Austral
ECOLOGY A Journal of ecology in the Southern Hemisphere

Ecological Society of Australia

Austral Ecology (2022) **47**, 828–840

Responses of floodplain birds to high-amplitude precipitation fluctuations over two decades

TIM REID,[1] HANIA LADA,[1] KATHERINE E. SELWOOD,[2,3]
GREGORY F. B. HORROCKS,[4] JAMES R. THOMSON[5] AND RALPH MAC NALLY[1,3]⋆
[1]Institute for Applied Ecology, The University of Canberra, Bruce, Australian Capital Territory, 2617, Australia (Email: ralph.macnally@gmail.com); [2]Wildlife and Conservation Science, Zoos Victoria, Parkville, Victoria, Australia; [3]School of BioSciences, The University of Melbourne, Parkville, Victoria, Australia; [4]Faculty of Science and Technology, Federation University, Mt Helen, Victoria, Australia; and [5]Department of Environment, Land, Water and Planning, Arthur Rylah Institute for Environmental Research, Heidelberg, Victoria, Australia

Abstract Globally, high-amplitude variation in weather (*e.g.* precipitation) is increasing in frequency and magnitude. This appears to be so for the southern Murray-Darling Basin, Australia, where droughts of unprecedented (in the instrumental record, extending back to the mid-1800s) depth and duration (1997–first half of 2010; second half of 2012–) are being punctuated by extreme wet periods, albeit of shorter duration (‘Big Wet’, second half of 2010–first half of 2012). We have previously reported on the responses of floodplain-forest birds to the cessation of the longest recorded drought (‘Big Dry’, 1997–first half of 2010), but we found little evidence of a rebound, at least shortly after the Big Wet. However, we reasoned that there may have been insufficient time for the birds to have responded in that short time, so we repeated the survey program 5 years after the end of the Big Wet (2017). Bird occurrences, reproductive activity and success were substantially greater compared with late in the Big Dry (2009) than they had been soon after the Big Wet (2013). However, bird occurrences still fell well below measurements in the early-Big Dry (1998), so that the avifauna appears to be in decline, most probably because the length of drought periods far exceeds that of wet periods giving the birds too little time to recover fully.

Key words: breeding success, climate variability, extreme events, floodplain forests, reporting rates, vegetation condition.

INTRODUCTION

Climate change is having major impacts on biodiversity by many mechanisms (Selwood *et al.* 2015b). Profound changes in precipitation alter the quantity, usually negatively, and temporal patterns of plant production and hence plant-food resources for many animals (Hovenden *et al.* 2019) and can lead to changes in spatial distributions of food arising from differences in spatial patterns in precipitation (Cowles *et al.* 2018; Hawkins *et al.* 2018). Rising temperatures associated with greenhouse-gas emissions affect organismal physiology, often by inducing high stress during heat waves (Dyderski *et al.* 2018; Smale *et al.* 2019), negatively affecting habitat quality (Mac Nally *et al.* 2014) or depressing or altering food availability (Telleria *et al.* 2016; Lister & Garcia 2018). All of these temperature-related aspects can depress reproductive success (Van de Ven *et al.* 2020; Schou *et al.* 2021). Of course, temperature and precipitation jointly affect plant primary production so that dry, hot spells can depress plant production to an even greater extent than either would singly (Muller-Landau *et al.* 2020). Generally, there has been a greater focus on biodiversity effects of projected gradual changes in mean climate rather than of more abrupt or high-amplitude variation in climate [*i.e.* extreme climatic events; (Gutschick & BassiriRad 2003; Thompson *et al.* 2018)]. However, there is much evidence that extreme climatic events are likely to have much more profound and immediately deleterious effects on biodiversity than gradual changes in means (Babcock *et al.* 2019).

Extreme temperature fluctuations are demonstrably important from a biodiversity perspective (Waldock *et al.* 2018), but our focal region, the Murray-Darling Basin of south-eastern Australia, has experienced ramped heating since the late 1990s. All mean annual temperatures exceeded the baseline mean (1961–1990, Australian Bureau of Meteorology standard) so that there are no high-amplitude fluctuations in temperature *per se* (see Appendix S7). Therefore, we focused on high-amplitude fluctuations in precipitation because these have occurred over that period

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⋆Corresponding author.

Accepted for publication February 2022.

doi:10.1111/aec.13164

(Appendix S6). Water availability has major impacts on habitat quality and food availability in floodplain forests, upon which we focus in this study (Mac Nally *et al.* 2014). Longer, more-frequent and more-intense droughts are projected to, and have occurred in, many parts of the world, including northern China, western North America, Mediterranean countries and southern Africa. The drying and heating in the Murray-Darling Basin broadly is consistent with consensus projections from global circulation models for the basin (Timbal 2015). Precipitation patterns are influenced to differing degrees by several large-scale forcing processes [El Niño-Southern Oscillation, Interdecadal Pacific Oscillation, Indian Ocean Dipole, Southern Annular Mode, (Heinrich *et al.* 2009; Verdon-Kidd & Kiem 2009)]. The longer-term expectation is for more-frequent, longer droughts that will be punctuated by short, intense periods of precipitation, a pattern that seems to be playing out (Leblanc *et al.* 2012; Timbal 2015). This changing precipitation pattern, relative to the instrumental record, had been accompanied by near-inexorable warming (Timbal 2015).

Here, we examined changes in forest birds in two floodplain forests, Gunbower Island and Barmah Forest, in northern Victoria, Australia (Fig. 2). These are the two largest extant native river red gum *Eucalyptus camaldulensis* Dehnh forests in the world. The weather patterns in the Murray-Darling Basin over the past two decades provided an opportunity to explore avian responses to precipitation fluctuations of an unprecedented degree (at least in the instrumental record, since the 1850s). A 13-year severe drought (1997–first half of 2010) was interrupted by a 2-year period of extraordinary precipitation (second half of 2010–first half of 2012), followed since by generally well-below average precipitation (2013–) (Ashcroft *et al.* 2019; Dey *et al.* 2019).

A consequence of the general drying and heating experienced in south-eastern Australia since 1990 has been a widespread decline in the health of floodplain forests (measured by forest stand condition, or SC, defined below) (Cunningham *et al.* 2018), to which forest birds respond (Mac Nally *et al.* 2014). Therefore, SC was taken into account alongside precipitation patterns by selecting in-forest locations that spanned the range of SC. While there was little evidence of a positive response by the floodplain birds to the high precipitation event of 2010–2012 in 2013 (Selwood *et al.* 2015a), it is possible that the 2013 results might not have allowed enough time for responses that might emerge after a longer-time. Here, we report on avifaunal responses 4 years after the initial avian investigations and 5 years (2017) after the end of the heavy precipitation event. We did not have firm expectations of whether there would be improvement in bird reporting rates and breeding. It is possible that gains arising from longer periods following the cessation of the Big Wet might be offset by the on-going generally sub-baseline precipitation since 2012.

METHODS

Climate patterns

The large-amplitude fluctuations in precipitation fell into three periods. The 1997–first half of 2010 drought is referred to as the ‘Big Dry’, while the 2-year extreme precipitation event from the second half of 2010 to the first half of 2012 is known as the ‘Big Wet’ (Verdon-Kidd & Kiem 2009; Leblanc *et al.* 2012). We refer to the period from the second half of 2012 onward, when precipitation generally was well-below average until at least 2020, as the ‘post-Big Wet’.

Precipitation in the Big Dry was well short of the baseline set by the Australian Bureau of Meteorology (1961–1990), and was succeeded by the 2 years of extreme precipitation in the Big Wet. Since 2012, there were several years of drought and two near-average years in 2016–2017 (Fig. 1a). The predominance of below- and well-below average years since 1991 has led to a cumulative net deficit of almost *two* full average years of precipitation (Fig. 1b). Mean temperature has increased, with many years exceeding the baseline by ≥1°C (Fig. 1c).

