



Resistance and resilience: can the abrupt end of extreme drought reverse avifaunal collapse?

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ABSTRACT

Aim Climate change is expected to increase the frequency and intensity of extreme climatic events, such as severe droughts and intense rainfall periods. We explored how the avifauna of a highly modified region responded to a 13-year drought (the ‘Big Dry’), followed by a two-year period of substantially higher than average rainfall (the ‘Big Wet’).

Location Temperate woodlands in north central Victoria, Australia.

Methods We used two spatially extensive, long-term survey programmes, each of which was repeated three times: early and late in the Big Dry, and in the Big Wet. We compared species-specific changes in reporting rates between periods in both programmes to explore the resistance (the ability to persist during drought) and resilience (extent of recovery post-drought) of species to climate extremes.

Results There was a substantial decline in the reporting rates of 42–62% (depending on programme) of species between surveys conducted early and late in the Big Dry. In the Big Wet, there was some recovery, with 21–29% of species increasing substantially. However, more than half of species did not recover and 14–27% of species continued to decline in reporting rate compared with early on in the Big Dry. Species’ responses were not strongly related to ecological traits. Species resistance to the drought was inversely related to resilience in the Big Wet for 20–35% of the species, while 76–78% of species with low resistance showed an overall decline across the study period.

Conclusions As declines occurred largely irrespective of ecological traits, this suggests a widespread mechanism is responsible. Species that declined the most during the Big Dry did not necessarily show the greatest recoveries. In already much modified regions, climate extremes such as extended drought will induce on-going changes in the biota.

Keywords

Big Dry, Big Wet, climate change, degradation, land-use change, recovery, species traits.

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INTRODUCTION

As the world’s climate warms, there will be greater numbers of extreme climatic events such as protracted droughts and floods (IPCC, 2013). Climatic extremes restructure ecological assemblages (Jimenez *et al.*, 2011), and their increased frequency may pose a greater threat to biodiversity than gradual

changes in average climatic conditions (Jentsch & Beierkuhnlein, 2008). However, most work on the effects of climate change has focused on increases in mean temperature to assess range shifts (Lenoir *et al.*, 2008) and changes in phenology (Cleland *et al.*, 2007), with few assessments of assemblage-level responses to extreme events (but see Thompson *et al.*, 2013).

Increases in extreme climatic events will occur over a template of massively transformed regions dominated by human activities (Opdam & Wascher, 2004). Much modified ecosystems may be particularly vulnerable to climate change due to regional shifts in the distribution of precipitation, local drying and warming (McAlpine *et al.*, 2009), and increased fire frequency and severity (Regan *et al.*, 2010). This overlap of disturbances may limit the capacity of the biota to 'bounce back' (Falkenberg *et al.*, 2013) following the release of a pressure, such as prolonged drought.

The net effect on species from wide variations in climatic conditions will be determined by their ability to absorb the pressure ('resistance'), and their capacity to recover following the release of the pressure ('resilience') (Harrison, 1979). The ability of an assemblage to return to its original state following the relaxation of a pressure requires that species-specific resistance be inversely related to resilience (Herbert *et al.*, 1999; Orwin *et al.*, 2006). Thus, species that decline most during climatic extremes (e.g. severe drought) will need to have a relatively great capacity to recover to return to their predisturbance state.

The capacity for animal species to resist, or to recover from, climate extremes is contingent on: (1) the extent and severity of a climatic pressure and the time lags in the replenishment of diminished resources (e.g. food and vegetation); (2) the extent of available habitat, especially in much modified landscapes, that can accommodate resistance or recovery (Morecroft *et al.*, 2012); and (3) species' ecological traits that affect resistance and resilience (Smith, 2011; Chessman, 2013). Our knowledge of the resistance and resilience of biota to prolonged droughts in much modified landscapes is limited because of a scarcity of consistently measured, large-scale, long-term data that track assemblages throughout severe droughts.

