Fire, drought and flooding rains: The effect of climatic extremes on bird species’ responses to time since fire

Jemima Connell1 | Mark A. Hall1,2 | Dale G. Nimmo3 | Simon J. Watson1 | Michael F. Clarke1

1Department of Ecology, Environment and Evolution, La Trobe University, Bundoora, VIC, Australia
2Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW, Australia
3School of Environmental Science, Institute for Land, Water and Society, Charles Sturt University, Albury, NSW, Australia

Correspondence
Jemima Connell, Department of Ecology, Environment and Evolution, La Trobe University, Bundoora, VIC, 3086, Australia. Email: jemima.connell@environment.nsw.gov.au

Funding information
Department of Environment, Land, Water and Planning, State Government of Victoria

Editor: Catherine (FIRE) Parr

Abstract
Aim: Climatic extremes and fire affect ecosystems across the globe, yet our understanding of how species are influenced by the interaction of these broadscale ecological drivers is poorly understood. Using a ten-year dataset, we tested how extreme drought and rainfall interacted with time since fire (TSF) to shape bird species’ distributions.

Location: Semi-arid mallee woodlands of south-eastern Australia.

Methods: We quantified the effects of climatic extremes on bird species’ occurrence, species richness and incidence at 180 sites across three climatic periods—an El Niño-associated drought (the “Big Dry”), immediately after La Niña drought-breaking rainfall (“Big Wet”) and three years following the La Niña event (“Post-Big Wet”). We then compared species’ responses with TSF across the three climatic periods using a chronosequence of sites from 1 to 117 years post-fire.

Results: La Niña rainfall had sustained impacts on species’ occurrence. Over half of species increased significantly during the Big Wet. Despite three intervening years of below-average rainfall, three quarters of these species remained comparably high, Post-Big Wet. By contrast, less than half of threatened and declining species benefited from high rainfall. Responses of species to TSF were found to differ contingent on climatic conditions: almost twice as many species responded to TSF during the Big Wet and almost three times as many Post-Big Wet, compared with the Big Dry. Across climatic periods, a majority of species showed preference for mid to older post-fire vegetation.

Main conclusions: Variation in responses to TSF is likely due to the effect of climatic variation on resources. We suggest that, at sites of different post-fire age, interactions between TSF and climate may differentially influence both the availability and longevity of resources. Given climatic extremes are predicted to become increasingly severe with climate change, accounting for their influence on fauna–fire dynamics will require careful management of fire.
Climate and fire are inextricably linked forces that shape ecosystems worldwide (Bowman et al., 2009; Ummenhofer & Meehl, 2017). Both drive the distribution and abundance of animal species through mortality and alteration of resources (Fox, 1982; Monamy & Fox, 2000; Parmesan et al., 2000). Fire incinerates vegetation, altering resources and triggering vegetation changes (i.e. succession) that can continue for years, decades or centuries (Haslem et al., 2011). Climatic extremes, such as major rainfall events occurring in water-limited systems, can increase primary productivity, leading to population pulses and expansion of animal distributions (Holmgren et al., 2006), whereas droughts can cause population crashes and range contractions (Maron et al., 2015). Despite increased knowledge of how climate and fire can drive ecosystem changes, there remains little understanding of how they interact to shape species occurrence.

Post-fire vegetation succession results in fluctuations in resources available to animals, which subsequently change in abundance, generating a species’ post-fire response (characterized as curves in the “habitat accommodation model”; Fox, 1982). Recent work has questioned how stable such responses are across space and time (e.g. Kelly et al., 2017; Nimmo et al., 2012). For example, Verdon et al. (2019) showed that the fire response of the Mallee Emu-wren (Stipiturus mallee) was influenced by the interaction of time since fire (TSF) with elevation, and Hale et al. (2016) showed that the response of mammals to fire fluctuated over time. An explanation for varying post-fire responses is that factors other than fire, such as climatic variation, also affect vegetation and resource availability. This results in variable trajectories of post-fire vegetation across space and time, in turn leading to variable responses of animals (Nimmo et al., 2014).

Climatic variations can strongly affect vegetation and resource availability for animals resulting in population fluctuations (Parmesan et al., 2000). Precipitation plays a crucial and limiting role, exemplified by its pronounced effects on plants and fast-reproducing mammals (Holmgren et al., 2006). Major rainfall events promote plant productivity, triggering changes in the distribution and abundance of animals (Jaksic, 2001; Schwinning & Sala, 2004; cf. Pavey & Nano, 2009). For example, following high rainfall Predavec (1994) showed rodent populations in an Australian arid system increased 40-fold, while Jaksic et al. (1997) demonstrated small mammal populations in a semi-arid Chilean desert fluctuated 20-fold. Broader impacts of climatic extremes, such as prolonged drought and wet periods, have also been highlighted for other taxa (e.g. bird communities, Albright et al., 2010; Bennett et al., 2014; Tischler et al., 2013). Changes to faunal assemblages can be attributed to rainfall-induced variation in food availability. On the Galápagos Islands, high rainfall events associated with the El Niño Southern Oscillation (ENSO) were acknowledged as driving greater seed, fruit, nectar, pollen and arthropod abundances and linked to greater breeding success for two species of Darwin’s finches (Grant et al., 2000). In south-eastern Australia, drought conditions have been associated with significant declines in flowering by eucalypt trees (Mac Nally et al., 2009), a dominant food resource providing nectar, other carbohydrates, fruits and flowers, supporting large invertebrate assemblages and many vertebrates. Decreased bird breeding, a lower proportion of juvenile birds and smaller resident bird populations were documented alongside this decline in food availability (Mac Nally et al., 2009).

Given that the frequency and severity of both wildfire and climatic extremes are becoming exacerbated by human-driven climate change (McKenzie et al., 2004; Weltzin et al., 2003), knowledge of the extent to which they interact is critical for understanding population trajectories of fauna and developing effective fire management for biodiversity conservation (Clarke, 2008). There is emerging evidence that fire and climatic extremes do indeed interact to shape species’ distributions. In an arid ecosystem, the abundance of small mammals increased more at newly burnt sites (<5 years post-fire) relative to long-unburnt sites (>25 years post-fire) following high La Niña rainfall. Differences were attributed to variation in food resource availability (Letnic & Dickman, 2005). In a temperate ecosystem, Hale et al. (2016) demonstrated that mammal species’ post-fire responses varied between periods of drought, drought-breaking rainfall and post-rainfall. Understanding the prevalence of such interactions is important from a fire management perspective. For example, if species’ responses often differ contingent on climatic conditions, then the optimal approach to fire management may also vary (e.g. see Hale et al., 2016). Further, some management practices (e.g. burning to promote particular post-fire seral stages) may be more effective or pose a lower risk to species, when conducted under particular climatic scenarios (Clarke, 2008).

Here, we capitalized on a rare opportunity to test the effects of drought and rainfall on birds and their response to TSF by building on long-term survey data in a fire-prone, semi-arid ecosystem of south-eastern Australia. These systems support a rich diversity of fauna, many of which show strong associations with TSF (e.g. birds, Connell et al., 2017; mammals, Kelly et al., 2011; reptiles, Nimmo et al., 2012) and have highly variable rainfall between years that affects plant recruitment and productivity (Holmgren et al., 2006). Recurring cycles of dry and wet—typical of arid regions—have become more severe and common in semi-arid zones, associated with climate change (Weltzin et al., 2003). We investigated whether bird species occurrence and the association of species with TSF were each influenced by extreme climatic variation. We compared species’ occurrences across space and time, in turn leading to variable responses of animals (Nimmo et al., 2014).
Sunset and the Hattah–Kulkyne National Parks—in southeastern Australia. Mean total annual rainfall for the region is 290 mm (Bureau of Meteorology, 2020a), and summer extremes are high (mean daily maxima >32°C), while winters are mild (mean daily minima ~16°C). The region is characterized by undulating dunes and swales of low relief (~2–15 m, Lawrence, 1980). Surveys were conducted across two major vegetation types, Triodia mallee and Chenopod mallee (as defined by Haslem et al., 2010), both of which are dominated by treed "mallee," a multi-stemmed eucalypt (Noble, 1984). Triodia mallee typically occurs on sandy dunes with a canopy comprising Eucalyptus dumosa and E. socialis, and an understorey featuring perennial hummock grass (Triodia scariosa) and sclerophyllous shrubs. Chenopod mallee occurs in loamy or clay swales with a canopy typified by E. oleosa subsp. oleosa and E. gracilis, with a sparse understorey of Chenopodioideae and succulent shrubs. Treed mallee is highly fire-prone, and fires typically consume all strata, with trees re-sprouting from lignotubers following wildfire (Noble, 1984). Large wildfires (>10,000 ha) typically occur decadal somewhere in the reserve system, but areas can remain unburnt for over a century (Avitabile et al., 2013). Variable amounts of prescribed burning are conducted within reserves, both to reduce fuel loads and to protect and promote biodiversity (Department of Sustainability & Environment, 2012).