Study floodplains

The floodplains of Barmah Forest (centred on 35°53′S, 145°07′E) and Gunbower Island (centred on 35°47′S, 144°16′E) are on the Murray River in south-eastern Australia (Fig. 2). These floodplains consist of open forests (trees 10–30 m tall, 30–45% projective foliage cover) and woodlands (trees 10–30 m tall, 20–25% projective foliage cover) that are dominated by the river red gum *Eucalyptus camaldulensis* Dehnh. There is a variable understory of shrubs, sedges and grasses and groundcover is low vegetation (<50 cm), fallen timber and litter (Cunningham *et al.* 2009). Mean historic annual precipitation was 428 mm (minimum 175–maximum 893) (Fig. 1: Echuca, 36°10′S, 144°46′E; Gunbower Circle, 35°58′S, 144°37′E; http://www.bom.gov.au/climate/averages/tables; accessed August 27th, 2020). The mean monthly maximum temperature ranges from 13.5 to 31.0°C (Echuca).

Stand condition

Forest stand condition (SC), which is a measure of forest health (Cunningham *et al.* 2009), affects avian occurrence and breeding in these floodplain forests (Mac Nally *et al.* 2014). SC is the average of three equally weighted variables: (i) percentage live basal area; (ii) plant area index (PAI) and (iii) crown extent (Cunningham *et al.* 2009). SC was measured for each bird-survey site in 2009, 2013 and 2017, and retrospectively estimated SC for the 1998 survey locations (Cunningham *et al.* 2018), to use as a covariate in our models.

doi:10.1111/aec.13164

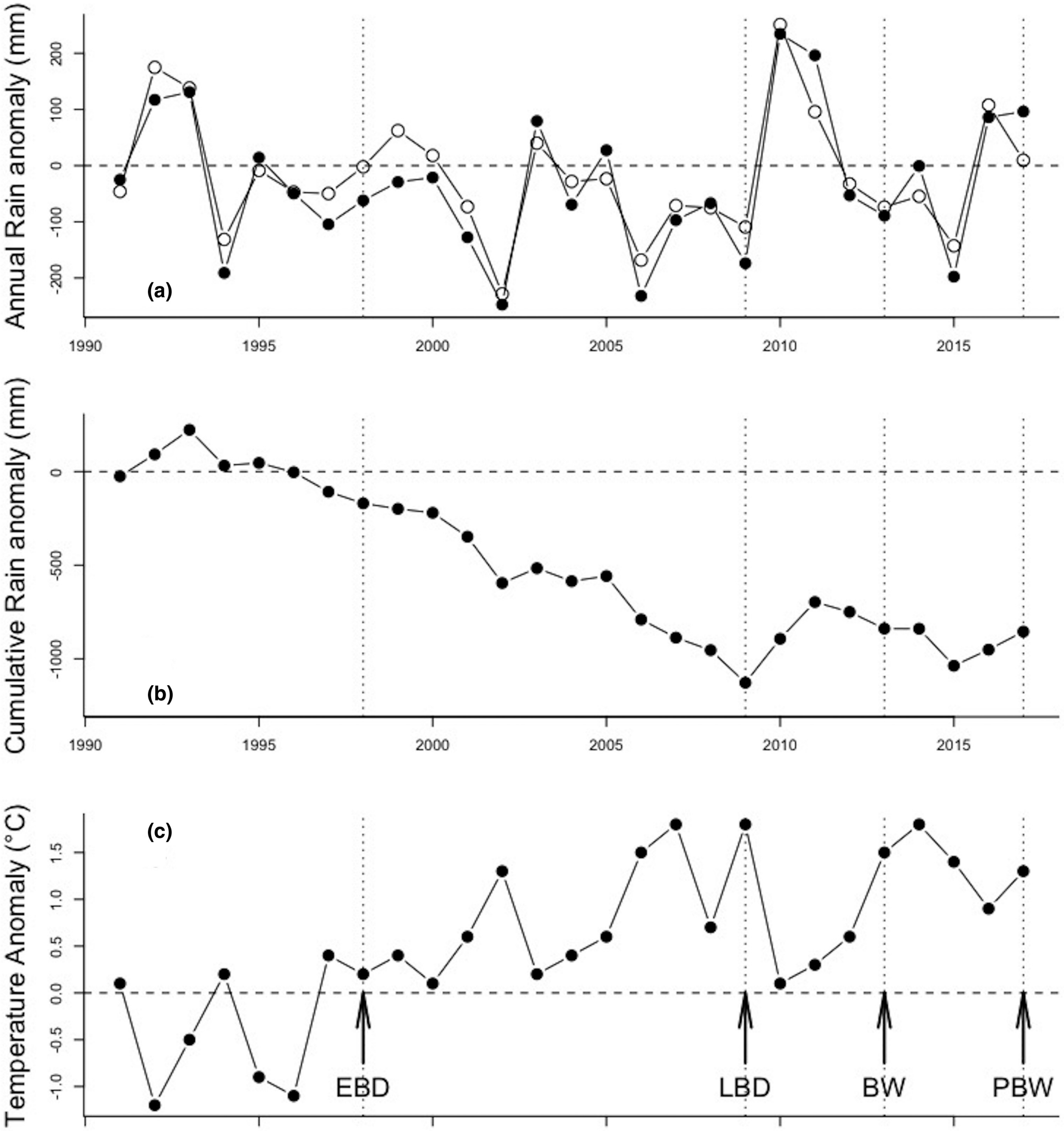

Fig. 1. (a) Patterns of annual precipitation anomalies at two stations (solid circles: Echuca Aerodrome; open circles: Gunbower Circle T Wiltipol) since the end of the baseline period of the Australian Bureau of Meteorology (1961–1990). (b) Cumulative precipitation anomalies at Echuca Aerodrome since 1991. (c) Temperature anomalies at Echuca Aerodrome since 1991; arrows indicate bird-survey years of this study: EBD = early-Big Dry (1998), LBD = late-Big Dry (2009), BW = Big Wet (2013) and PBW = post-Big Wet (2017).

Selection of study sites in floodplains

The general survey program to assess temporal patterns in species' occurrences involved four survey programs in the breeding seasons (July–November), which we labelled the 'early-Big Dry' (1998), 'late-Big Dry' (2009), immediate post-Big Wet, hereafter called 'Big Wet' (2013) and long post-Big Wet, hereafter called 'post-Big Wet' (2017). The later three survey programs were undertaken in the same way as one-another at the same locations, and included information on bird breeding activity and success (Mac Nally 2007).