South-eastern Australia has experienced the interaction between land-use and climate change. The region was subjected to massive land transformation over the past 200 years, primarily for agriculture (ECC, 2001). There have been major declines in several taxa (Brown *et al.*, 2008; Mac Nally *et al.*, 2009; Thomson *et al.*, 2012). The area has warmed, with increases in mean annual temperature over several decades (Jones, 2012). Increases in mean temperature were compounded by an extended drought – 'the Big Dry' – from 1997 to 2010 (Leblanc *et al.*, 2012). The duration and accumulated precipitation deficit was at least twice that of other droughts since instrumental records from the 1880s began (Leblanc *et al.*, 2012). Climate-change scenarios project a 1–5 °C increase in mean annual temperature (IPCC, 2013) and a 5–15% decrease in mean annual precipitation for the region by 2070 (relative to 1990) (IPCC, 2007). These observed, and projected, climate-change measures are consistent with other regions at similar latitudes (e.g. the North American southwest, the Mediterranean Basin, southern Africa and northern China) (IPCC, 2013).

The Big Dry and the ramping of temperature, in conjunction with land-use change, were linked to a regional

'collapse' of avifauna in the box and ironbark ecosystems of south-eastern Australia (Mac Nally *et al.*, 2009). Avifaunal declines occurred both inside and outside of protected areas, and irrespective of species' ecological traits (Mac Nally *et al.*, 2009). The Big Dry ended with heavy spring and summer rains between mid-2010 and 2012 – 'the Big Wet' (Leblanc *et al.*, 2012). A key question is: did the breaking of the Big Dry provide the region's biota a reprieve (Mac Nally *et al.*, 2014), and if so, how has the region's avifauna responded?

We use two extensive monitoring programmes that tracked changes in the avifauna throughout an entire region, the box and ironbark ecosystem of Victoria, Australia, during the Big Dry (Mac Nally *et al.*, 2009), and into the Big Wet (total span: 1995–2012). These large-scale, complementary data sets provided an opportunity to assess the extent to which the abrupt end of a protracted drought 'unwound' the collapse of a regional fauna in a much modified region. Specifically, we asked: (1) did the Big Wet reverse the collapse of the avifauna witnessed during the Big Dry? (2) What is the relationship between the resistance and resilience of species in the Big Dry–Big Wet period? And (3) are ecological traits (e.g. nesting, foraging, geographic range) associated with differing resistance during drought or with resilience following the drought's breaking?

METHODS

The region (30,000 km², central Victoria, Australia, Fig. 1) is characterized by forest and woodland vegetation with an open canopy of moderate height (10–25 m) dominated by eucalypts. The understorey consists of small shrubs and herbs, such as acacias (Mimosaceae), heaths (Epacridaceae) and bush peas (Fabaceae), and tussock grasses (*Poa* spp., *Austrodanthonia* spp.). Local forest composition is dependent on soils, elevation, drainage and aspect (ECC, 2001; Mac Nally & Horrocks, 2002).

Climate data

Rainfall and temperature data were obtained from spatial data modelled for 500-m grids from the Bureau of Meteorology Data Library (BoM, 2013). Mean annual temperature and rainfall anomalies are based on a historical baseline (1961–1990). Historically, precipitation fell mostly in winter and spring with hot, dry summers. Precipitation during the Big Dry was below the Australian Bureau of Meteorology baseline (1961–90) for 11 of the 13 years (Fig. 2), with an accumulated deficit of almost 2.5 years of baseline average precipitation (Fig. 2). Declines were disproportionately large in autumn and early winter (Leblanc *et al.*, 2012). The Big Wet replenished about 1 year of the baseline precipitation deficit from the Big Dry (BoM, 2013).

In south-eastern Australia, there were step changes in temperature in 1968 and 1997, which led to a total rise in mean minimum (+1.16 °C) and maximum (+1.08 °C) tempera-