### 2.2 | Sampling design

Sites selected for the present study formed part of a broader project (the Mallee Fire and Biodiversity Project, see Watson, Taylor, Spence-Bailey, et al., 2012) and were clustered in eleven landscapes (4 km diameter) across the region. Sampling was performed using a TSF chronosequence from 1 to approximately 170 years post-fire, comprising a subset (n = 180 sites) of those surveyed by Watson, Taylor, Nimmo, et al. (2012). While use of space-for-time substitution was necessary to study a multi-decadal post-fire successional trajectory, it assumes that factors driving both spatial variation and temporal variation in ecological processes are commensurate (Pickett, 1989). Sites within landscapes were a minimum distance of 500 m apart to allow for independence, and landscapes were separated by a minimum of 2 km. Surveys were performed in Triodia and Chenopod mallee vegetation types. Heathy and Shrubby mallee vegetation types are also typical of the region but were excluded from analyses because surveying was not conducted across an adequate distribution of post-fire ages within either type. Similarly, due to poor sampling representation, sites older than 117 years post-fire were excluded. Post-fire age of vegetation at sites was determined during the first survey round using two methods. For those sites burnt after 1972, age was established using fire scars mapped from satellite imagery (Avitabile et al., 2013), and for sites burnt prior to this, age was established using a regression technique developed by Clarke et al. (2010), who were able to model a strong relationship between post-fire mallee tree age and stem diameter and validated this with independent data.

### 2.3 | Bird data

Repeat bird surveys were conducted at all sites in three periods of extreme climatic variation: during the Millennium Drought (the "Big Dry," surveys conducted in 2006–2008); 6 months to 1 year following the first and highest rainfall peak of the 2010–2012 La Niña event (the "Big Wet," surveys conducted in 2011–2012 during the second, more moderate La Niña rainfall peak, Bureau of Meteorology, 2020a,
and following the La Niña event ("Post-Big Wet," surveys conducted in 2014–2015). The Big Dry was one of two of the most severe and extended drought periods for the Murray Darling Basin since records began in 1880, with below-average annual rainfall from 2001 to 2009 (Leblanc et al., 2012; see Figure 1; raw data taken from Mildura Airport weather station, Bureau of Meteorology, 2020a). Records from the Big Wet were collected following exceptionally high, drought-breaking rains, which comprised the highest annual rainfall means recorded for the Basin (Leblanc et al., 2012). Records from the Post-Big Wet period were conducted in a period of below-average rainfall, which occurred from 2012 onwards.

Four repeat visits were conducted at all sites for each climatic period, comprising two separate springs (2006, 2007) and autumns (2007, 2008) during the Big Dry, and twice in each of a single spring and autumn season for both the Big Wet (2011, 2012) and Post-Big Wet (2014, 2015) periods. Five-minute point surveys were performed, with all individuals seen or heard within a 60 m radius of a site recorded (see Appendix Table S1.1 in Supporting Information for complete species list). Using the same survey sites and methodology, Watson, Taylor, Nimmo, et al. (2012) previously modelled variation in detectability of individual bird species against observer distance and vegetation density. They found that vegetation density, which varies with post-fire age (Haslem et al., 2011), did not significantly bias the detectability of any species within the 60 m radius.

2.4 | Response and predictor variables

We first compared changes in the occurrence of individual species, species richness and incidence (as specified below) across the study landscape between climatic periods (climate-only models). We then assessed changes in the occurrence of individual species, species richness and incidence with post-fire age (from 1–117 years post-fire) to the interaction between climatic period (Big Dry, Big Wet and Post-Big Wet) and vegetation type (Triodia and Chenopod mallee, as defined by Haslem et al., 2010, climate+fire models). TSF response models for the Big Dry, originally built for the wider Murray Mallee region (Watson, Taylor, Nimmo, et al., 2012), were here reconstructed using a subset of data from the Victorian region only, to allow for direct comparison for each species across climatic periods.

Individual species’ occurrences were modelled using presence/absence data, as measured by the number of sites at which a species was recorded at least once within any of the four survey rounds within each climatic period. This was deemed more appropriate than use of abundance data, for which counts were low for many rarer species in the region (Watson, Taylor, Nimmo, et al., 2012). Species richness was measured by the cumulative total number of species recorded at least once at a site across four repeat surveys within each climatic period. Species incidence was measured by the cumulative total number of presences of all species at a site, pooled across the four repeat surveys within a period (i.e. for any given species, a maximum of four incidences within a period was possible). For climate-only models, individual species’ occurrences, species richness and incidence were pooled across all sites within each climatic period, while for climate+fire models, these response data were separated by post-fire age and vegetation type.

Threatened and declining mallee bird species were identified as threatened with extinction or experiencing significant declines using state and federal agency listings (see Appendix Table S1.2). Temporary resident bird species (i.e. migrants, long-distance nomads and those species for which there is evidence of locally nomadic movement, e.g. in response to flowering events) were identified using reference material from Schodde (1981) and Marchant and Higgins (1993).
2.5 Statistical analyses

We used a mixed-effects modelling framework to accommodate the repeated-measures design and account for spatial clustering of data (Zuur et al., 2009). For climate-only models, the association of species with climatic period was determined using generalized linear mixed models (GLMMs, using the lme4 package; Bates et al., 2015). For climate+fire models, the association of species with TSF in each vegetation type was determined for each climatic period using generalized additive mixed models (GAMMs, using the gamm4 package; Wood & Scheipl, 2013), which allow for nonlinear relationships between predictors and response variables (Zuur et al., 2009).

For both sets of models, climatic period was included as a fixed effect, and sites and landscapes were included as random effects to account for both repeated sampling across each of the survey periods and the spatial clustering of sites within landscapes. For climate+fire models, post-fire responses were assessed for each level of the interaction between vegetation type (Triodia mallee, Chenopod mallee) and climatic period (Big Dry, Big Wet and Post-Big Wet). These models were fitted by applying an additional smoothing term to TSF, with a “by” function for the vegetation x rainfall period categories. Nonparametric smoothing parameters were estimated from the data using a Laplace approximate maximum-likelihood approach, where smoothing is optimized through an iterative procedure during model fitting (Wood, 2008). As smoothers were not excessively wiggly, no upper limit was set to the number of basic functions.

Total species richness and incidence response models were constructed assuming a Poisson distribution and log link function, as count data were used (Zuur et al., 2009). Models were assessed for overdispersion, and none was found. Individual species models were constructed assuming a binomial error distribution and logit link function, as presence/absence data were used. Models were built only for those species, which occurred at ≥20 sites, following Watson, Taylor, Nimmo, et al. (2012), and for climate+fire models, post-fire responses were assessed only for species with ≥10 records in a given combination of climatic period and vegetation type (see recommendations by Harrison et al., 2018). For climate-only models, 35 species were able to be modelled (Table 1). For climate+fire models, 27 species were able to be modelled (Tables 2 and 3), with 25 fire responses able to be assessed in the Big Dry, 39 in the Big Wet and 38 Post-Big Wet (note that models fitted in multiple vegetation types were counted separately).

For climate-only models, pairwise comparisons between climatic periods were tested using estimated marginal means (EMMs, using the emmeans package; Lenth et al., 2018). EMMs are generated using the fitted model to make predictions over a grid of predictor combinations in order to assess the effects of individual factors. The grid comprises a reference level for each unique level of a categorical predictor, and a single reference level representing the mean value of any numeric predictor (Lenth et al., 2018). These predict species occurrence in each climatic period and estimate the significance of differences between terms, using Tukey’s HSD (honestly significant difference) test. Odds ratios were used to convey the constant effect of the predictor (climatic period) on species occurrence. The odds ratio represents the multiplicative factor by which species occurrence changes between each combination of climatic period. Its use allows for direct comparison of the magnitude of change experienced between species. Odds ratios were derived from EMM pairwise contrasts and are shown on the log odds ratio scale.

For climate+fire models, significant smoothing functions (p < .05, estimated using chi-square as per Wood, 2017) were predicted to new data representing a chronosequence from 1-120 years, and subsequent response curves were assigned to a priori types developed by Watson, Taylor, Nimmo, et al. (2012), adapted from Whelan et al. (2002). A priori response types were incline, decline, bell, plateau, delayed and irruptive (see Appendix Figure S1.1). Non-significant smoothing functions were assigned a “null” response.

Evaluation of climate+fire models was performed using deviance explained as a measure of model fit, and cross-validation as a measure of predictive capacity (using source code adapted from Elith et al., 2008). For each model, the dataset was randomly split into fivefold, of which fourfold were used to build a model, and the fifth was used to test it. This process was repeated five times, with a different fold held out for testing at each iteration. The Spearman rank correlation coefficient was used as a measure of predictive ability for Poisson models (Potts & Elith, 2006). This measure ranks predicted and observed values, providing a score between −1 and 1. The mean area under the receiver operating curve (AUC) value was calculated for binomial models. An AUC value of >0.5 indicates a predictive ability no better than random, 0.5–0.7 indicates some predictive ability, 0.7–0.9 indicates reasonable predictive ability, and >0.9 indicates strong predictive ability (Pearce & Ferrier, 2000).

Data analyses were conducted in RStudio V 1.2.1335 (R Core Team, 2019). See Appendix S2 for examples of R scripts used.