doi:10.1111/aec.13164

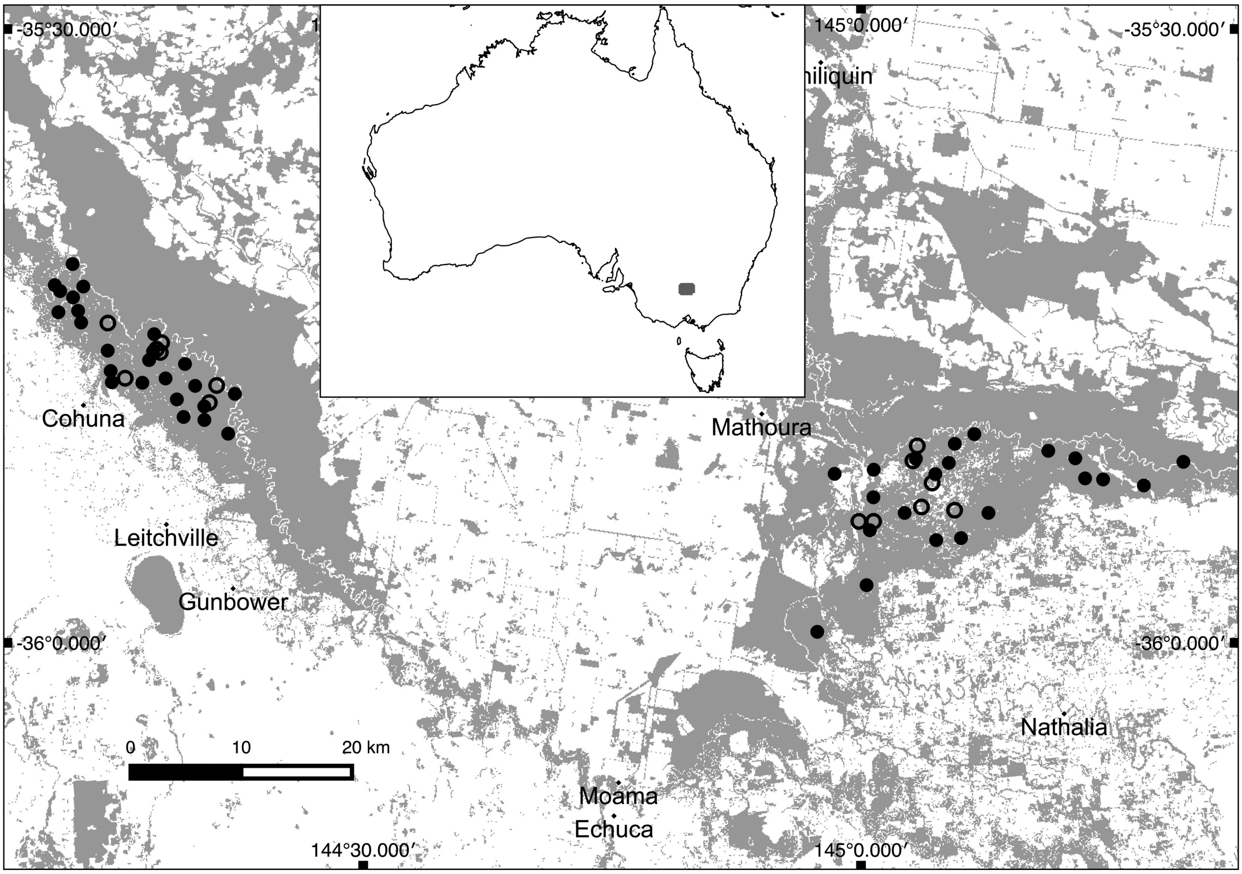

Fig. 2. Locations of sites from the early-Big Dry (1998; open circles) and late-Big Dry, Big Wet and post-Big Wet (2009, 2013 and 2017 respectively; black circles). Light-grey shading is native forest and woodland cover, most of which is floodplain forest.

The early-Big Dry sites

The seven sites on Gunbower Island and seven sites at Barmah Forest surveyed in 1998 originally were chosen to determine avian responses to variation in fallen-timber load (Mac Nally *et al.* 2001). SC was retrospectively estimated from spatially explicit models using historical Landsat imagery for the 1998 sites (Cunningham *et al.* 2009), for which we had retrospective estimates of SC in 1990, 2003 and 2006. We deemed that SC midway into the Big Dry (2003) would be the best estimate for the 1998 surveys (Cunningham *et al.* 2018).

The late-Big Dry, Big Wet, and post-Big Wet sites

We used a classified raster image of SC in 2009 and Hawth's Tools for stratified random sampling in ARCGIS (http://www.spatialecology.com/htools/rndselss.php) to choose potential study sites on Gunbower Island (55, of which 24 were selected after on-ground confirmation of suitability) and at Barmah Forest (50, 21 selected). We did ground measurements within 50 × 50 m plots to select sites for bird surveys (2-ha circular sites) centred on the 0.25 ha stand-condition plots. We also measured levels of fallen timber and numbers of dead trees, which influence avian occurrence and breeding activity in these floodplain forests (Mac Nally *et al.* 2014). Sites in late-Big Dry, Big Wet and the post-Big Wet programs were not selected specifically to span the ranges of these covariates as they were for SC.

Bird surveys

Bird-occurrence surveys

Each of the 14 sites in early-Big Dry was surveyed eight times in the breeding season (August–December). For the late-Big Dry, Big Wet and post-Big Wet survey programs, the 45 sites each was visited five times during the breeding season. Sites were not visited at Barmah Forest in 2013 due to the Big Wet, where residual water-logging made surveys logistically impossible. Otherwise, visits were conducted at most 2 weeks apart because intervals between hatching and fledging in some species of birds are short (Selwood *et al.* 2009). The difference in numbers of surveys (8 *vs.* 5) was accounted for statistically (see Statistical analyses). One difference was that the 1998 survey plots were 250 × 80 m strips, while the later survey plots were circular ones with radii of 80 m.

Surveys were not done on hot (>35°C), rainy or strong-wind days, which diminish bird activity. Surveys were conducted within 3 h of dawn or dusk because birds become somewhat quiescent during the middle of the day. We visited the two floodplain forests alternately between the survey periods within any given year to limit systematic temporal biases between forests. Sites within forests were surveyed in randomized order to avoid potential systematic sampling biases (weather, observer fatigue). We used a fixed-time (20 min), fixed-area (2 ha) search method, which involved a systematic scan and recording of all birds and their behaviours (Selwood *et al.* 2009). Only data for birds undertaking activities *within* the site were used for analyses, so data for birds flying non-stop through, or over, the sites were not included.

The bird-survey programs used a similar standard protocol (Mac Nally *et al.* 2001; Mac Nally *et al.* 2014). Calibration surveys were conducted between successive sets of observers to establish consistency in recording; such calibration data were not used for the analyses reported here. The physical structure of river red gum forests make bird detectability high (mean detection distance 23.9 m) (Selwood *et al.* 2015a). Bird surveys were done by very experienced observers (GH, C. Tzaros or L. Conole in 1998, HL in 2009, KES in 2013, and TR in 2017).

Analyses are mainly for passerines and parrots. We excluded data for raptors, nocturnal or water birds because observations of these species were not recorded well by the methods used here and many of these species range widely (> 2 ha) on a daily basis. Data are reported only for species that were recorded in ≥2 years, on ≥5 occasions, and ≥2 times in a single year; models for species that did not satisfy these criteria invariably failed to converge or fitted poorly.

Breeding-behaviour scores

For the 2009, 2013 and 2017 programs, we scored behaviour and other observations, such as occupied and vacant nests, which provided evidence of breeding. Each behaviour score was based on a consensus weighting derived from the opinions of 25 experienced Australian ornithologists [see Acknowledgements in (Mac Nally 2007)]. The evidence classes for breeding were: feeding of young out of the nest (9.0), young birds seen (9.0), feeding of young in the nest (8.0), presence of juveniles (7.5), young birds heard (7.5), adults carrying food (6.0), adult sitting on a nest (6.0), current breeding season's nest (5.0), past breeding season's nest (an indicator that the site had been regarded as potentially suitable for breeding in recent seasons, 3.5), adult gathering nest material (3.0), courtship (2.0), territorial behaviour (1.0) and male and female pairs (1.0). Only the observed behaviour with *highest* score for a given nest or territory was used in statistical analyses. For example, if courtship (weighting 3.0) and presence of juveniles (weighting 7.5) were scored for a given nest, then the assigned value would be 7.5.

Nest locations were recorded with GPS and with site-sketch maps. We summed breeding scores for all territories and species in each year for an overall measure of bird breeding activity at each site ('total breeding score'). We analysed changes in the number of breeding species by comparing the number of species at each site that showed breeding behaviour ('number of breeding species'). The summed number of young produced at each site for all species in each year was used to estimate the effective breeding output ('number of young'). We assessed species-specific changes in total breeding scores for the nine most common breeding bird species based on their total breeding scores (Brown treecreeper *Climacteris picumnus*, Buff-rumped thornbill *Acanthiza reguloides*, Red-capped robin *Petroica goodenovii*, White-plumed honeyeater *Lichenostomus penicillata*, Striated pardalote *Pardalotus striatus*, Jacky winter *Microeca fascinans*, White-throated treecreeper *Cormobates leucophaeus*, Superb fairy-wren *Malurus cyaneus*, Yellow rosella *Platycercus elegans flaveolus*; see Appendix S1 for complete list of Linnean names).