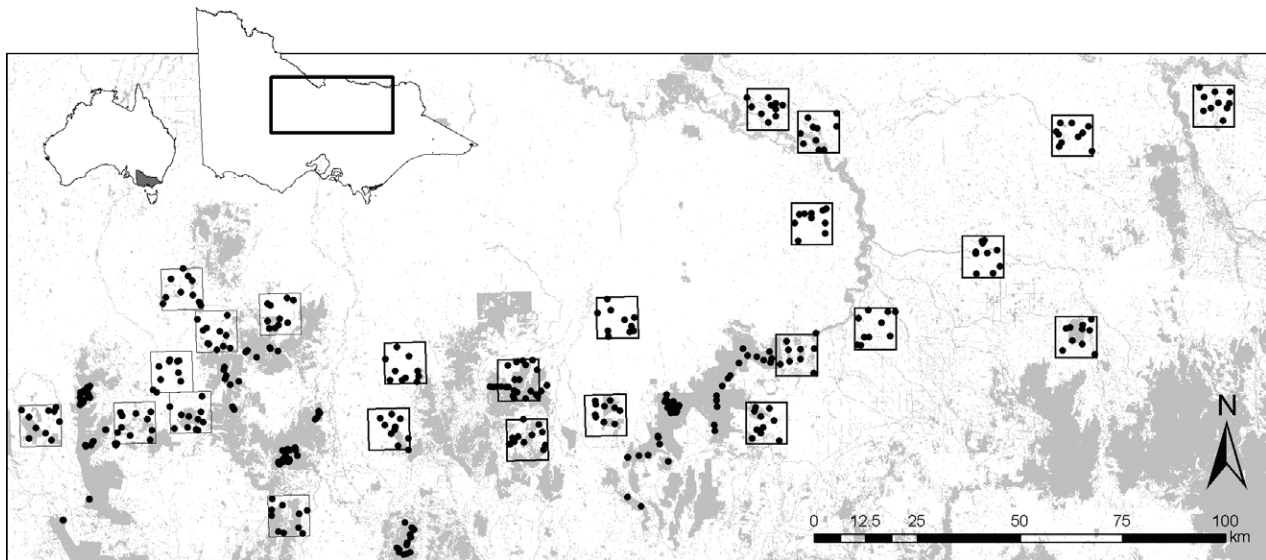


Figure 1 The location of study sites in both survey programmes in north-central Victoria, Australia (remnant vegetation is shown in grey shading). Study sites enclosed in boxes are those of the landscape programme.

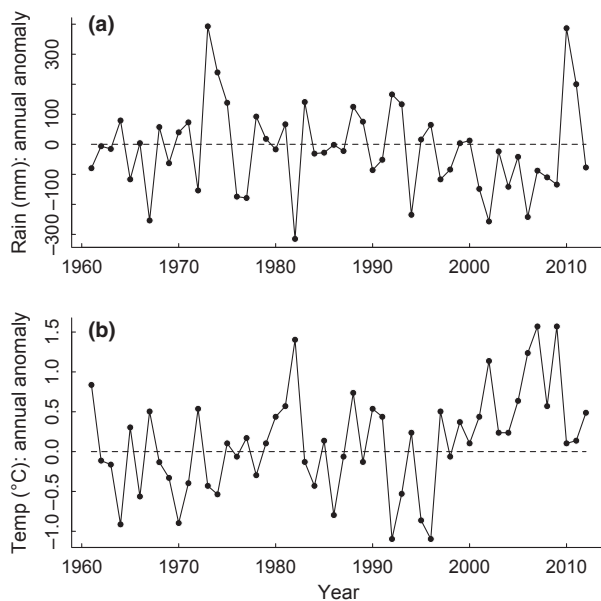


Figure 2 Annual anomalies relative to the 1961–90 baselines used by the Australian Bureau of Meteorology, for rainfall (mm; a) and mean maximum temperature (°C; b). Data are means from six representative stations across central Victoria, Australia (Australian Bureau of Meteorology stations: Dunolly, Bendigo prison, Bendigo airport, Waranga Shores, Maryborough, Creswick).

tures for the region (Jones, 2012). Mean temperature increased by 0.58 °C.

Bird occurrence data

Data were obtained from six intensive survey periods sampled in fragments of native vegetation across the region (1995–97, 2004–05 and 2010–11) ('fragment programme') and in a series

Table 1 Details of bird-occurrence studies. A 'site' is a 2 ha transect that was surveyed between four to eight times (No. surveys/site) within a sampling period. See source papers for further information on site selection

Programme	No. sites	No. surveys/site	Years	Sources
Fragment	139	8	1995–97	Mac Nally <i>et al.</i> (2000), Mac Nally & Horrocks (2002)
Fragment	65	8	2004–05	Thomson <i>et al.</i> (2007)
Fragment	120	8	2010–11	This study
Landscape	240	4	2002–03	Radford <i>et al.</i> (2005)
Landscape	240	4	2006–07	This study
Landscape	240	4	2011–12	This study

of landscapes (2002–03, 2006–07 and 2011–12) ('landscape programme') (Table 1). The programmes used a similar standard protocol for bird surveys (strip transects of 2 ha) (Barrett *et al.*, 2003). The programmes were conducted in the same region, but differed in the way transects were grouped [into 'study landscapes' (see Radford *et al.*, 2005) or habitat fragments (see Mac Nally *et al.* 2000)] and the years in which the three rounds in each programme were undertaken. Each site was visited multiple times throughout the year. Birds are active throughout the year, and several of the dominant eucalypts (e.g. *Eucalyptus tricarpa*) may flower profusely in the colder months, which attracts nectarivorous birds (Mac Nally & McGoldrick, 1997).