3 RESULTS

3.1 Influence of climatic extremes on bird species’ occurrence

Bird species richness and incidence increased significantly, both more than doubling during the Big Wet compared with the Big Dry. Post-Big Wet, both species richness and incidence remained high, compared with the Big Wet (c.f. the Big Dry, climate-only models; Table 1). Over half of individual bird species modelled (20 of 35) increased significantly in occurrence during the Big Wet compared with the Big Dry. Of those species that increased significantly Big Wet, more than three quarters (16) showed sustained increases Post-Big Wet (i.e. their odds ratio did not significantly decline, Post-Big Wet compared with Big Wet). Six species increased exclusively Post-Big Wet (i.e. their odds ratio increased significantly compared with the Big Dry or Big Wet). Increases in individual species occurrence were dominated by resident species in both the Big Wet and Post-Big Wet (16 of 20 and 18 of 22, respectively). Six species decreased significantly Post-Big Wet. Of these, three were listed as
| Response variable          | n       | Big Wet vs. Big Dry | Post-Big Wet vs. Big Wet | Post-Big Wet vs. Big Dry |
|---------------------------|---------|---------------------|--------------------------|--------------------------|
|                           |         | Odds ratio | SE | Z ratio | p value | Odds ratio | SE | Z ratio | p value | Odds ratio | SE | Z ratio | p value |
| Community measure         |         |            |    |         |          |            |    |         |          |            |    |         |          |
| Bird species richness     | 785     | 2.29       | 0.10 | 19.53   | <.01    | 0.95       | 0.03 | -1.65   | .23     | 2.17       | 0.09 | 18.08   | <.01    |
| Bird species incidence    | 985     | 2.82       | 0.10 | 28.22   | <.01    | 0.99       | 0.03 | -0.23   | .97     | 2.80       | 0.10 | 28.04   | <.01    |
| Individual species        |         |            |    |         |          |            |    |         |          |            |    |         |          |
| Common Bronzewing         | 3       | 2.43       | 1.71 | 1.26    | .42     | 2.88       | 1.35 | 2.26    | .06     | 7.01       | 4.49 | 3.04    | .01     |
| Australian Ringneck       | 13      | 1.58       | 0.63 | 1.16    | .48     | 0.87       | 0.32 | -0.37   | .93     | 1.38       | 0.55 | 0.80    | .71     |
| Mulga Parrot              | 7       | 3.45       | 1.85 | 2.30    | .06     | 0.64       | 0.28 | -1.04   | .55     | 2.20       | 1.18 | 1.46    | .31     |
| Splendid Fairy-wren       | 12      | 1.82       | 0.72 | 1.51    | .28     | 0.77       | 0.28 | -0.73   | .75     | 1.39       | 0.57 | 0.81    | .70     |
| Variegated Fairy-wren     | 4       | 5.60       | 4.33 | 2.23    | .07     | 0.54       | 0.35 | -0.94   | .61     | 3.02       | 2.33 | 1.43    | .32     |
| Mallee Emu-wren\textsuperscript{a} | 10 | 2.16       | 1.39 | 1.21    | .45     | 0.13       | 0.10 | -2.71   | .02     | 0.27       | 0.21 | 1.73    | .20     |
| Striated Grasswren\textsuperscript{a} | 14 | 1.93       | 1.02 | 1.24    | .43     | 0.18       | 0.11 | -2.72   | .02     | 0.35       | 0.22 | 1.71    | .20     |
| Shy Heathwren\textsuperscript{a} | 31 | 1.06       | 0.35 | 0.17    | .98     | 0.75       | 0.26 | -0.85   | .68     | 0.79       | 0.27 | 0.68    | .77     |
| Weebill                   | 65      | 2.87       | 0.38 | 7.55    | <.00    | 0.52       | 0.33 | 1.60    | .25     | 3.39       | 0.42 | 8.06    | <.00    |
| Chestnut-rumped Thornbill | 23      | 7.89       | 2.52 | 6.48    | <.00    | 0.21       | 0.06 | -5.40   | <.00    | 1.69       | 0.53 | 1.67    | .22     |
| Inland Thornbill          | 28      | 1.79       | 0.51 | 2.05    | .10     | 1.42       | 0.36 | 1.38    | .35     | 2.53       | 0.70 | 3.34    | <.00    |
| Spotted Pardalote         | 61      | 6.88       | 1.88 | 7.05    | <.00    | 1.79       | 0.49 | 2.13    | .08     | 12.34      | 3.77 | 8.23    | <.00    |
| Striated Pardalote        | 30      | 4.55       | 1.28 | 5.40    | <.00    | 0.77       | 0.18 | -1.09   | .52     | 3.51       | 0.98 | 4.52    | <.00    |
| White-eared Honeyeater    | 66      | 29.43      | 12.26 | 8.12   | <.00    | 0.22       | 0.07 | -4.58   | <.00    | 6.35       | 1.99 | 5.90    | <.00    |
| Yellow-plumed Honeyeater  | 85      | 3.29       | 1.05 | 3.72    | <.00    | 0.79       | 0.24 | -0.77   | .72     | 2.60       | 0.81 | 3.05    | .01     |
| White-fronted Honeyeater\textsuperscript{b} | 29 | 10.39      | 3.35 | 7.27    | <.00    | 0.09       | 0.03 | -7.42   | <.00    | 0.91       | 0.28 | 0.31    | .95     |
| Spiny-cheeked Honeyeater\textsuperscript{b} | 41 | 8.43       | 2.36 | 7.63    | <.00    | 0.67       | 0.16 | -1.74   | .19     | 5.62       | 1.49 | 6.49    | <.00    |
| Red Wattlebird\textsuperscript{b} | 9  | 2.50       | 1.07 | 2.13    | .08     | 0.40       | 0.17 | -2.13   | .08     | 1.00       | 0.49 | 0.00    | 1.00    |
| Brown-headed Honeyeater\textsuperscript{b} | 8  | 6.24       | 2.61 | 4.38    | <.00    | 0.53       | 0.16 | -2.15   | .08     | 3.27       | 1.42 | 2.74    | .02     |

(Continues)
| Response variable          | Big Dry | Big Wet | Post-Big Wet | Big Wet versus Big Dry | Odds ratio | SE    | Z ratio  | p value | Post-Big Wet versus Big Wet | Odds ratio | SE   | Z ratio  | p value | Post-Big Wet versus Big Dry | Odds ratio | SE   | Z ratio  | p value |
|---------------------------|---------|---------|--------------|------------------------|------------|-------|----------|---------|----------------------------|------------|------|----------|---------|----------------------------|------------|------|----------|---------|
| Striped Honeyeater        | 5       | 23      | 19           | 7.27                   | 4.13       | 3.50  | <.00     |         | 0.75                       | 0.29       | 0.76 | .73      |         | 5.45                       | 3.09       | 2.99 | .01      |         |
| White-browed Babbler      | 5       | 23      | 19           | 6.36                   | 3.49       | 3.38  | <.00     |         | 0.77                       | 0.28       | 0.72 | .75      |         | 4.91                       | 2.71       | 2.89 | .01      |         |
| Chestnut Quail-thrush     | 29      | 37      | 85           | 1.41                   | 0.42       | 1.17  | .47      |         | 4.65                       | 1.32       | 5.43 | <.00     |         | 6.56                       | 1.98       | 6.23 | <.00     |         |
| Red-lored Whistler        | 11      | 33      | 9            | 4.44                   | 1.84       | 3.60  | <.00     |         | 0.18                       | 0.08       | −3.91| <.00     |         | 0.79                       | 0.39       | −0.49| .88      |         |
| Golden Whistler           | 11      | 25      | 19           | 6.85                   | 4.14       | 3.19  | <.00     |         | 0.50                       | 0.25       | −1.39| .34      |         | 3.43                       | 2.00       | 2.11 | <.00     |         |
| Rufous Whistler           | 2       | 8       | 17           | 13.05                  | 14.92      | 2.25  | .06      |         | 11.10                      | 10.12      | 2.64 | .02      |         | 144.88                     | 188.74     | 3.82 | <.00     |         |
| Grey Shrike-thrush         | 29      | 98      | 104          | 7.23                   | 2.01       | 7.10  | <.00     |         | 1.16                       | 0.26       | 0.67 | .78      |         | 8.38                       | 2.37       | 7.53 | <.00     |         |
| Crested Bellbird          | 10      | 67      | 102          | 10.45                  | 3.79       | 6.47  | <.00     |         | 2.26                       | 0.49       | 3.72 | <.00     |         | 23.61                      | 8.56       | 8.72 | <.00     |         |
| Masked Woodswallow         | 9       | 12      | 35           | 1.43                   | 0.70       | 0.73  | .75      |         | 4.81                       | 2.03       | 3.73 | <.00     |         | 6.87                       | 3.17       | 4.17 | <.00     |         |
| White-browed Woodswallow  | 8       | 30      | 30           | 6.20                   | 2.94       | 3.85  | <.00     |         | 1.00                       | 0.33       | 0.00 | 1.00     |         | 6.20                       | 2.94       | 3.85 | <.00     |         |
| Grey Butcherbird          | 45      | 77      | 87           | 2.30                   | 0.54       | 3.55  | <.00     |         | 1.26                       | 0.27       | 1.07 | .53      |         | 2.89                       | 0.68       | 4.52 | <.00     |         |
| Australian Magpie         | 3       | 8       | 20           | 2.76                   | 1.88       | 1.49  | .30      |         | 2.71                       | 1.17       | 2.31 | .05      |         | 7.48                       | 4.69       | 3.21 | <.00     |         |
| Grey Currawong            | 3       | 14      | 26           | 5.02                   | 3.23       | 2.51  | .03      |         | 2.02                       | 0.71       | 2.01 | .11      |         | 10.15                      | 6.27       | 3.75 | <.00     |         |
| Willie Wagtail            | 12      | 21      | 20           | 2.01                   | 0.81       | 1.73  | .20      |         | 0.94                       | 0.34       | −0.18| .98      |         | 1.88                       | 0.77       | 1.56 | .26      |         |
| Jacky Winter              | 17      | 51      | 62           | 4.47                   | 1.47       | 4.56  | <.00     |         | 1.40                       | 0.35       | 1.35 | .37      |         | 6.27                       | 2.08       | 5.55 | <.00     |         |
| Southern Scrub-robin      | 2       | 12      | 14           | 21.03                  | 21.21      | 3.02  | .01      |         | 1.45                       | 0.89       | 0.61 | .82      |         | 30.51                      | 31.21      | 3.34 | <.00     |         |

Notes: Significant odds ratios (p < .05) indicated in bold.