STATISTICAL ANALYSES

Species-specific reporting rates

The reporting rate for a single site i in program j [1: early-Big Dry, 1998; 2: late-Big Dry, 2009; 3: Big Wet, 2013; or 4: post-Big Wet, 2017] is the proportion of visits to that site in program j in which a species was recorded. The mean reporting rate for program j is the expected proportion of occupied sites at any given time. We estimated changes in reporting rates among the four programs using hierarchical Bayesian models, which accounted for inherent spatial structure by having floodplain random effects. We used a zero-inflated binomial model that consisted of a 'prevalence sub-model', the probability of finding a species at any site in a survey program, and an in-site, reporting-rate (denoted by 'RR') sub-model, which is the number of times a species would be recorded at a given site in N repeated visits, if present. The model (1) was:

$$y_{ij} \sim \text{Binomial}\left(q_{ij}, N_{ij}\right); q_{ij} = I_{ij}\lambda_{ij}; I_{ij} \sim \text{Bernoulli}\left(p_{ij}\right); \tag{1a}$$

$$\text{prevalence submodel}: \text{logit}\left(p_{ij}\right) = \alpha_{\text{p}} + \rho_j + \xi S_{ij} + \varepsilon_k + \varepsilon_{i(k)}; \tag{1b}$$

$$\text{in–site RR submodel}: \text{logit}\left(\lambda_{ij}\right) = \alpha_\lambda + \phi_j. \tag{1c}$$

y_{ij} is the number of times the species was recorded in site i (nested within floodplain k) during program j, and N_{ij} is the number of surveys performed (8 in 1998, and 5 for other three programs). p_{ij} is the probability of occurrence, which is distributed as a Bernoulli variate derived from the binary indicator value (*i.e.* species was reported or not) I_{ij}. This value was modelled on the log-odds scale (logit-transform) as an intercept α_{p} and a program-specific effect (*i.e.*

1998, 2009, …) ρ_j; we set $\rho_1 = \rho_{\text{early Big Dry}} = 0$ so that the values for later programs are deviations from values in the early-Big Dry. λ_{ij} is the number of occurrences expected if the species were present, and was modelled on the log-odds scale as a function of an intercept (α_λ), program-specific effect ($\phi_j; \phi_1 = \phi_{\text{early Big Dry}} := 0$). There were random effects for floodplain (ε_k), and site nested within floodplain ($\varepsilon_{i(k)}$). We set the random effect for Barmah Forest to 0, so the random effect for Gunbower Island is relative to Barmah forest ('the Gunbower Island effect'). The term ξ is the potential effect of stand condition (S_{ij}) on prevalence. These relatively uninformative priors were used: $\alpha_p, \alpha_\lambda, \rho_j, \phi_j, \xi \tilde{N}(0, \sigma^2 = 4)$, $\varepsilon_k \tilde{N}(0 \sigma^2 = \sigma^2_{\text{floodplain}})$, $\varepsilon_i \tilde{N}(0, \sigma^2 = \sigma^2_{\text{transect}})$, and $\sigma_{\text{floodplain}}, \sigma_{\text{transect}} \text{Uniform}(0, 8)$.

We calculated the estimated program-specific RRs by averaging over the values of q_{ij} for each program. Differences in RRs for all rounds were monitored, from which posterior probability distributions for the differences were computed. We considered posterior probabilities ≥ 0.91 to be 'strong evidence' of an increase in mean RR in a later round compared with an earlier round while posterior probabilities ≤ 0.09 were 'strong evidence of a decrease in mean RR (Kass & Raftery 1995). These values correspond to a 10:1 posterior: prior odds-ratio given uninformative priors, which is regarded as strong evidence for a difference (Kass & Raftery 1995). The same means of inference was used for parameter values for ρ_j, ϕ_j, which were indicators of differences in prevalence (ρ_j) and in-site RR if present (ϕ_j) respectively. Note that values ≥ 0.75 or ≤ 0.25 are regarded as 'substantial evidence of increases or decreases, and values between 0.25 and 0.75 are 'barely worth mentioning' (Kass & Raftery 1995).

Breeding responses

Breeding was measured only for the late-Big Dry (2009), Big Wet (2013) and post-Big Wet (2017). All response models had these fixed effects: the 'effect' of Year 2013 compared to 2009 (Big Wet *vs.* late-Big Dry) and the 'effect' of Year 2017 compared to 2009 (post-Big Wet *vs.* late-Big Dry). There were random effects for site and forest, and the effect of the latter again was expressed as the 'Gunbower Island effect' relative to Barmah Forest. There were three covariates for the analyses (Mac Nally *et al.* 2014): (i) SC; (ii) fallen timber (t ha^{-1}); and (iii) number of dead trees (ha^{-1}). Upon inspection, fallen timber and numbers of dead trees were right-skewed, which was remedied by log-transformation. We used centred versions of stand condition (SC), log(fallen timber) and log(dead trees) to speed and stabilize model convergence.

The response variables for breeding were: (i) total breeding score (summed scores of breeding behaviours of all species at each site over the entire study, which were based on the maximum per-nest or per-territory scores); (ii) the number of breeding species; (iii) the total number of young irrespective of species; and (iv) the breeding scores of the nine most breeding-active species.

All responses were log-normally distributed, and so, were modelled on a log-transformed scale as:

$$\mu = \tau_{2013\ v\ 2009} + \tau_{2017\ v\ 2009} + \text{centred}(\text{covariates}) + \rho_{\text{site}} + \rho_{\text{Gunbower}}; \log(\text{Response}) \sim \text{Gaussian}(\mu, \sigma^2).$$

The primary responses of interest are the differences between programs ($\tau_{2013\ v\ 2009}$, $\tau_{2017\ v\ 2009}$), conditional on the covariates, and taking into account site (ρ_{site}) and forest (ρ_{Gunbower}) random effects.

Estimation, model adequacy and parameter inference

We fitted models in JAGS (Plummer 2003) using the jagsUI 'wrapper' (Kellner 2019). We sampled parameter distributions for 50 000 MCMC iterations, after 10 000 iteration burns-in (values discarded). We assessed overall model adequacy with posterior predictive assessment (Gelman *et al.* 1996), which is a function provided in jagsUI providing that the observed and simulated residuals are monitored. If the observed value (posterior predictive probability, PPP) is ≤ 0.05 or ≥ 0.95, then the fitted model is regarded as being *unlikely* to have generated the observed data (Gelman *et al.* 1996). As corroboration, we also used the leave-one-out (LOO) cross-validation method to check residuals distributions (Vehtari *et al.* 2016; Vehtari *et al.* 2017).

RESULTS

Trends in reporting rates among programs

Fifty-seven species were seen in 1998, 44 in 2009, 41 in 2013 and 68 species in 2017; 31 species were common to all survey programs. Overall, reporting rates were lower in the late-Big Dry (2009) and Big Wet (2013) than in the early-Big Dry (1998), although there was some evidence of increases in the post-Big Wet (2017) relative to the late-Big Dry and Big Wet, but rates still were lower than in the early-Big Dry (Fig. 3a,b). Prevalence was lower in the late-Big Dry and Big Wet than in the early-Big Dry, with some rebound in the post-Big Wet (Fig. 3c). If birds were present at a site, there was little difference in their in-site reporting rates (Fig. 3d).