Fragment programme

All fragment surveys were repeated eight times at regular intervals throughout the year. Each strip transect of

80 × 250 m (2 ha) was surveyed for 20 min by one observer proceeding along the transect line. Transects were spatially clustered in sites within woodland fragments and large forest blocks depending on the area of native vegetation (Mac Nally & Horrocks, 2002). We do not consider fragment area (our focus is on regional prevalence), but included site identity in analyses to account for spatial patterns. In the 1995–1997 survey, 139 sites were surveyed. In 2004–2005, a subset (25 sites) of those 139 sites was resurveyed, and 40 new sites were used (Thomson *et al.*, 2007). There were no apparent differences in the avifaunal assemblages between the original and new sites (Mac Nally, 2007). In 2010–2011, 120 sites of the original 139 fragment programme transects were surveyed; 19 had been cleared or access was denied.

The 1995–1997 and 2004–2005 surveys were conducted by G. F. B. Horrocks, but the 2010–2011 surveys were conducted by J. M. Bennett. To ensure that observations between the two observers were compatible, two full rounds of ‘calibration surveys’ (240 transects, both observers) were conducted prior to the commencement of the 2010–2011 surveys. Differences between the observers were very few during the second calibration survey round. Calibration data were excluded.

Landscape programme

Sites in the landscape programme were arranged as ten 2-ha sites in each of twenty-four 100 km² ‘landscapes’ (Fig. 1) (Radford *et al.*, 2005). Each site was visited four times, twice in the breeding period (September to December) and twice in the autumn/winter period (March to July), in each of the three survey periods. Species recorded during a 20-min survey and a 10-min supplementary period were regarded as present; both on and off transect data were used, which was consistent with data used by Radford & Bennett (2007) and by Mac Nally *et al.* (2009) for the landscape programme. All of the 240 sites established in the 2002–2003 survey programmes were revisited in 2006–2007 and in 2011–2012. The landscape surveys were conducted by G. Cheers, apart from half of the 2002–2003 surveys, which were done by J. Radford; both are highly experienced ornithologists in this ecosystem.

All surveys were conducted from sunrise to sunset but not if weather conditions were poor for bird activity and detection (e.g. rain, high temperature or high wind). The dry forests and woodlands of the study area characteristically have a similar open structure with a canopy 10–25 m so that woodland birds are relatively conspicuous. We did not correct for detectability because the statistical bias introduced by such corrections is potentially large (Royle & Link, 2006; Banks-Leite *et al.*, 2014), and we do not believe detectability at a site would differ systematically due to climatic extremes. The analyses excluded nocturnal, non-native, and aquatic species, of which there were few records. Only species recorded in at least two survey periods were analysed.

Ecological traits

Species were classified into guilds (Radford & Bennett, 2005) based on ecological traits that may lead birds in one guild to respond similar to change, that is, species’ ‘response traits’ (Lavelle & Garnier, 2002; Luck *et al.*, 2012). Response traits were as follows: nesting, foraging (diet and substrate), degree of conservation concern, dependence on the amounts of remnant vegetation in landscapes, migratory status (resident, migrant) and geographic range (i.e. mesic, semi-arid or arid environments or widespread) (Blakers *et al.*, 1984). Species were allocated to the single trait category deemed most appropriate (e.g. frugivore), although trait categories may not be completely distinct and a species may belong to multiple trait classes (e.g. both insectivore and nectarivore). Five independent expert ornithologists reviewed the classifications to confirm their suitability. Sources of trait data are provided in the studies described by Radford & Bennett (2005), and an explanation of the choice of response traits is provided in Table 2.