Cells highlighted dark grey—odds ratios significantly >1 (i.e. higher); light grey, significantly <1 (i.e. lower).

n (species richness)—cumulative total number of species recorded across all sites (pooled across post-fire age classes and vegetation types).

n (species incidence)—total number of presences of all species recorded across all sites (pooled across post-fire age classes and vegetation types).

n (individual species)—total number of presences of all species recorded across all sites (pooled across post-fire age classes and vegetation types).

a Declining and/or threatened mallee bird species.

b Temporary resident species.
| Community measure   | Big Dry |   | Big Wet |   | Post-Big Wet |   |
|---------------------|---------|---|---------|---|--------------|---|
|                     | n      | Response | Edf | Chi-square | p value | n      | Response | Edf | Chi-square | p value | n      | Response | Edf | Chi-square | p value |
| Bird species richness | 544    | Null | 1.00 | 0.09       | .77     | 1,294  | Null | 1.00 | 0.41       | .52     | 1,214  | Plateau | 2.59 | 26.64       | <.00    |
| Bird species incidence | 684    | Null | 1.00 | 1.84       | .17     | 2026   | Null | 1.00 | 0.35       | .55     | 1,998  | Plateau | 2.96 | 34.32       | <.00    |

| Individual species |   |   |   |   |   |   |
|---------------------|---|---|---|---|---|---|
| Common Bronzewing    | 3 |   |   |   |   |   |
| Australian Ringneck  | 7 |   |   |   |   |   |
| Splendid Fairy-wren  | 10| Null | 1.00 | 0.24           | .62     | 15   | Null | 1.00 | 0.00           | .97     | 14   | Null | 1.00 | 0.28           | .60     |
| Shy Heathwren a      | 25| Decline | 1.00 | 7.14           | .01     | 25   | Decline | 1.00 | 12.37           | <.00   | 20   | Decline | 1.00 | 9.17           | <.00     |
| Weebill              | 45| Null | 1.00 | 3.15           | .08     | 103  | Null | 1.00 | 0.08           | .77     | 106  | Null | 1.00 | 1.24           | .27     |
| Chestnut-rumped Thornbill | 14| Null | 1.00 | 2.92           | .09     | 55   | Null | 1.00 | 0.00           | .95     | 20   | Null | 1.00 | 0.44           | .51     |
| Inland Thornbill     | 24| Null | 1.00 | 0.16           | .69     | 33   | Null | 1.00 | 0.00           | .99     | 39   | Null | 1.00 | 2.54           | .11     |
| Spotted Pardalote     | 45| Null | 1.00 | 2.52           | .11     | 101  | Null | 1.00 | 1.74           | .19     | 111  | Null | 1.00 | 1.06           | .30     |
| Striated Pardalote   | 12| Null | 1.00 | 2.61           | .11     | 46   | Null | 1.00 | 1.23           | .26     | 45   | Incline | 1.00 | 13.66          | <.00     |
| White-eyed Honeyeater | 53| Decline | 1.00 | 6.86           | .01     | 109  | Null | 1.00 | 3.24           | .07     | 90   | Decline | 1.74 | 7.30           | .01     |
| Yellow-plumed Honeyeater | 57| Incline | 1.00 | 23.83          | <.00   | 76   | Plateau | 2.75 | 21.84          | <.00   | 74   | Plateau | 3.90 | 28.10          | <.00     |
| White-fronted Honeyeater b | 27| Null | 1.00 | 1.05           | .31     | 77   | Irruptive | 3.18 | 7.39           | .05     | 25   | Null | 1.00 | 2.42           | .12     |
| Spiny-cheeked Honeyeater b | 32| Delayed | 2.90 | 9.57           | .01     | 88   | Null | 1.00 | 0.29           | .59     | 80   | Null | 1.00 | 1.23           | .27     |
| Red Wattlebird b     | 6  |   |   |   |   |   |
| Brown-headed Honeyeater b | 4 |   |   |   |   |   |
| Chestnut Quail-thrush a | 16| Null | 1.00 | 0.70           | .40     | 25   | Null | 1.00 | 0.19           | .67     | 51   | Null | 2.06 | 3.93           | .12     |
| Red-lobed Whistler a | 8  |   |   |   |   |   |
| Golden Whistler      | 9  |   |   |   |   |   |
| Grey Shrike-thrush    | 18 | Null | 1.00 | 0.56           | .45     | 71   | Null | 1.00 | 0.09           | .77     | 72   | Bell  | 2.32 | 8.92           | .03     |

(Continues)
| Response variable          | Big Dry |  |  |  |  | Big Wet |  |  |  |  | Post-Big Wet |  |  |  |
|---------------------------|---------|---|---|---|---|---------|---|---|---|---|--------------|---|---|---|
|                           | n       | Response | Edf | Chi-square | p value | n       | Response | Edf | Chi-square | p value | n       | Response | Edf | Chi-square | p value |
| Crested Bellbird<sup>a</sup> | 7       |          |     |            |         | 43      | Null     | 1.00 | 1.90     | .17     | 74      | Bell     | 2.28 | 9.56   | .02     |
| Masked Woodswallow<sup>b</sup> | 5       |          |     |            |         | 7       |          |     |          |         | 26      | Incline  | 1.00 | 6.60   | .01     |
| White-browed Woodswallow<sup>b</sup> | 7       |          |     |            |         | 22      | Null     | 1.00 | 0.12     | .73     | 21      | Incline  | 1.00 | 9.90   | <.00     |
| Grey Butcherbird          | 29      | Null     | 1.00 | 0.63      | .43     | 48      | Null     | 1.00 | 0.00     | .96     | 63      | Null     | 1.00 | 0.01   | .95     |
| Australian Magpie         | 2       |          |     |            |         | 3       |          |     |          |         | 12      | Null     | 1.00 | 0.02   | .90     |
| Grey Currawong            | 2       |          |     |            |         | 11      | Null     | 1.00 | 2.64     | .10     | 18      | Null     | 1.00 | 0.03   | .87     |
| Willie Wagtail            | 4       |          |     |            |         | 15      | Delayed  | 1.00 | 4.50     | .03     | 11      | Delayed  | 1.00 | 8.45   | <.00     |
| Jacky Winter              | 5       |          |     |            |         | 31      | Incline  | 1.00 | 9.31     | <.00     | 40      | Incline  | 1.00 | 13.34  | <.00     |

Notes: Significant smoothing functions for time since fire were assessed using the chi-square (bold indicates \( p < .05 \)).

<sup>a</sup>Edf—estimated degrees of freedom.

<sup>n</sup>(species richness)—cumulative total number of species recorded across all sites (pooled across post-fire age classes).

<sup>n</sup>(species incidence)—total number of presences of all species recorded across all sites (pooled across post-fire age classes).

<sup>n</sup>(individual species)—number of sites at which species was detected within any survey round within each climatic period (pooled across post-fire age classes).

Italicized \( n \) values—time since fire responses not assessed for given combination of climatic period and vegetation type as \( n < 10 \).

Coefficients of the linear term also included in the models (climatic period) are presented in Table S1.3.

<sup>a</sup>Declining and/or threatened mallee bird species.

<sup>b</sup>Temporary resident species.
Table 3: Summary of climate–fire interaction effects (i.e. time since fire responses) for bird species occurrence during three periods of climatic extreme (Big Dry, Big Wet and Post-Big Wet) in Chenopod mallee (climate+fire models). Models were developed using generalized additive mixed models (GAMMs).