doi:10.1111/aec.13164

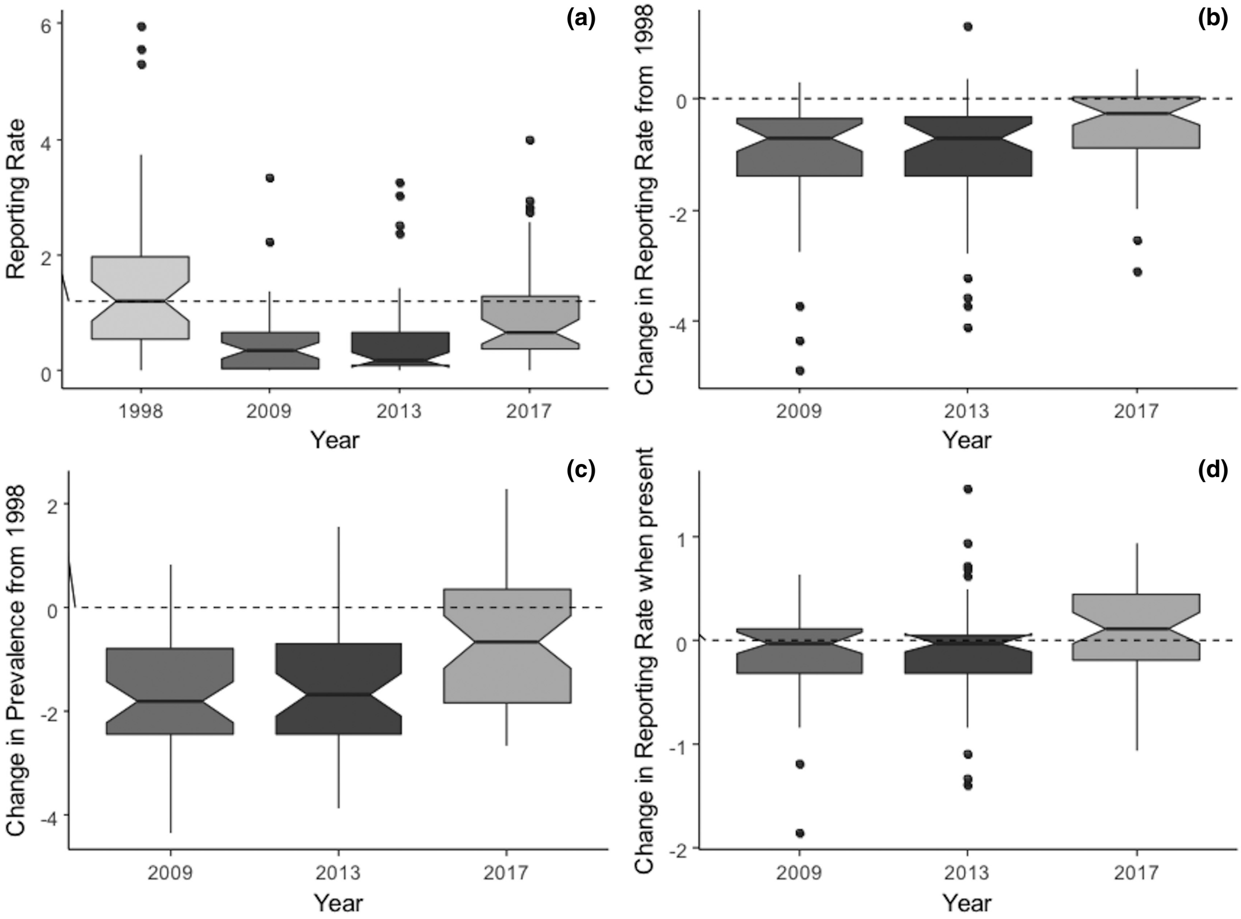

Fig. 3. Notched box-and-whiskers plots summarizing distributions for all modelled species. (a) Estimated overall reporting rates (RR) expressed as per eight visits per site for each survey program. The dotted line is overall mean reporting rate for the reference survey program of the early-Big Dry. (b) Changes in estimated on-site overall reporting rates, (c) prevalence (on logistic scale) and (d) in-site log reporting rates relative to the early-Big Dry (dotted lines indicate no change relative to the early-Big Dry).

Of the 45 species that satisfied the inclusion criteria, there was strong evidence for declines in reporting rates for 35 species (78%) during the Big Dry (2009 *vs.* 1998), with only one species (Silvereye) having a greater reporting rate (Fig. 4). Until 2013, nine Big Dry-declining species (36%) had increased reporting rates, including four species (12%) with increases equal to or greater than their declines (Appendix S1). The other species either declined further (eight species, 23%) or their reporting rates did not change (18 species, 51%). Three of the 10 species that did not decline through the Big Dry had declined by 2013. Over the entire duration 1998–2017, 23 species (51%) declined, one increased (2%) and 21 species (46%) did not change much (Fig. 4).

Associations with stand condition

Twelve of the 45 species were negatively associated with SC [Pr(>0) < 0.09] and another three probably were [Pr(>0) < 0.25] (Appendix S2). Eleven were positively associated with SC [Pr(>0) > 0.91] and another three probably were [Pr(>0) > 0.75] (Appendix S2). The other 16 appeared to have little association with SC. We list statistics for associations of individual species with SC from previous analyses (Selwood *et al.* 2015a). While some of the strong associations, both negative and positive, found for 2017 were less evident in 2013, the association for only one species, the Laughing kookaburra *Dacelo novaeguineae*, a large kingfisher, changed from a strong positive relationship in the 2013 analyses to a strong negative one in the 2017 calculations (Appendix S2). Strong positive associations in 2013 were not evident for two species in 2017 (Mistletoebird *Dicaeum hirundinaceum*, Striated thornbill). Six species went from probably negative to almost certainly negative between 2013 and 2017, while associations for another six species went from marginal positive to strongly positive (Appendix S2).

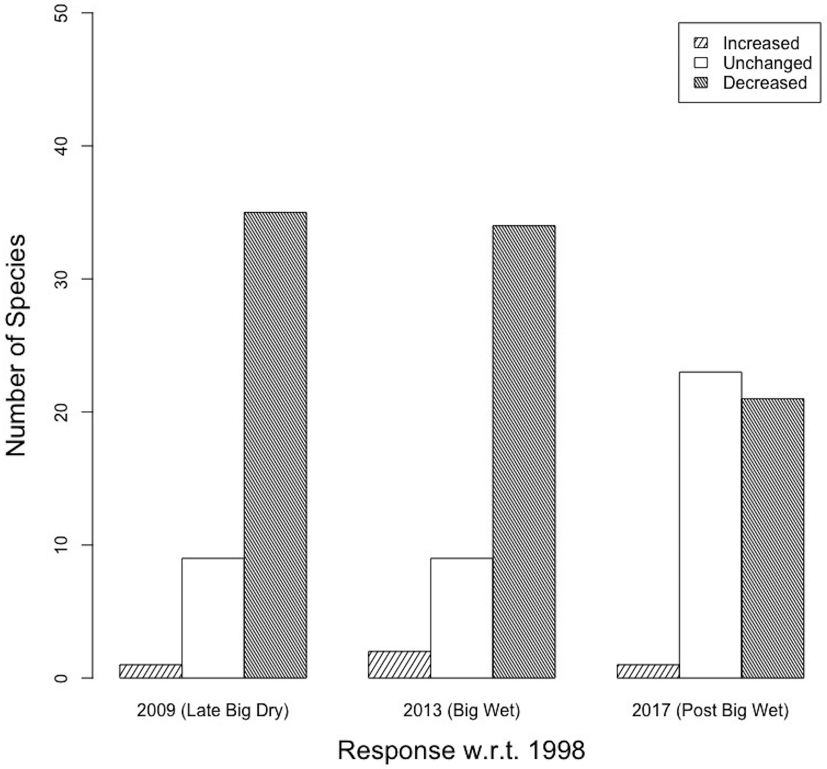

Fig. 4. Summary of numbers of species that increased [Pr (>0) ≥ **0.91**], decreased [Pr (>0) < *0.09*] or probably remained unchanged (Pr(>0) otherwise] in the three later survey programs relative to the first survey program (1998).

Breeding behaviours and success

Temporal trends

Breeding activity by three species (Brown treecreeper, Red-capped robin, Yellow rosella) was lower in the Big Wet than in the late-Big Dry (2009), while that of the white-plumed honeyeater was greater (Table 1). Six response measures (log scale) were greater in the post-Big Wet than in the late-Big Dry, including numbers of breeding species and young produced, and breeding activity by the Jacky winter, Striated pardalote, White-plumed honeyeater and White-throated treecreeper (Table 1, Appendix S3). Breeding activity was reduced for three species between the late-Big Dry and the post-Big Wet: Brown treecreeper, Superb fairy-wren and Yellow rosella (Table 1, Appendix S4).