Statistical analyses

We analysed data for the fragment and landscape programmes separately for four reasons. First, the three rounds in each programme were conducted in different sets of years. Second, the survey methods were slightly different, with the fragment programme using the standard 2 ha–20 min Birds Australia second-atlas method while the landscape programme employed an extra 10 min of observation. Third, there were different sets of observers. Last, the programmes complemented each other by covering somewhat different vegetation. The fragment sites generally were located on relatively dry and infertile sites on hill slopes, often dominated by red ironbark *E. tricarpa*. A greater proportion of sites in the landscape programme was located on plains, with more fertile soils, often mainly grey box *Eucalyptus microcarpa*.

Species-specific reporting rates were the response variables in all analyses. The reporting rate for a single transect i in period j (1, 2, or 3) is the proportion of visits in period j in which a species was recorded. The mean reporting rate for period j is the expected proportion of occupied transects at any given time or, equivalently, the probability of observing a species in a single visit to a randomly chosen transect. We estimated changes in mean reporting rates between the three survey periods of each programme. We used hierarchical Bayesian models to estimate changes in reporting rates and to account for spatial structure. The model was:

$$y_{i(l)j} \sim \text{Binomial}(v_{ij}, p_{ij}); \text{logit}(p_{ij}) \\ = \alpha + \delta_l^1 \cdot I_{j>1} + \delta_l^2 \cdot I_{j=3} + \varepsilon_l + \varepsilon_i$$

$$\delta_l^1 \sim N(\Delta_1, \sigma_{\delta_1}^2); \delta_l^2 \sim N(\Delta_2, \sigma_{\delta_2}^2)$$

Table 2 Explanation for the choice of avian response traits used in analyses

Trait	Explanation	
	Resistance	Resilience
Nesting substrate	Drought caused decreases in canopy and shrub cover, and changes in ground cover (e.g. leaf litter) (Bennett <i>et al.</i> , 2013), such that drought may disproportionately affect species dependent on these resources for nesting (Albright <i>et al.</i> , 2010b)	There is likely to be a lag in the response of species associated with nesting substrates affected by the drought because these substrates (e.g. shrub cover) take time to recover (Bennett <i>et al.</i> , 2013)
Foraging (diet and substrate)	Drought will differentially affect food resources (e.g. nectar, invertebrate abundance) and foraging substrates (e.g. canopy vs. ground cover; Bennett <i>et al.</i> , 2013), resulting in different rates of decline between broad foraging guilds	The rapidity of response to the breaking of drought will differ among food types (e.g. invertebrates vs. nectar), resulting in different rates of recovery between broad dietary guilds
Migratory status	Migratory species will respond most strongly to drought because their higher mobility allows them to avoid drought-affected regions (Albright <i>et al.</i> , 2010a,b)	Migratory species will respond more quickly to the end of drought due to their ability to make long-distance movements and their lack of dependence on <i>in situ</i> reproduction
Habitat	Species dependent on woodlands have undergone historic declines in the study region. Reduction in regional population size may cause woodland-dependent species to be more negatively affected by drought	Woodland-dependent species may respond less quickly to the end of drought due to historical declines and degradation of habitat
Geographic range	Species with geographic ranges associated with drier climates (e.g. semi-arid or arid zones) should be more able to cope with regional drying than species associated with mesic bioregions	Species associated with mesic bioregions may benefit disproportionately from the end of drought
Degree of conservation concern	Species that are already experiencing decline may be more vulnerable to the effects of extreme drought	Species experiencing decline may be compromised in their ability to respond positively to the end of drought

Here, $y_{i(l)j}$ is the number of times the species was recorded in transect i (within landscape/fragment l), during period j , v_{ij} is the number of surveys, and p_{ij} is the corresponding reporting rate, which was modelled on the log-odds scale as a function of: an overall mean reporting rate for the first period, α ; spatial random intercepts ε_b , ε_{fs} and spatially varying change parameters, which estimate the change in reporting rate between the first and second survey periods, δ_1^1 , and between the second and third periods, δ_1^2 . The change parameters were modelled hierarchically, with overall mean changes, Δ_1 and Δ_2 , and random variation among landscapes/fragments, $\sigma_{\delta_1}^2$ and $\sigma_{\delta_2}^2$. Note that $I_j > 1$ is a binary indicator variable with value 1 for surveys in the second and third periods, and $I_j = 3$ had value 1 for the third period only. We estimated the mean changes in reporting rate during the Big Dry Δ_1 , in response to the Big Wet Δ_2 , and over the full period of study, $\Delta_3 = \Delta_1 + \Delta_2$. For each species, we calculated posterior probabilities that reporting rates declined, $\Pr(\Delta_n < 0)$, or increased $\Pr(\Delta_n > 0)$, during each period. We considered posterior probabilities > 0.9 to be strong evidence of a change in mean reporting rate (decrease or increase).