| Response variable          | Big Dry | Big Wet | Post-Big Wet |
|---------------------------|---------|---------|--------------|
|                           | n       | Response| Edf | Chi-square | $p$ | n | Response| Edf | Chi-square | $p$ | n | Response| Edf | Chi-square | $p$ |
| **Community measure**     |         |         |     |            |     |     |         |     |            |     |     |         |     |            |     |
| Bird species richness     | 241     | Null    | 1.00| 1.02 | .31 | 506 | Null    | 1.00| 0.25 | .61 | 453 | Incline | 1.00| 9.06 | <.00 |
| Bird species incidence    | 301     | Null    | 1.00| 0.04 | .84 | 755 | Null    | 1.00| 0.85 | .36 | 716 | Incline | 1.00| 10.25 | <.00 |
| **Individual species**    |         |         |     |            |     |     |         |     |            |     |     |         |     |            |     |
| Common Bronzewing         | 0       |         |     |            |     |     |         |     |            |     |     |         |     |            |     |
| Australian Ringneck       | 6       |         |     |            |     |     |         |     |            |     |     |         |     |            |     |
| Splendid Fairy-wren       | 2       |         |     |            |     |     |         |     |            |     |     |         |     |            |     |
| Shy Heathwren             | 6       |         |     |            |     |     |         |     |            |     |     |         |     |            |     |
| Weebill                   | 20      | Null    | 1.00| 0.98 | .32 | 41  | Null    | 1.00| 0.79 | .38 | 46  | Null    | 1.00| 0.43 | .51 |
| Chestnut-rumped Thornbill | 9       |         |     |            |     |     |         |     |            |     |     |         |     |            |     |
| Inland Thornbill          | 4       |         |     |            |     |     |         |     |            |     |     |         |     |            |     |
| Spotted Pardalote         | 16      | Null    | 1.00| 0.16 | .69 | 34  | Null    | 1.00| 0.79 | .37 | 38  | Plateau | 1.00| 4.99 | .03 |
| Striated Pardalote        | 17      | Null    | 1.00| 0.66 | .42 | 27  | Null    | 1.00| 1.85 | .17 | 19  | Incline | 1.00| 4.55 | .03 |
| White-eared Honeyeater    | 13      | Null    | 2.13| 6.70 | .07 | 41  | Decline | 1.00| 6.90 | .01 | 26  | Decline | 1.00| 6.67 | .01 |
| Yellow-plumed Honeyeater  | 26      | Incline | 1.00| 8.98 | <.00| 33  | Indine  | 1.00| 5.73 | .02 | 30  | Incline | 1.00| 7.82 | .01 |
| White-fronted Honeyeater$^b$ | 2     |         |     |            |     |     |         |     |            |     |     |         |     |            |     |
| Spiny-cheeked Honeyeater$^b$ | 8    |         |     |            |     |     |         |     |            |     |     |         |     |            |     |
| Red Wattlebird$^b$         | 3       |         |     |            |     |     |         |     |            |     |     |         |     |            |     |
| Brown-headed Honeyeater$^b$ | 4     |         |     |            |     |     |         |     |            |     |     |         |     |            |     |
| Chestnut Quail-thrush$^b$  | 13      | Null    | 1.00| 0.12 | .73 | 12  | Null    | 1.00| 2.33 | .13 | 33  | Null    | 1.00| 0.31 | .58 |
| Red-bered Whistler$^a$     | 3       |         |     |            |     |     |         |     |            |     |     |         |     |            |     |
| Golden Whistler           | 2       |         |     |            |     |     |         |     |            |     |     |         |     |            |     |
| Grey Shrike-thrush         | 10      | Null    | 1.00| 0.40 | .53 | 26  | Indine  | 1.00| 3.88 | .05 | 30  | Incline | 1.00| 7.99 | <.00 |

(Continues)
| Response variable     | Big Dry |          |          |          |          | Big Wet |          |          |          |          | Post-Big Wet |          |          |          |
|----------------------|---------|----------|----------|----------|----------|---------|----------|----------|----------|----------|----------------|----------|----------|----------|
|                      | n       | Response | Edf      | Chi-square | p value | n       | Response | Edf      | Chi-square | p value | n       | Response | Edf      | Chi-square | p value |
| Crested Bellbirda    | 3       | Null     | 1.00     | 0.15      | .70      | 23      | Null     | 1.00     | 0.13      | .72      | 26      | Null     | 1.00     | 0.71      | .40     |
| Masked Woodswallowb  | 3       |          |          |           |          | 5       |          |          |           |          | 8       |          |          |           | .11     |
| White-browed Woodswallowb | 1 |          |          |           |          | 8       |          |          |           |          | 7       |          |          |           | .40     |
| Grey Butcherbird     | 16      | Null     | 1.00     | 0.15      | .70      | 29      | Null     | 1.00     | 0.13      | .72      | 23      | Null     | 1.00     | 0.71      | .40     |
| Australian Magpie    | 1       |          |          |           |          | 5       |          |          |           |          | 6       |          |          |           | .40     |
| Grey Currawong       | 1       |          |          |           |          | 2       |          |          |           |          | 8       |          |          |           | .40     |
| Willie Wagtail       | 8       |          |          |           |          | 6       |          |          |           |          | 7       |          |          |           | .40     |
| Jacky Winter         | 11      | Null     | 1.00     | 0.70      | .40      | 19      | Null     | 1.00     | 1.27      | .26      | 21      | Incline  | 1.00     | 4.20      | .04     |

Notes: Significant smoothing functions for time since fire were assessed using the chi-square (bold indicates p < .05).

*aEdf*—estimated degrees of freedom.

*n* (species richness)—cumulative total number of species recorded across all sites (pooled across post-fire age classes).

*n* (species incidence)—total number of presences of all species recorded across all sites (pooled across post-fire age classes).

*n* (individual species)—number of sites at which species was detected within any survey round within each climatic period (pooled across post-fire age classes).

Italicized *n* values—time since fire responses not assessed for given combination of climatic period and vegetation type as *n* < 10.

Coefﬁcients of the linear term also included in the models (climatic period) are presented in Table S1.3.

*a* Declining and/or threatened mallee bird species.

*b* Temporary resident species.
threatened and/or declining mallee bird species, including two (the Mallee Emu-wren and Striated Grasswren [Amytornis striatus]) for which no significant increases in the Big Wet were documented.

3.2 Influence of climatic extremes on bird species' responses to fire

Bird species richness and incidence increased substantially across all post-fire age classes during both the Big Wet and Post-Big Wet, compared with the Big Dry, in both vegetation types (climate+fire models, Tables 2 and 3 and Figure 2; see Appendix Table S1.3). No significant associations between species richness or incidence and TSF were found during the Big Dry or Big Wet. However, both species richness and incidence were positively associated with TSF Post-Big Wet. In both vegetation types, lower species richness and incidence were observed in younger post-fire age classes than during the Big Wet.

Of 27 species modelled, 15 responded to TSF in at least one climatic period, and 31 significant responses (where the p value of the smooth term was <.05) were observed in total (multiple responses by a single species in different vegetation types and/or climatic periods were counted separately; Tables 2 and 3). Six species responded to fire across multiple climatic periods—three species responded to fire in all three periods (Shy Heathwren [Calamanthus cautus], White-eared Honeyeater [Lichenostomus leucotis], responding across vegetation types] and Yellow-plumed Honeyeater [Lichenostomus ornatus]) and three species responded in two periods (Grey Shrike-thrush...
[**Colluricincla harmonica**, Willie Wagtail [*Rhipidura leucophrys*] and Jacky Winter [*Microeca fascinans*]). Nine species responded to fire in only one climatic period. No relation with TSF was detected in 12 species (in any climatic period, across both vegetation types; see also Appendix Table S1.3).

Contrary to our prediction that associations with TSF would be more evident during the Big Dry, almost twice as many responses to TSF occurred during the Big Wet (nine responses, with one species responding exclusively in this period—White-fronted Honeyeater [*Purnella albifrons*], Triodia mallee; Table 2). Only three species showed evidence of expansion into a broader range of TSF age classes during the Big Wet. The White-eared Honeyeater (Triodia mallee; Table 2, Figure 3d) and Spiny-cheeked Honeyeater (Triodia mallee; Table 2, Figure 3g) both ceased to respond to TSF and had substantially higher occurrence across all or most post-fire age classes compared with the Big Dry. The Yellow-plumed Honeyeater (responding in

![Figure 3](image.png)

**FIGURE 3** Predicted probability of occurrence with relation to time since fire in Triodia mallee for individual species with statistically significant time since fire responses in at least one of three periods of climatic extreme (Big Dry, Big Wet and Post-Big Wet): (a) Australian Ringneck, (b) Shy Heathwren, (c) Striated Pardalote, (d) White-eared Honeyeater, (e) Yellow-plumed Honeyeater, (f) White-fronted Honeyeater, (g) Spiny-cheeked Honeyeater, (h) Red-lored Whistler, (i) Grey Shrike-thrush, (j) Crested Bellbird, (k) Masked Woodswallow, (l) White-browed Woodswallow, (m) Willie Wagtail and (n) Jacky Winter. Solid lines represent predicted probability of occurrence, shaded regions represent 95% confidence intervals, and points represent observed data. Regions shaded in colour and with a bold line indicate a significant response for that period. Regions shaded grey indicate a null response. Responses unable to be assessed due to low sample size are not shown. Models were built using generalized additive mixed models (GAMMs, climate+fire).
each vegetation type) retained an association with TSF in both the Big Dry and Big Wet, but showed a more muted response (i.e. less marked differences in peaks of occurrence) in the Big Wet compared with Big Dry (Triodia mallee, Table 2, Figure 3e; Chenopod mallee, Table 3, Figure 4d).

Post-Big Wet, few species resumed TSF associations formerly exhibited in the Big Dry. The highest number of responses to TSF was observed in this period—over three times as many responses occurred Post-Big Wet (17 responses) compared with the Big Dry and eight species responded exclusively in this period (Tables 2 and 3). Seven species (comprising eight responses) showed comparatively high occurrence in both the Big Wet and Post-Big Wet (c.f. the Big Dry) but only responded to fire Post-Big Wet (Tables 2 and 3; Australian Ringneck [Barnardius zonarius], Triodia mallee, Figure 3a; Striated Pardalote [Pardalotus striatus], Triodia mallee, Figure 3c; White-eared Honeyeater, Triodia mallee, Figure 3d; Grey Shrike-thrush, Triodia mallee, Figure 3i; White-browed Woodswallow [Artamus superciliosus], Triodia mallee, Figure 3l; Spotted Pardalote [Pardalotus punctatus], Chenopod mallee, Figure 4a; Striated Pardalote, Chenopod mallee, Figure 4b; and Jacky Winter, Chenopod mallee, Figure 4f).