Associations with covariates

Only four breeding response variables were positively associated with SC, namely, total breeding score and breeding activity of the Buff-rumped thornbill, White-plumed honeyeater and White-throated treecreeper (Table 1, Appendix S5). Fallen-timber loads and numbers of dead trees were 'covariates' and did not form part of the site-selection criteria, which was driven by SC. Five response variables (on the log scale) were negatively associated with fallen-timber load and only one, breeding activity by the White-plumed honeyeater, was positively associated (Table 1). The latter and that of the Brown treecreeper were positively associated with numbers of dead trees (log scale), while breeding activity by the Jacky winter and the Yellow rosella were negatively associated.

Values for most variables were greater on Gunbower Island (*i.e.* a positive 'Gunbower Island effect'), with four being substantially so, including total breeding activity and number of breeding species (log scale) (Table 1).

DISCUSSION

The most recent surveys of the two floodplain forests, some 5 years after the end of the Big Wet, showed that occurrence of birds had not yet reached their early-Big Dry (1998) levels. Of the 45 most regularly occurring birds within these forests, 35 species declined in occurrence over the Big Dry (1998–2009) and, while most species (31) had increased in the subsequent 8 years, 21 of the 45 species had occurrences substantially less than in the early-Big Dry; only one species (Silvereye) had a greater occurrence than 19 years before (Fig. 4).

Notwithstanding these multi-decadal overall declines, results from the post-Big Wet (2017) were more promising compared with those from the late-Big

doi:10.1111/aec.13164

Table 1. Estimates of model parameters (±SD) and probabilities that parameters differed from zero for three assemblage-wide measures of bird breeding activity at Barmah Forest and Gunbower Island, and for breeding activity of nine individual species

	PPP	LOO residuals	Stand condition	log(fallen timber)	log(N.dead trees)	2013 v 2009	2017 v 2009	Gunbower effect
Assemblage-wide measures								
Total activity	0.488	111 good	**0.089** ± **0.059**	−0.141 ± 0.145	−0.019 ± 0.109	−0.214 ± 0.253	0.097 ± 0.154	**0.298** ± **0.172**
Breeding species	0.511	110 good, 1 ok	0.027 ± 0.030	*−0.154* ± *0.075*	−0.026 ± 0.056	0.033 ± 0.111	**0.253** ± **0.063**	**0.236** ± **0.086**
Young produced	0.799	110 good, 1 ok	0.009 ± 0.031	0.029 ± 0.077	0.022 ± 0.058	0.015 ± 0.128	**0.152** ± **0.078**	0.012 ± 0.090
Individual species								
Buff-rumped thornbill	0.59	101 good, 10 ok	**0.127** ± **0.068**	*−0.305* ± *0.172*	0.070 ± 0.128	−0.148 ± 0.273	−0.008 ± 0.16	0.139 ± 0.202
Brown treecreeper	0.41	108 good, 3 ok	0.020 ± 0.066	0.175 ± 0.165	**0.186** ± **0.123**	*−1.164* ± *0.272*	*−0.758* ± *0.166*	**0.493** ± **0.197**
Jacky winter	0.92	105 good, 6 ok	−0.050 ± 0.045	−0.052 ± 0.109	*−0.127* ± *0.083*	0.038 ± 0.191	**0.296** ± **0.119**	−0.035 ± 0.132
Red-capped robin	0.86	95 good, 16 ok	−0.066 ± 0.061	0.021 ± 0.154	−0.001 ± 0.115	*−0.457* ± *0.247*	−0.095 ± 0.149	−0.105 ± 0.184
Superb fairy-wren	0.84	107 good, 4 ok	−0.004 ± 0.042	*−0.122* ± *0.104*	−0.068 ± 0.078	0.173 ± 0.179	*−0.162* ± *0.11*	0.019 ± 0.121
Striated pardalote	0.81	109 good, 2 ok	−0.046 ± 0.046	−0.062 ± 0.111	−0.026 ± 0.084	−0.060 ± 0.192	**0.393** ± **0.121**	0.052 ± 0.135
White-plumed honeyeater	0.74	100 good, 11 ok	**0.100** ± **0.064**	**0.264** ± **0.167**	**0.178** ± **0.123**	**0.446** ± **0.235**	**0.210** ± **0.130**	0.199 ± 0.19
White-throated treecreeper	0.94	104 good, 7 ok	**0.076** ± **0.038**	*−0.127* ± *0.092*	0.031 ± 0.069	0.116 ± 0.161	**0.129** ± **0.098**	0.033 ± 0.108
Yellow rosella	0.75	108 good, 3 ok	−0.017 ± 0.035	*−0.244* ± *0.086*	*−0.121* ± *0.065*	*−0.398* ± *0.151*	*−0.125* ± *0.094*	**0.291** ± **0.104**

Two measures of model fit are provided (see text): posterior predictive probabilities [PPP, (Gelman *et al.* 1996)] and leave-one-out cross-validation residuals [LOO, (Vehtari *et al.* 2016)]. **Bold**/*italic* text indicates a substantial **increase**/*decrease* [Pr (>0) ≥ **0.91** or Pr(>0) < *0.09*]. Linnean names are listed in Appendix S1. *Note*: 2009 = late-Big Dry, 2013 = Big Wet, and 2017 = post-Big Wet.

Dry (2009) than were the comparisons between the Big Wet (2013) and the late-Big Dry, suggesting that the longer period had allowed more time for recovery. The numbers of species that increased: remained unchanged: decreased in occurrence between the Big Wet and the late-Big Dry were 16:18:11, while the analogous figures for the post-Big Wet *vs.* late-Big Dry comparisons were 31:11:3 (Fig. 4). Between the post-Big Wet and the Big Wet, 26 species had greater occurrences, 18 remained unchanged, and only the Superb fairy-wren decreased.

These more positive occurrence trends were reflected in most comparisons of breeding statistics between the Big Wet and the late-Big Dry and post-Big wet and the late-Big Dry (Table 1). Numbers of breeding species and young produced both changed from essentially zero values to substantial positive ones between the Big Wet and the post-Big Wet. There were similar increases in the breeding activity of the Jacky winter, Striated pardalote, and White-throated treecreeper (Table 1). While not substantial in either temporal comparison, values for these comparisons were more positive in the post-Big Wet *vs.* late-Big Dry comparison than in the Big Wet *vs.* late-Big Dry contrasts for total breeding activity and breeding activities of the Buff-rumped thornbill, Brown treecreeper, Red-capped robin, and Yellow rosella. Only two breeding statistics were lower. Breeding activity of the White-plumed honeyeater, although still substantially greater in post-Big Wet than in the late-Big Dry (**0.210** ± **0.130**), was not as pronounced as in the Big Wet *vs.* late-Big Dry comparison (**0.446** ± **0.235**). Breeding activity of the Superb fairy-wren was less in the post-Big Wet than in the late-Big Dry (*−0.162* ± *0.11*) (from somewhat positive between the Big Wet and the late-Big Dry, 0.173 ± 0.179), consistent with the decline in the species' occurrence (Table 1). Of course, many of these increases in breeding statistics reflect the greater occurrences of many species in the post-Big Wet compared to Big Wet (26 species increased, 18 remained unchanged, the Superb fairy-wren declined; Fig. 4).

Yet the more positive outcomes for species' occurrence and breeding statistics seen in the post-Big Wet than in the Big Wet should not overlook that the avifauna of these floodplain forests has declined since the early-Big Dry (1998), with 21 of 45 species having substantially lower occurrence rates in the post-Big Wet than in the early-Big Dry (Fig. 4). It is possible that the results of the 1998 surveys were the culmination of a series of good (rainfall) years, so that the bird occurrence may have been relatively 'inflated'. However, the rainfall anomalies were negative from 1994 to 1998 (averaged over the two weather stations) so that we do not believe that the 1998 bird assemblages would have benefited from a stretch of excellent conditions occurring before the 1998 surveys (Fig. 1a). It also is possible that the slightly different methods used in 1998 than in the later survey programs might influence our inferences. However, comparisons of reporting rates between our data and independent data from the 2nd BirdLife Australia Atlas program suggest that our inferences generally are robust to the different survey methods used in 1998 compared with 2009, 2103 and 2017 (Appendix S8). Therefore, the avifauna of these floodplain forests seems to be falling short of full recovery and that the periods of high precipitation, typically for a couple of years at most, probably are not providing sufficient time for the birds to recover before extended dry spells re-emerge. This pattern of long drought–short wet has been projected to be the future for the region in which our floodplain forests are located [the Murray-Darling Basin, (Timbal 2015)], and the pattern of precipitation since 1991 (Appendix S6) appears to be consistent with this projection.