Mean reporting rate and change parameters were assigned independent normal prior distributions: $\alpha \sim N(0, 100)$, $\Delta_n \sim N(0, 1)$. Random-intercept parameters were assigned exchangeable normal prior distributions ($\varepsilon_l \sim N(0, \sigma_l^2)$), with

uniform priors on the corresponding standard deviations, $\sigma_l^2 \sim U(0, 2)$. Standard deviations for random-slopes parameters $\sigma_{\delta_1}^2$ and $\sigma_{\delta_2}^2$ were assigned more constrained uniform priors, namely $U(0, 1)$.

We used Bayesian multilevel analysis of variance (Gelman, 2005; Qian & Shen, 2007) to partition variation in estimated trends Δ_1 , Δ_2 and Δ_3 , and among ecological traits. The model for the trend estimate for species s in survey programme r was: $\Delta_{sr} = \beta_0 + \sum_{g=1}^6 \beta_{j(s)}^g + \text{species}_s + \text{survey program}_r + \varepsilon_{sr}$, where β_0 is the overall mean trend, β_j^g is the estimated effect (mean deviation) associated with level j (e.g. nectarivore) of trait g (e.g. diet), and species and survey programme (i.e. fragment or landscape surveys) are random effects (note that the residual error $\varepsilon = \text{survey programme} \times \text{species variation}$). The coefficients for all levels of a particular trait were assigned exchangeable normal prior distributions; $\beta_j^g \sim N(0, \sigma_g^2)$, and the finite population standard deviation of each 'batch' of coefficients, $\text{SD}(\beta_j^g)$ was used as an estimate of the 'variance component' for that trait (Gelman, 2005).

All models were estimated using WinBUGS (Spiegelhalter *et al.*, 2003). Posterior distributions were sampled with three independent chains of 10,000 iterations each, after 5000 iteration burn-in periods. We examined chain histories and Gelman-Rubin diagnostics to check for adequate mixing and convergence.

RESULTS

The Big Dry

In the fragment programme, 42% of species (41 of 98 species) declined during the Big Dry (i.e. had substantially lower reporting rates in 2004–05 vs. 1995–97), whereas only 6% of species increased (Fig. 3a). In the landscape programme, 62% of species (82 of 132 species) declined during the Big Dry (i.e. 2006–07 vs. 2002–03), compared to 2% of species that increased substantially (Fig. 3d).

The Big Wet

For the fragment programme, 21% of species increased relative to their reporting rates during the Big Dry. However,

27% of species declined, which included some species that had previously not declined and already-declining species that declined further during this period (Fig. 3b). For the landscape programme, 29% of species increased substantially during the Big Wet compared with the Big Dry (Fig. 3e), while 14% of species declined despite the onset of the Big Wet (Fig. 3e).

Long-term change

Some 54% of species in the fragment programme had substantially lower reporting rates during the Big Wet compared to *before* the Big Dry (Fig. 3c). Only 18% of species increased substantially over that period. In the landscape programme, 55% of species had substantially lower reporting rates during the Big Wet compared with the initial surveys