Unexpectedly, of six species that were associated with TSF across multiple climatic periods, only one resumed the same response Post-Big Wet as exhibited in the Big Dry (White-eared Honeyeater, Triodia mallee, Figure 3d). However, of six species which responded to fire in both the Big Wet and Post-Big Wet, all retained

---

**FIGURE 4** Predicted probability of occurrence with relation to time since fire in Chenopod mallee for individual species with statistically significant time since fire responses in at least one of three periods of climatic extreme (Big Dry, Big Wet and Post-Big Wet): (a) Spotted Pardalote, (b) Striated Pardalote, (c) White-eared Honeyeater, (d) Yellow-plumed Honeyeater, (e) Grey Shrike-thrush and (f) Jacky Winter. Solid lines represent predicted probability of occurrence, shaded regions represent 95% confidence intervals, and points represent observed data. Regions shaded in colour and with a bold line indicate a significant response for that period. Regions shaded grey indicate a null response. Responses unable to be assessed due to low sample size are not shown. Models were built using generalized additive mixed models (GAMMs, climate+fire).
the same response type (Tables 2 and 3; Shy Heathwren, Triodia mallee, Figure 3b; Yellow-plumed Honeyeater, Triodia mallee, Figure 3e; Willie Wagtail, Triodia mallee, Figure 3m; Jacky Winter, Triodia mallee, Figure 3n; White-eared Honeyeater, Chenopod mallee, Figure 4c; Yellow-plumed Honeyeater, Chenopod mallee, Figure 4d; and Grey Shrike-thrush, Chenopod mallee, Figure 4e). Two of these species retained the same response type across all three climatic periods (Shy Heathwren; and Yellow-plumed Honeyeater, Chenopod mallee).

Across climatic periods, where species responded to fire, preference for intermediate (as indicated by bell or plateau response) or older (incline, delayed) vegetation was shown (three of five responses in the Big Dry, five of nine in the Big Wet, and 14 of 17 Post-Big Wet, pooled across vegetation types; Tables 2 and 3, Figures 3 and 4).

While model evaluation measures were reasonably high for species occurrence and incidence models, they were generally low to moderate for individual species (Table 4). Model fit and predictive ability were higher for species with a significant association with TSF (n = 15 species, average deviance explained 12.93%, range 1.68%–24.07%; average AUC 0.71, AUC range 0.64–0.78; Table 4) than for species with no TSF association (n = 12 species, average deviance explained 7.27%, range 0.39%–15.98%; average AUC 0.61, AUC range 0.51–0.74). Of 15 species with at least one significant response to TSF, models for half (eight) had both modest fit (deviation explained >10%) and reasonable predictive capacity (AUC ≥0.7; Figure S1.2).

**4 | DISCUSSION**

We found that climatic extremes can interact with TSF to shape bird species’ occurrence. For many species, occurrences associated with the Big Wet were higher and sustained compared with the Big Dry. Over half of species, and both species richness and incidence, increased significantly in occurrence during the Big Wet. Three years after the deluge, three quarters of those species, and species richness and incidence, remained comparably high with the Big Wet (c.f. the Big Dry). While model predictions indicated interactions between climate and fire did not strongly influence most species, there were distinct differences in the number and type of associations with TSF between climatic periods. Contrary to expectations, more species responded to TSF during and following the Big Wet, than during the Big Dry. There was also little support for our prediction that species would quickly return to Big Dry responses to TSF after the Big Wet. The influence of TSF on bird species richness and incidence also fluctuated, with no detectable effect during the Big Dry or Big Wet, but a significant effect following the Big Wet. We suggest that interactions between climate and fire may differentially influence resource availability in different post-fire habitats, and thus the extent and nature of animal species’ relationships to TSF.

Using a long-term dataset, we showed how a sequence of extreme climatic events can have persistent effects on a semi-arid bird community. As anticipated, we found the Big Wet was associated
with significant increases in bird species richness and incidence. These increases were sustained into the Post-Big Wet, despite three intervening years of below-average rainfall. Fluctuations in occurrence were overwhelmingly dominated by resident rather than nomadic species, unlike in many arid systems (e.g. South America, Jacobs & Lazo, 1999; South Africa, Dean & Milton, 2001; Dean, 2004; but see Australia, Pavey & Nano, 2009), suggesting changes in occurrence result from rain-stimulated breeding within the study area (e.g. see Jordan et al., 2017). Extreme rainfall events are expected to mitigate the deleterious effects of drought by facilitating the recovery of fauna populations (Holmgren et al., 2006). However, following the same Millennium Drought in south-eastern Australia, reporting rates for a temperate bird assemblage did not increase for more than half of species during the Big Wet, and up to a quarter in fact continued to decline (Bennett et al., 2014). Selwood et al. (2015) reported ~60%–85% of bird species across the Murray–Darling river basin failed to recover during the same climatic period. The more beneficial effect of the Big Wet detected in our study may be because arid-zone species are better adapted to both capitalize on, and persist through, the climatic extremes of resource boom-bust cycles (Holmgren et al., 2006). For example, Morton et al. (2011) proposed that perennial plants in woody arid systems continue to produce carbon-rich products (e.g. vegetative growth, flowering, seeding, fruiting, plant exudates) for several years following major rainfall, capable of sustaining associated herbivorous and insectivorous activity. This prolonged resource availability (over months to years) would likely sustain high bird populations for extended periods. However, the cumulative impact of increasingly severe, frequent and protracted droughts as a result of human-induced climate change (IPCC, 2013) will likely compromise the ability of many ecosystems to adequately recover during future La Niña periods (e.g. Saatchi et al., 2013). Such impacts are expected to be particularly acute in arid and semi-arid regions because they are primarily water-limited (Weltzin et al., 2003).

Less than half of the threatened and declining species benefited from the resource boom, and several highly vulnerable species showed declines in the Post-Big Wet, relative even to the Big Dry (e.g. Mallee Emu-wren, Striated Grasswren). Small, vulnerable populations may be less able than large populations to capitalize on resource-rich conditions. During such periods, other pre-existing biotic pressures may counter attempts by these species to breed and/or rear young. For example, several threatened mallee bird species have specialized post-fire habitat requirements (Connell et al., 2017), yet availability of preferred post-fire age classes can be limited and/or disjunct at the landscape scale (e.g. Connell et al., 2019). Life history traits can exacerbate this impact. The poor dispersal ability of the Mallee Emu-wren, which has mid- to older post-fire vegetation requirements (Verdon et al., 2019), has led to the isolation of small populations and subsequent population bottlenecks (Brown et al., 2009). Further, small populations may be more susceptible to biotic stresses associated with resource fluctuations. For example, in an arid Australian ecosystem, populations of an introduced predator, the red fox (Vulpes vulpes), increased substantially during and following La Niña rainfall, leading authors to identify this as a critical “bust” period for wildlife management (Letnic & Dickman, 2006). Red foxes are prevalent at both the landscape and site scale in our study system (Payne et al., 2014). They have been implicated as a cause of mortality for the Malleefowl (Leipoa ocellata, e.g. Wheeler & Priddel, 2009), and other threatened mallee bird species may be vulnerable due to their ground-nesting or ground-foraging habits (e.g. Mallee Emu-wren, Red-lored Whistler, Department of Environment, Land, Water and Planning, 2016). Such compounding pressures may contribute to persistent population declines.

Consistent with a growing view that species’ responses to fire history are spatially and temporally dynamic, we observed changes in the type of response that species displayed over time to TSF. The most common of these was a shift from a response type indicative of a preference for a particular fire age (e.g. decline, plateau) to a null response (or vice versa). The most likely explanation for variation in responses to fire is the effect of climatic variation on resources. The “dynamic vegetation” hypothesis proposes that temporal and spatial differences in environmental drivers can variably influence post-fire habitat structure, and thus the extent and nature of species’ relationships to TSF (see Nimmo et al., 2014). For example, Hale et al. (2016) found small mammals varied in their response to fire during contrasting periods of climatic extremes in a temperate system, and Nimmo et al. (2014) documented geographically variable fire responses by reptiles in a semi-arid system. This hypothesis provides one explanation for the variable responses to fire exhibited by birds here. In arid and semi-arid systems, exceptionally large rainfall pulses stimulate increased recruitment, growth, flowering, fruiting, production of seeds and other carbohydrates (e.g. nectar) for ephemeral, annual and perennial plants (e.g. Gutiérrez et al., 1997; Letnic & Dickman, 2010). These pulses also promote the regeneration of woody vegetation, such as mulga, eucalypts and conifer woodlands in Australian systems (Austin & Williams, 1988), and increases in associated primary consumers, particularly invertebrates (e.g. Grant et al., 2000; Langlands et al., 2006). Resource availability in post-fire habitat thus varies temporally, and concomitant changes in habitat use by fauna may be seen.