Forest stand condition and the avifauna

There is wide variation in the stand condition of the floodplain forests; the proportion of floodplain forests in good condition plummeted after the Big Dry, but seems to have stabilized to about 25% (Cunningham *et al.* 2018). Good-condition areas typically are near to main river channels, anabranches and ready access to the water table, providing the groundwater is not overly saline (Cunningham *et al.* 2011). Given the associations between bird species' occurrence rates and breeding activity with SC, we previously projected how the floodplain-forest bird assemblages might change into the long future (Mac Nally *et al.* 2014). Many of these projected deleterious avifaunal changes seem inevitable given the likely future climates for the region (King *et al.* 2017). However, associations between birds and stand condition have identified locations within the forests that would serve as important areas for forest birds during *both* drought and benign precipitation periods, which we refer to as 'havens' (Selwood *et al.* 2019). The significance of the identification of havens into the future is to prioritize management actions and investments in locations that offer the greatest ecological benefits during sequences of high-amplitude precipitation events (Selwood *et al.* 2019). This may become even more important if floodplain forests maintain better condition than upland and plains forests due to access to water from snowmelt or rainfall events in montane regions because all of the bird species, bar the Yellow rosella, which is a sub-species of the broadly distributed Crimson rosella, also occupy non-floodplain forests (Selwood *et al.* 2017).

While we have no data for birds or stand condition for 2018 onwards, the avian results that we report are likely to be at their peak given the on-going drought that has occurred in much of eastern Australia since 2017 (King *et al.* 2020). The severity and duration of the drought (Appendix S6; 2019 had the greatest deficit over the past 30 years), coupled with the more-or-less inexorable rise in temperatures (Appendix S7), probably has continued to exert downward pressure on SC and hence on much of the avifauna.

High-amplitude precipitation variation and biodiversity

A prominent feature of greenhouse-gas induced climate change is an increase in frequency and severity of extreme climatic events throughout the world (Moreno & Møller 2011; Diffenbaugh *et al.* 2017). We have focused on high-amplitude precipitation swings (droughts and floods), which now appear to be characteristic of many parts of the world (Chun-Yu *et al.* 2013; Roque-Malo & Kumar 2017), including mid-latitude and Mediterranean regions such as that upon which we report (Deitch *et al.* 2017). Tree cover, a key component of our stand-condition measure, is linked to precipitation variability at global scales (Xu *et al.* 2018). So, a logical train for this floodplain-forest system seems to be increasing greenhouse gases leading to more extreme precipitation fluctuations, which produce negative impacts on tree cover and health (SC), and subsequent adverse effects on the dependent fauna (Lada *et al.* 2013; Selwood *et al.* 2015a). Understanding how weather extremes affect the biota needs approaches that recognize *sequences* of extremes alternating with beneficial or benign periods [*e.g.* (Thompson *et al.* 2018)], which appear to characterize many systems. Last, the timing of extreme events in relation to species' life histories (*e.g.* longevity, fecundity, survivorship curves) is likely to be a critical component of how species fare in relation to high-amplitude climatic fluctuations (Selwood *et al.* 2015b).

ACKNOWLEDGEMENTS

The study was carried out under Monash University School of Biological Sciences Animal Ethics Committee permit BSCI/2007/05 and the University of Canberra permit #AEC17-15 and a Victorian Government Department of Environment, Land, Water and

Planning National Parks Research Permit 10008379. Chris Tzaros, Laurie Conole, Anna Lada, Michael Kaplan, Peter Selwood and Justine Smith assisted with fieldwork, while Erica Fleishman, Peter Griffioen, Matt White, Rohan Clarke, Melanie McGeoch and the late Shaun Cunningham helped in other stages of the project. We thank reviewers and editors for stimulating important clarifications in the MS. Open access publishing facilitated by The University of Melbourne, as part of the Wiley - The University of Melbourne agreement via the Council of Australian University Librarians. [Correction added on 6 June 2022, after first online publication: CAUL funding statement has been added.]

CONFLICTS OF INTEREST

The authors declare that they have no competing interests or conflicts.

AUTHOR CONTRIBUTIONS

Tim Reid: Data curation (supporting); Investigation (supporting); Project administration (supporting); Writing-original draft (co-lead); Writing-review & editing (supporting). **Hania Lada**: Data curation (supporting); Investigation (supporting); Project administration (supporting); Writing-original draft (supporting); Writing-review & editing (supporting). **Katherine Selwood**: Conceptualization (supporting); Investigation (supporting); Methodology (supporting); Writing-original draft (supporting); Writing-review & editing (supporting). **Gregory Ford Byron Horrocks**: Investigation (supporting); Methodology (supporting); Writing-review & editing (supporting). **Jim Thomson**: Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Software (supporting); Writing-original draft (supporting); Writing-review & editing (supporting). **Ralph Mac Nally**: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Resources (lead); Software (lead); Supervision (lead); Validation (lead); Writing-original draft (co-lead); Writing-review & editing (lead).

FUNDING

This work was supported by the Australian Research Council Grants DP0984170, DP120100797 and LP120200217. Stand-condition mapping was supported by grant LP0560518, and funds from the Murray-Darling Basin Authority (MD1114).

REFERENCES

Ashcroft L., Karoly D. J. & Dowdy A. J. (2019) Historical extreme rainfall events in southeastern Australia. *Weather. Clim. Extremes* **25,** 100210.

Babcock R. C., Bustamante R. H., Fulton E. A. *et al.* (2019) Severe continental-scale impacts of climate change are happening now: Extreme climate events impact marine habitat forming communities along 45% of Australia's coast. *Front. Mar. Sci.* **6,** 411.

Chun-Yu Z., Ying W., Xiao-Yu Z. *et al.* (2013) Changes in climatic factors and extreme climate events in Northeast China during 1961–2010. *Adv. Clim. Change Res.* **4,** 92–102.

Cowles J., Boldgiv B., Liancourt P., Petraitis P. S. & Casper B. B. (2018) Effects of increased temperature on plant communities depend on landscape location and precipitation. *Ecol. Evol.* **8,** 5267–78.

Cunningham S., Mac Nally R., Read J. *et al.* (2009) A robust technique for mapping vegetation across a major river system. *Ecosystems* **12,** 207–19.

Cunningham S. C., Griffioen P., White M. D. & Mac Nally R. (2018) Rapid assessment of ecosystems in a changing world: a method for rigorous and rapid mapping of floodplain forest condition for a major river. *Land Degrad. Dev.* **29,** 127–37.

Cunningham S. C., Thomson J. R., Mac Nally R., Read J. & Baker P. J. (2011) Groundwater change forecasts widespread forest dieback across an extensive floodplain system. *Freshw. Biol.* **56,** 1494–508.

Deitch M. J., Sapundjieff M. J. & Feirer S. T. (2017) Characterizing precipitation variability and trends in the world's Mediterranean-climate areas. *Water* **9,** 259.

Dey R., Lewis S. C., Arblaster J. M. & Abram N. J. (2019) A review of past and projected changes in Australia's rainfall. *Wiley Interdiscip. Rev. Clim. Change* **10,** e577.

Diffenbaugh N. S., Singh D., Mankin J. S. *et al.* (2017) Quantifying the influence of global warming on unprecedented extreme climate events. *Proc. Natl. Acad. Sci.* **114,** 4881–6.

Dyderski M. K., Paź S., Frelich L. E. & Jagodziński A. M. (2018) How much does climate change threaten European forest tree species distributions? *Glob. Chang. Biol.* **24,** 1150–63.

