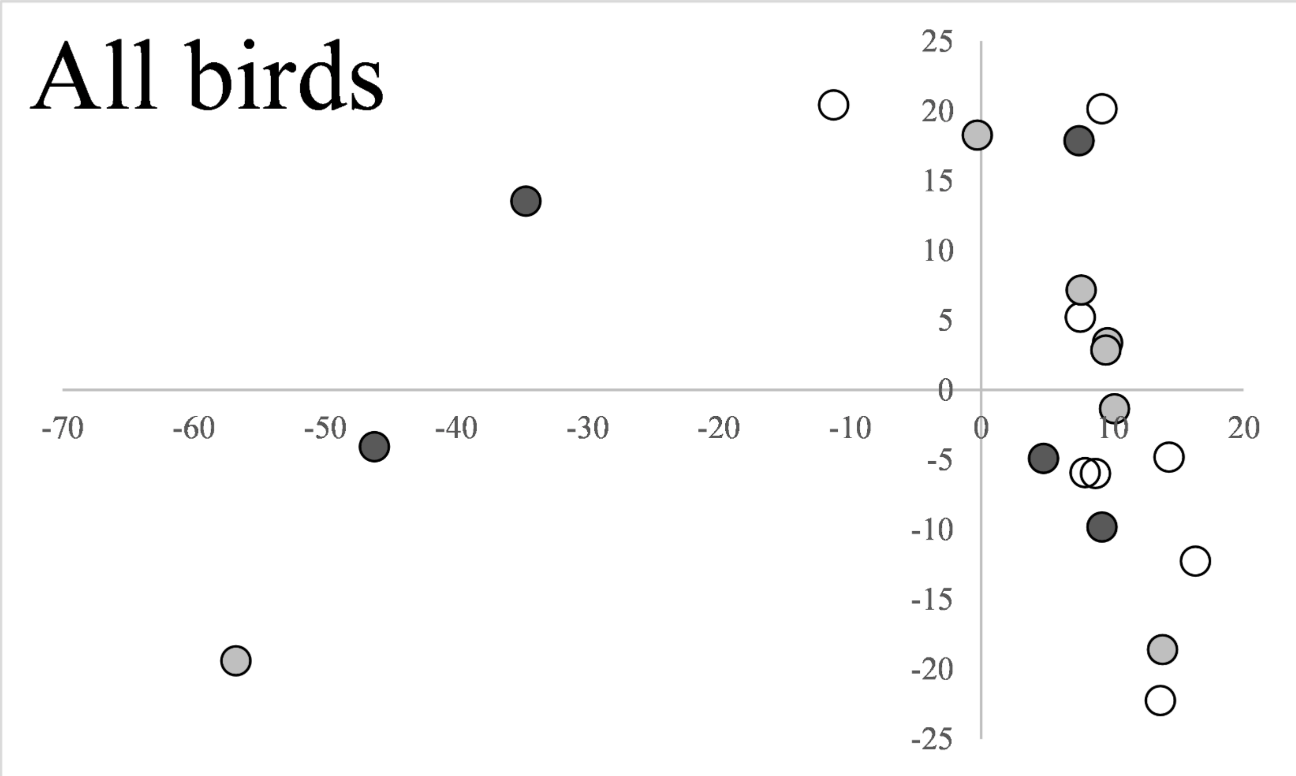
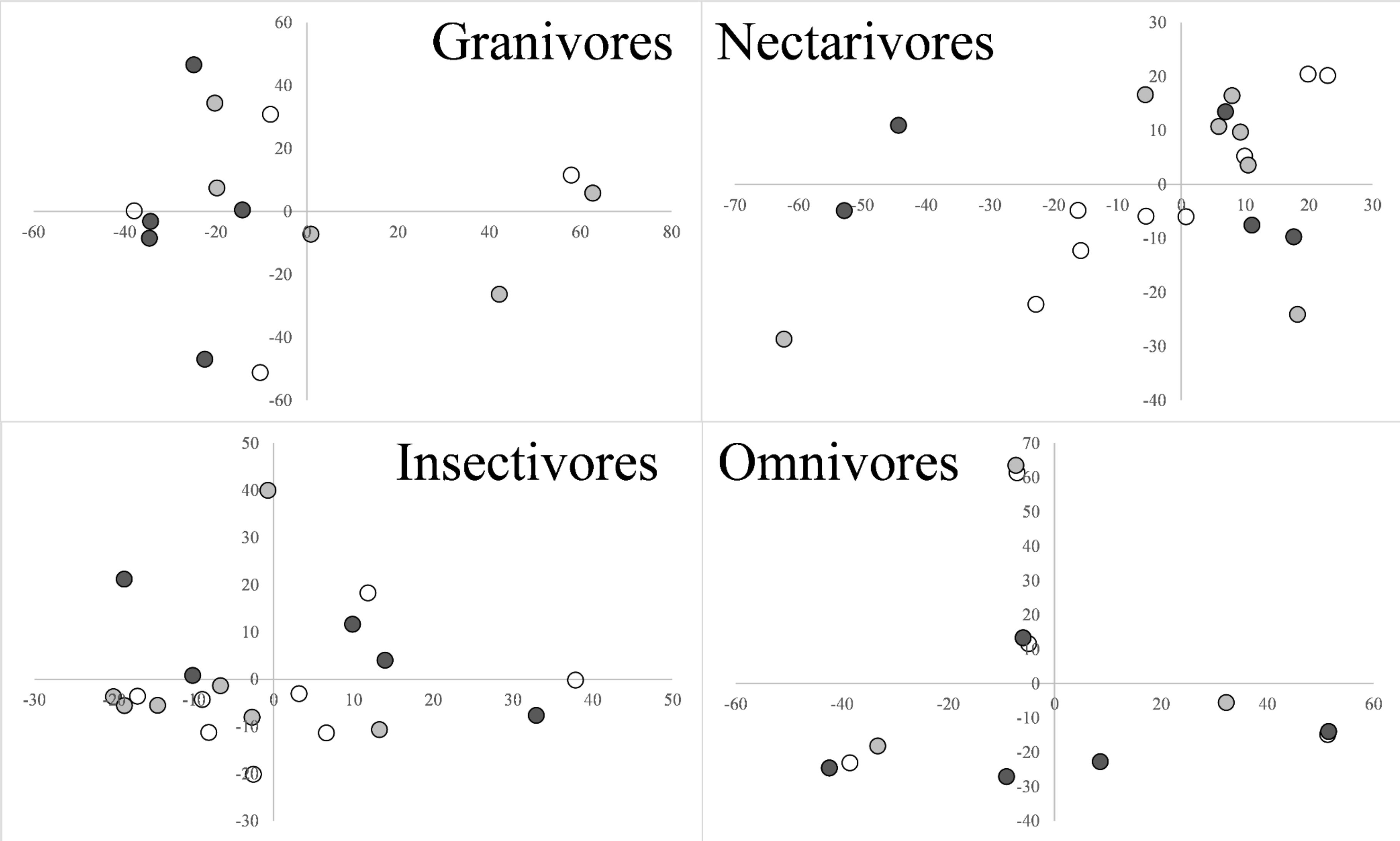
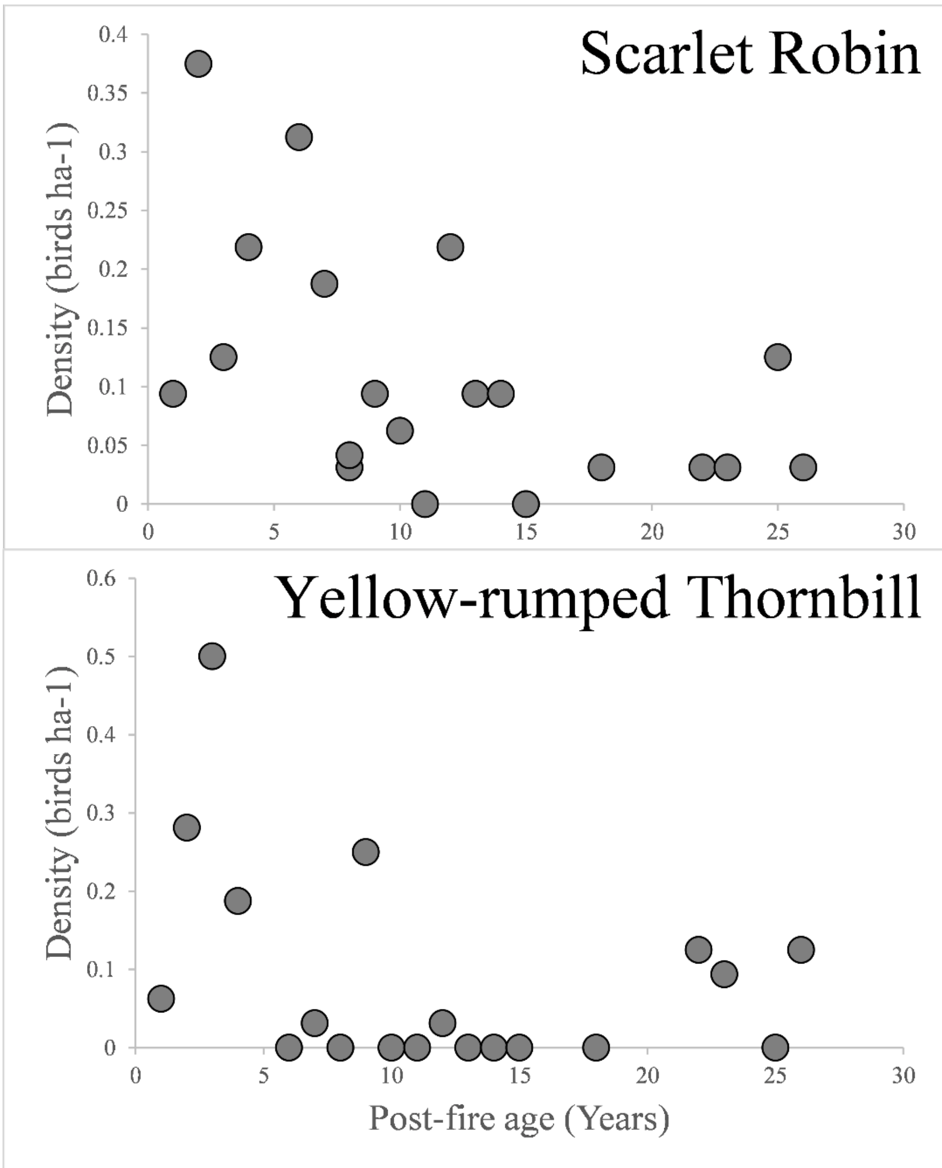


Fig. 2. Principal Coordinates Analysis (PCO) of the overall bird community in relation to post-fire age. Young sites (≤8 years post-fire) are shown as white circles, intermediate site (9–15 years post-fire) as light grey circles and old sites (≥18 years post-fire) as dark grey circles. Note there is no difference between the three post-fire stages and no directional post-fire succession.



Granivores
Nectarivores
Insectivores
Omnivores

Fig. 3. Principle Coordinates Analysis (PCO) of the four most abundant bird guilds in relation to post-fire age; granivores (*n* = 4), nectarivores (*n* = 7), omnivores (*n* = 4) and insectivores (*n* = 28). Young sites (≤8 years post-fire) are shown as white circles, intermediate site (9–15 years post-fire) as light grey circles and old sites (≥18 years post-fire) as dark grey circles. Note there is no difference between the three post-fire stages for any of the guilds nor any directional post-fire succession.



Fig, 4. Densities of Scarlet Robins and Yellow-rumped Thornbills in relation to post-fire age. Potential relationships for Scarlet Robins include decreasing densities with post-fire age (linear), decreasing then persisting at low densities (threshold) or decreasing and then increasing in older ages (quadratic). The potential relationship for Yellow-rumped Thornbills is decreasing with post-fire age with an increase in older ages (quadratic).