Although we predicted fewer responses to TSF during the Big Wet owing to more plentiful resources across a broader range of fire ages, we found the opposite—more species displayed an association with fire during the Big Wet than the Big Dry. It is possible that above-average rainfall may have triggered the boom of certain resources at sites of particular post-fire age classes, leading to congregations of species in habitat not otherwise preferred. For example, prolonged high rainfall in mallee shrublands triggers mast seeding in Triodia spp. (Wright et al., 2014), which occurs at greater densities >20 years post-fire (Haslem et al., 2011). Similarly, profuse flowering by mallee eucalypts is rarely observed in trees less than 10 years post-fire (unpublished data, Mallee Fire and Biodiversity Project). Our finding of fewer fire responses during the Big Dry contrasts to findings of Hale et al. (2016), who observed more responses to TSF by small mammals during drought, and speculated...
that restricted use of preferred habitat in a period of climatic stress could explain the heightened role of fire history. We suggest that responses to the interaction between fire and climatic extremes differ between taxa. In contrast to small mammals (e.g. Holland & Bennett, 2007; Monamy & Fox, 2010), birds are a highly mobile taxa, with many species likely able to exploit a broader range of habitat types and track variations in resource availability at the landscape scale (Thomson et al., 2007). In our study, widespread scarcity of resources during drought may in fact have required broader use of the available environment, including less-preferred post-fire age classes (sensu optimal foraging theory, Stephens & Krebs, 1986; e.g. Feinsinger & Swarm, 1982).

We suggest that evidence of the expansion of habitat use is not limited to incidences where a species ceases to show a fire response. We originally predicted that the extension of species’ distributions across a broader range of post-fire age classes would be demonstrated by fewer associations with fire history. Based on observed fire response changes here, different degrees of expansion may occur in response to varying resource availability (Figure 5). This includes when a species’ preferred successional window broadens (i.e. a change in fire response type to include peaks of occurrence across a greater range of post-fire ages, as observed in the Yellow-plumed Honeyeater in Triodia mallee) or becomes muted (i.e. to retain the same fire response type but show less marked differences in peaks of occurrence, as seen by the Yellow-plumed Honeyeater in Chenopod mallee). In contrast, contraction of habitat use would be evidenced by an amplification of the fire response (with peaks of occurrence across a narrower range of post-fire ages).

Changes in the relationship between species richness and incidence with TSF were also observed. During both the Big Dry and Big Wet, species richness was unrelated to TSF. These results are inconsistent with previous work that incorporated the same study region (but also occurred across a wider area) during the Big Dry, which showed higher bird species richness in landscapes dominated by long unburned vegetation (Taylor et al., 2012). This may be attributable to differences in the classification of long unburned vegetation and the spatial scales at which species richness was measured.

Site data in our study were analysed on a finer post-fire continuum from 1–117 years, while Taylor et al. (2012) used a coarser classification, considering all vegetation >35 years post-fire as old. While the current study was undertaken at the site scale (i.e. alpha diversity at individual sites), work by Taylor et al. (2012) was conducted at the landscape scale, measuring gamma diversity, which takes into account variation in species assemblages between sites (i.e. beta diversity). Therefore, increased diversity observed by that study is likely to be the result of higher beta diversity (i.e. differences in communities at different sites) between long unburned sites of differing post-fire age.

The only time period in which fire was found to exert an influence on bird species richness and incidence was Post-Big Wet. During this period, species richness and incidence remained comparably high to the Big Wet in older age classes (≥50 years post-fire) but declined in recently burned areas. This suggests that the longevity of rainfall effects on ecosystems might itself have a successional basis, where resources boosted by rainfall persist for longer periods in old fire age classes than in recently burned vegetation.

**FIGURE 5** Conceptual diagram depicting possible changes to a species’ generalized time since fire response curve in response to varying resource availability. Here, a species with a bell-shaped response is used as an example. The predicted nature of possible changes to its relationship to time since fire during changed climatic conditions includes the following: (a) different degrees of expansion—ceasing to show a response (i.e. expansion across all post-fire age classes); broadening of its successional window (i.e. to include peaks of occurrence across a greater range of post-fire ages, and here assuming a plateau type); or muting (i.e. retaining its fire response type but showing less marked differences in peaks of occurrence). Alternatively, (b) contraction of the response type may be seen, for example amplification of the response, with peaks of occurrence across a narrower range of post-fire ages.
Long-unburnt (>38 years) semi-arid vegetation has been found to have greater water absorbing capacities, and significantly higher primary productivity than recently burnt (<5 years) vegetation (Mappin et al., 2003). Thus, in addition to its unique range of structural attributes (e.g. hollows, logs, deep litter layers, decorticating bark; see Haslem et al., 2011), older vegetation may offer a greater and/or more prolonged resource flush than other fire age classes in the years after major rainfall. Landscapes with a greater extent of older vegetation may also augment the recuperation of bird populations after drought (acting as a temporal “ecological refuge”; see Collins et al., 2019; Letnic & Dickman, 2010) and enhance their resistance to future below-average or drought conditions (Mac Nally et al., 2014; Nimmo et al., 2016).

Different aspects of the fire regime may interact with extreme drought and rainfall to influence the provision of resources and in turn species occurrence. Mallee shrublands predominantly experience high severity, infrequent and stand-replacing fires, and TSF strongly influences the post-fire development of important habitat attributes (Haslem et al., 2011; Rainsford et al., 2020). In other fire-prone systems, fire regime characteristics such as fire severity (e.g. in forested and woodland systems, Swan et al., 2018; Tingley et al., 2016) or fire frequency may also strongly influence habitat attributes, and so interact strongly with climatic extremes. Because mallee shrublands have a long fire-return interval (>100 years; Clarke et al., 2010) and regenerate slowly (Haslem et al., 2011), any changes in responses to time since fire under differing climatic conditions need to be well understood to effectively manage fire in this system. The interaction of climatic extremes with a range of structurally distinct post-fire age classes likely promotes heterogeneous fauna responses. In systems with fewer post-fire seral stages, or which experience fast post-fire recovery (such as less-structurally complex grasslands), interactions with TSF may be less pronounced, although the timing of extreme drought or rainfall following fire may influence fire frequency or severity.

Despite the dynamic effects of climatic extremes on TSF, some habitat preferences retained importance for individual bird species. Mid to older mallee vegetation has previously been identified as being of disproportionate importance for multiple taxa (Kelly et al., 2015, during El Niño conditions), and here, we found that, even through periods of extreme climatic variation, more than half of species responding to TSF showed preference for these older age classes. In mallee shrublands, many important post-fire habitat attributes such as hollows, bark and canopy cover continue to develop beyond 40–60 years post-fire (Haslem et al., 2011). Further, responses of some species to interactions between TSF and climatic period differed between Triodia mallee and Chenopod mallee, and a higher total number of responses were seen in the former. Contrasting responses to TSF between these vegetation types have previously been identified for diverse taxa including birds (Watson, Taylor, Nimmo, et al., 2012, but also mammals, Kelly et al., 2011, and reptiles, Nimmo et al., 2012). This is likely driven by variation in the post-fire development of several key habitat attributes between the two vegetation types (primarily under- and mid-storey vegetation cover, which are higher in Triodia mallee; Haslem et al., 2011).

Caution is required in the interpretation of TSF models with only modest model fit. Among 15 species with a significant response to TSF, only half were of at least modest fit and provided reasonable predictive capacity. This is broadly consistent with previous work in this system (Watson, Taylor, Nimmo, et al., 2012) and with other studies that have modelled fauna species occurrence in relation to time since fire (e.g. Kelly et al., 2017; Swan et al., 2015), and reinforces the importance of non-fire variables in helping to shape the occurrence of fire-sensitive species across large landscapes. However, potential effects of individual variables can still be important. For example, despite low model fit (deviance explained, 10.21%) for the Jacky Winter, there is a 0.10 (10%) difference in the species’ predicted probability of occurrence under Big Wet versus Post-Big Wet climatic conditions at a site 90 years post-fire (Figure 3n). This may indicate considerable population changes can result from climate and fire interactions. Further, the ability to detect species’ relationships to TSF could potentially be influenced by prevailing climatic conditions that impact the occurrence rates of each species. Here, almost half of responses detected exclusively during the Post-Big Wet were for species with comparatively high occurrence rates in both this period and the Big Wet. However, fewer responses to TSF were found in the Big Dry and this may have been influenced by substantially lower species occurrences during this period (i.e. small populations—leading to higher likelihood of type II error with inaccurate designation of a “null” response, an issue highlighted by Smith et al., 2013; and observed by Hale et al., 2016). For example, a number of species for which no fire response was identified during the Big Dry were found to respond to fire when larger datasets, encompassing a larger study region, were used (Connell et al., 2017; Watson, Taylor, Nimmo, et al., 2012). While it was not feasible to examine this here, it is an important area for future investigation. This inconsistency could reflect either insufficient data at the scale studied here to successfully detect a response to TSF or in fact the scale-dependent nature of species’ associations with fire (e.g. Nimmo et al., 2014).

### 4.1 Management implications

Climatic extremes are predicted to increase in frequency, duration and severity (Weltzin et al., 2003), and accounting for their influence on fauna–fire dynamics will require careful management of fire. Using a long-term dataset, we highlight the contextual nature of the effects of fire on animal species. Our work indicates that species may be more vulnerable to the timing of fire management actions in certain climatic conditions than others—for example, prescribed fires conducted in key preferred post-fire age classes (e.g. older
vegetation) during periods when a species' population is very low (e.g., following prolonged drought) may pose high risk (Clarke, 2008). Our work can assist managers in determining appropriate "windows of opportunity," both spatially and temporally, for conducting burns to create and protect habitat.