Gelman A., Meng X.-L. & Stern H. (1996) Posterior predictive assessment of model fitness via realized discrepancies. *Stat. Sin.* **6,** 733–87.

Gutschick V. P. & BassiriRad H. (2003) Extreme events as shaping physiology, ecology, and evolution of plants: toward a unified definition and evaluation of their consequences. *New Phytol.* **160,** 21–42.

Hawkins B. A., Thomson J. R. & Mac Nally R. (2018) Regional patterns of nectar availability in subtropical eastern Australia. *Landsc. Ecol.* **33,** 999–1012.

Heinrich I., Weidner K., Helle G., Vos H., Lindesay J. & Banks J. C. G. (2009) Interdecadal modulation of the relationship between ENSO, IPO and precipitation: insights from tree rings in Australia. *Clim. Dyn.* **33,** 63–73.

Hovenden M. J., Leuzinger S., Newton P. C. D. *et al.* (2019) Globally consistent influences of seasonal precipitation limit grassland biomass response to elevated CO 2. *Nat. Plants* **5,** 167–73.

Kass R. E. & Raftery A. E. (1995) Bayes factors. *J. Am. Stat. Assoc.* **90,** 773–95.

Kellner K. (2019) jagsUI: a Wrapper Around 'rjags' to Streamline 'JAGS' Analyses.1.5.1. https://github.com/kenkellner/jagsUI.

King A. D., Karoly D. J. & Henley B. J. (2017) Australian climate extremes at 1.5 C and 2 C of global warming. *Nat. Clim. Change* **7,** 412–6.

King A. D., Pitman A. J., Henley B. J., Ukkola A. M. & Brown J. R. (2020) The role of climate variability in Australian drought. *Nat. Clim. Change* **10,** 177–9.

Lada H., Thomson J. R., Cunningham S. C. & Mac Nally R. (2013) Rainfall in prior breeding seasons influences population size of a small marsupial. *Austral Ecol.* **38,** 581–91.

Leblanc M., Tweed S., Van Dijk A. & Timbal B. (2012) A review of historic and future hydrological changes in the Murray-Darling Basin. *Glob. Planet. Change* **80,** 226–46.

Lister B. C. & Garcia A. (2018) Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proc. Natl. Acad. Sci.* **115,** E10397–406.

Mac Nally R. (2007) Consensus weightings of evidence for inferring breeding success in broad-scale bird studies. *Austral Ecol.* **32,** 479–85.

Mac Nally R., Lada H., Cunningham S. C., Thomson J. R. & Fleishman E. (2014) Climate-change-driven deterioration of the condition of floodplain forest and the future for the avifauna. *Glob. Ecol. Biogeogr.* **23,** 191–202.

Mac Nally R., Parkinson A., Horrocks G., Conole L. & Tzaros C. (2001) Relationships between terrestrial vertebrate diversity, abundance and availability of coarse woody debris on south-eastern Australian floodplains. *Biol. Conserv.* **99,** 191–205.

Moreno J. & Møller A. P. (2011) Extreme climatic events in relation to global change and their impact on life histories. *Curr. Zool.* **57,** 375–89.

Muller-Landau H. C., Cushman K. C., Arroyo E. E., Martinez C. I., Anderson-Teixeira K. J. & Backiel B. (2020) Patterns and mechanisms of spatial variation in tropical forest productivity, woody residence time, and biomass. *New Phytol.* **229,** 3065–87.

Plummer M. (2003) JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*. Vienna.

Roque-Malo S. & Kumar P. (2017) Patterns of change in high frequency precipitation variability over North America. *Sci. Rep.* **7,** 1–12.

Schou M. F., Bonato M., Engelbrecht A. *et al.* (2021) Extreme temperatures compromise male and female fertility in a large desert bird. *Nat. Commun.* **12,** 1–10.

Selwood K., Mac Nally R. & Thomson J. R. (2009) Native bird breeding in a chronosequence of revegetated sites. *Oecologia* **159,** 435–46.

Selwood K. E., Clarke R. H., Cunningham S. C., Lada H., McGeoch M. A. & Mac Nally R. (2015a) A bust but no boom: responses of floodplain bird assemblages during and after prolonged drought. *J. Anim. Ecol.* **84,** 1700–10.

Selwood K. E., Clarke R. H., McGeoch M. A. & Mac Nally R. (2017) Green tongues into the arid zone: river floodplains extend the distribution of terrestrial bird species. *Ecosystems* **20,** 745–56.

Selwood K. E., Cunningham S. C. & Mac Nally R. (2019) Beyond refuges: Identifying temporally dynamic havens to support ecological resistance and resilience to climatic disturbances. *Biol. Conserv.* **33,** 131–8.

Selwood K. E., McGeoch M. A. & Mac Nally R. (2015b) The effects of climate change and land-use change on demographic rates and population viability. *Biol. Rev.* **90,** 837–53.

Smale D. A., Wernberg T., Oliver E. C. J. *et al.* (2019) Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nat. Clim. Change* **9,** 306–12.

Telleria J. L., Fernandez-Lopez J. & Fandos G. (2016) Effect of climate change on mediterranean winter ranges of two migratory passerines. *PLoS One* **11,** e0146958.

Thompson R. M., King A., Kingsford R. T., Mac Nally R. & Poff N. L. (2018) Legacies, lags, and shifting baselines: environmental flow restoration in a changed and changing world. *Freshw. Biol.* **63,** 986–95.

Timbal B. (2015) Murray Basin Cluster Report. Climate Change in Australia Projections for Australia's Natural Resource Management Regions: Cluster Reports, eds. Ekström, M. et al., CSIRO and Bureau of Meteorology, Australia.

Van de Ven T., McKechnie A. E., Er S. & Cunningham S. J. (2020) High temperatures are associated with substantial reductions in breeding success and offspring quality in an arid-zone bird. *Oecologia* **193,** 225–35.

Vehtari A., Gelman A. & Gabry J. (2016) loo: efficient leave-one-out cross-validation and WAIC for Bayesian models. R package version 1.0.0. Available from URL: https://github.com/stan-dev/loo [Accessed 15th March 2018].

Vehtari A., Gelman A. & Gabry J. (2017) Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat. Comput.* **27,** 1413–32.

Verdon-Kidd D. C. & Kiem A. S. (2009) Nature and causes of protracted droughts in southeast Australia: comparison between the Federation, WWII, and Big Dry droughts. *Geophys. Res. Lett.* **36,** GL041067.

Waldock C., Dornelas M. & Bates A. E. (2018) Temperature-driven biodiversity change: disentangling space and time. *Bioscience* **68,** 873–84.

Xu X., Medvigy D., Trugman A. T., Guan K., Good S. P. & Rodriguez-Iturbe I. (2018) Tree cover shows strong sensitivity to precipitation variability across the global tropics. *Glob. Ecol. Biogeogr.* **27,** 450–60.

SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. Estimated reporting rates for each year (for eight surveys) for the 45 species analyzed (*i.e.* whose models adequately converged), and the estimated posterior probability of change in reporting rates between pairs of programs.

Appendix S2. Estimated associations of reporting rates with stand condition for the post-Big Wet analyses, ordered by increasing association with stand condition.

Appendix S3. Differences in six measures (log scale) that were greater in the post-Big Wet (2017) than in the late-Big Dry (2009).

doi:10.1111/aec.13164

Appendix S4. Differences in six measures (log scale) that were reduced in the post-Big Wet (2017) than in the late-Big Dry (2009).

Appendix S5. Associations between forest-stand condition (SC) and log scores.

Appendix S6. Precipitation anomalies (mm) relative to the baseline of the Australian Bureau of Meteorology (1961–1990) for the Murray-Darling Basin.

Appendix S7. Mean annual temperature anomalies (°C) relative to the baseline of the Australian Bureau of Meteorology (1961–1990) for the Murray-Darling Basin.

Appendix S8. Statistical significance levels[†] for comparisons of our data with independent data from the 2nd BirdLife Australia Atlas program (20-min-2 ha data).

doi:10.1111/aec.13164