ACKNOWLEDGEMENTS
This study formed part of a larger collaborative research project, the Mallee Hawkeye Project, between La Trobe and Deakin universities, with funding and support from the Department of Environment, Land, Water and Planning and support from Parks Victoria. J. Connell was supported by grants provided by the Stuart Leslie Bird Research Award, Stuart Leslie Conference Award (both through BirdLife Australia) and the M.A. Ingram Trust. We acknowledge the many fieldworkers who have contributed substantial effort to data collection. This research was approved under La Trobe University Animal Ethics Committee Permit No. AEC12-47, and research on public land and national parks was undertaken under Department of Environment, Land, Water and Planning Permit No. 10006404.

PEER REVIEW
The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13287.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.5x69p8d2h.

ORCID
Jemima Connell https://orcid.org/0000-0002-8485-4665
Mark A. Hall https://orcid.org/0000-0003-4273-980X
Dale G. Nimmo https://orcid.org/0000-0002-9814-1009
Simon J. Watson https://orcid.org/0000-0001-6063-7327
Michael F. Clarke https://orcid.org/0000-0003-1138-2908

REFERENCES
Albright, T. P., Pidgeon, A. M., Rittenhouse, C. D., Clayton, M. K., Flather, C. H., Culbert, P. D., Wardlow, B. D., & Radeloff, V. C. (2010). Effects of drought on avian community structure. Global Change Biology, 16, 2158–2170. https://doi.org/10.1111/j.1365-2486.2009.02120.x
Austin, M. P., & Williams, O. B. (1988). Influence of climate and community composition on the population demography of pasture species in semi-arid Australia. In Temporal and spatial patterns of vegetation dynamics (pp. 43–49). Springer.
Avitabile, S. C., Callister, K. E., Kelly, L. T., Haslem, A., Fraser, L., Nimmo, D. G., Watson, S. J., Kenny, S. A., Taylor, R. S., Spence-Bailey, L. M., Bennett, A. F., & Clarke, M. F. (2013). Systematic fire mapping is critical for fire ecology, planning and management: A case study in the semi-arid Murray Mallee, south-eastern Australia. Landscape and Urban Planning, 117, 81–91. https://doi.org/10.1016/j.landurbplan.2013.04.017
Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67, 1–48.
Bennett, J. M., Nimmo, D. G., Clarke, R. H., Thomson, J. R., Cheers, G., Horrocks, G. F. B., Hall, M., Radford, J. Q., Bennett, A. F., & Mac Nally, R. (2014). Resistance and resilience: Can the abrupt end of extreme drought reverse avifaunal collapse? Diversity and Distributions, 20, 1321–1332. https://doi.org/10.1111/ddi.12230
Bowman, D. M. J. S., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M., Cochrane, M. A., D’Antonio, C. M., DeFries, R. S., Doyle, J. C., Harrison, S. P., Johnston, F. H., Keeley, J. E., Krawchuk, M. A., Kull, C. A., Marston, J. B., Moritz, A. A., Prentice, I. C., Roos, C. I., Scott, A. C., … Pyne, S. J. (2009). Fire in the earth system. Science, 324, 481–484. https://doi.org/10.1126/science.1163886
Brown, S., Clarke, M., & Clarke, R. (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 malleus). Biological Conservation, 142, 432–445. https://doi.org/10.1016/j.biocon.2008.11.005
Burbidge, A. A., & Fuller, P. J. (2007). Gibson Desert birds: Responses to drought and plenty. Emu, 107, 126–134. https://doi.org/10.1071/jb0501
Bureau of Meteorology (2020b). Climate Data Online [WWW Document]. Retrieved from http://www.bom.gov.au/climate/data/index.shtml
Bureau of Meteorology. (2020a). La Niña – Detailed Australian Analysis [WWW Document]. Retrieved from http://www.bom.gov.au/climate/enso/inlist/index.shtml
Clarke, M. F. (2008). Catering for the needs of fauna in fire management: Science or just wishful thinking? Wildlife Research, 35, 385–394. https://doi.org/10.1071/WR07137
Clarke, M. F., Avitabile, S. C., Brown, L., Callister, K. E., Haslem, A., Holland, G. J., Kelly, L. T., Kenny, S. A., Nimmo, D. G., Spence-Bailey, L. M., Taylor, R. S., Watson, S. J., & Bennett, A. F. (2010). Ageing mallee eucalypt vegetation after fire: Insights for successional trajectories in semi-arid mallee ecosystems. Australian Journal of Botany, 58, 363–372. https://doi.org/10.1071/BT10051
Collins, L., Bennett, A. F., Leonard, S. W. J., & Penman, T. D. (2019). Wildfire refugia in forests: Severe fire weather and drought mute the influence of topography and fuel age. Global Change Biology, 25, 3829–3843. https://doi.org/10.1111/gcb.14735
Connell, J., Watson, S. J., Taylor, R. S., Avitabile, S. C., Clarke, R. H., Bennett, A. F., & Clarke, M. F. (2017). Testing the effects of a century of fires: Requirements for post-fire succession predict the distribution of threatened bird species. Diversity and Distributions, 23, 1078–1089. https://doi.org/10.1111/ddi.12597
Connell, J., Watson, S. J., Taylor, R. S., Avitabile, S. C., Schedvin, N., Schneider, K., & Clarke, M. F. (2019). Future fire scenarios: Predicting the effect of fire management strategies on the trajectory of high-quality habitat for threatened species. Biological Conservation, 232, 131–141. https://doi.org/10.1016/j.biocon.2019.02.004
Dean, W. R. J. (2004). Nomadic Desert Birds. Adaptations of Desert Organisms, Berlin, Heidelberg: Springer.
Dean, W. R. J., & Milton, S. J. (2001). Responses of birds to rainfall and seed abundance in the southern Karoo, South Africa. Journal of Arid Environments, 47, 101–121. https://doi.org/10.1006/jare.2000.02120.x
Department of Environment, Land, Water and Planning (2016). National Recovery Plan for the Mallee Emu-Wren (Stipiturus malleus), Red-lored Whistler (Pachycephala rufogularis) and Western Whipbird (Psophodes nigrogularis leucogaster). Canberra: Australian Government.
Department of Sustainability and Environment. (2012). Code of Practice for Bushfire Management on Public Land. Melbourne: Department of Sustainability and Environment.
Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. Journal of Animal Ecology, 77, 802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x
Feinsinger, P., & Swarm, L. A. (1982). "Ecological release", seasonal variation in food supply, and the hummingbird Amazilia Tobaci
Biodiversity Project. *Proceedings of the Royal Society of Victoria*, 124, 38–46. https://doi.org/10.1071/RS12038

Weltzin, J. F., Loik, M. E., Schwinning, S., Williams, D. G., Fay, P. A., Haddad, B. M., Harte, J., Huxman, T. E., Knapp, A. K., Lin, G., Pockman, W. T., Shaw, R. M., Small, E. E., Smith, M. D., Smith, S. D., Tissue, D. T., & Zak, J. C. (2003). Assessing the response of terrestrial ecosystems to potential changes in precipitation. *BioScience*, 53, 941–952.

Wheeler, R., & Priddel, D. (2009). The impact of introduced predators on two threatened prey species: A case study from western New South Wales. *Ecological Management & Restoration*, 10, S117–S123. https://doi.org/10.1111/j.1442-8903.2009.00457.x

Whelan, R. J., Rodgerson, L., Dickman, C. R., & Sutherland, E. F. (2002). Critical life cycles of plants and animals: Developing a process-based understanding of population changes in fire-prone landscapes. In R. A. Bradstock, J. E. Williams, & A. M. Gill (Eds.), *Flammable Australia: The fire regimes and biodiversity of a continent* (pp. 94–124). Cambridge University Press.

Wood, S. N. (2008). Fast stable direct fitting and smoothness selection for generalized additive models. *Journal of the Royal Statistical Society Series B*, 70, 495–518. https://doi.org/10.1111/j.1467-9868.2007.00646.x

Wood, S. N. (2017). *Generalized Additive Models: An Introduction with R* (2nd edition). Boca Raton, FL: CRC Press.

Wood, S., & Scheipl, F. (2013). gamm4: Generalised additive mixed models using mgcv and lme4 [WWW Document]. Retrieved from http://CRAN.R-project.org/package=gamm4

Wright, B. R., Zuur, A. F., & Chan, G. C. K. (2014). Proximate causes and possible adaptive functions of mast seeding and barren flower shows in spinifex grasses (*Triodia* spp.) in arid regions of Australia. *The Rangeland Journal*, 36, 297–308. https://doi.org/10.1071/RJ13104

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer.

**BIOSKETCH**

Jemima Connell conducted this study as part of her PhD thesis in the Landscape and Conservation Ecology (LACE) group at the LaTrobe University. Her PhD investigated how two major ecological disturbance processes, fire and climatic extremes, influence the distributions and persistence of a semi-arid bird community, with particular focus on threatened species.

Author contributions: J.C., S.J.W., M.A.H., D.G.N. and M.F.C. conceived and developed the concept; J.C. and M.A.H. collected and collated data; J.C. carried out the research; J.C. and M.A.H. conducted analysis with support from S.J.W. and D.G.N.; J.C. led the writing of the manuscript; and all authors contributed critically to drafts and gave final approval for publication.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Connell J, Hall MA, Nimmo DG, Watson SJ, Clarke MF. Fire, drought and flooding rains: The effect of climatic extremes on bird species’ responses to time since fire. *Divers Distrib*. 2021;00:1–22. https://doi.org/10.1111/ddi.13287