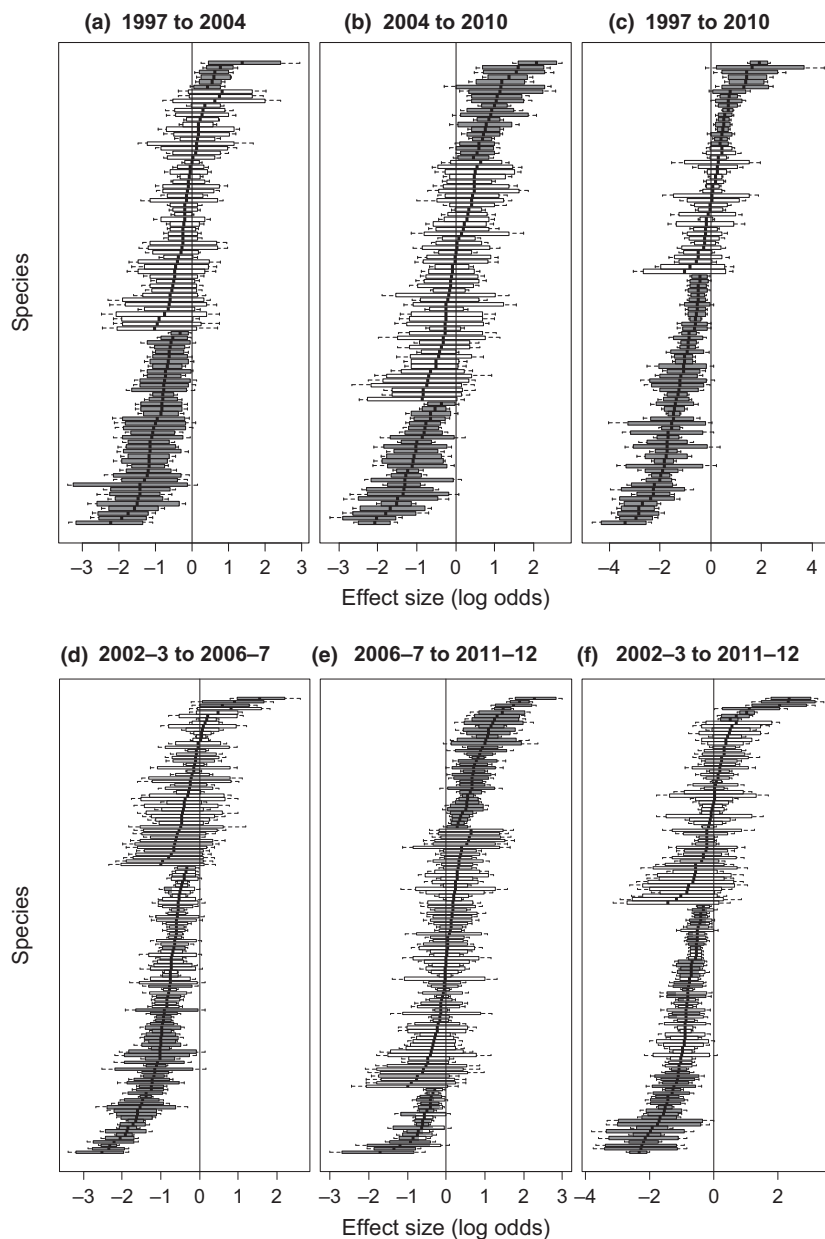


Figure 3 Ranked changes in the reporting rate (log odds) of bird species derived from Bayesian logistic regression, from the fragment programme, (a) 1997 vs. 2004 (b) 2004 vs. 2010 and (c) 1997 vs. 2010, and the landscape programme; (d) 2002–2003 vs. 2006–2007, (e) 2006–2007 vs. 2011–2012, and (f) 2002–2003 vs. 2011–2012. Horizontal bars show posterior distributions of change coefficients (log-odds transformed reporting rates) for each species: dark line = posterior median; bars extend to 90% credible intervals; dashed lines extend to 95% CIs. Grey shading indicates a change in reporting rate with > 90% certainty, white bars indicate < 90% certainty.

conducted early in the Big Dry (Fig. 3f). Only 5% of species increased substantially over that period.

Consistency between survey programmes

Widespread declines in reporting rate, in which species declined in both the landscape and fragment data sets over the entire period, were recorded for 43% (41 of 95) of species (Table 3). Widespread decliners included the fuscous honeyeater *Lichenostomus fuscus*, yellow-tufted honeyeater *Lichenostomus melanops*, musk lorikeet *Glossopsitta concinna*, eastern yellow robin *Eopsaltria australis*, restless flycatcher *Myiagra inquieta*, superb fairy-wren *Malurus cyaneus* and white-bellied cuckoo-shrike *Coracina papuensis*. There was weaker widespread decline for 24% (23 of 95) of species, with declines in only one or other programme (Table 3). Only the painted buttonquail *Turnix varius* and the yellow-faced honeyeater *Lichenostomus chrysops*, consistently increased over the entire period in both programmes.

Another 8% (8 of 95) of species increased in one but not the other programme (Table 3). There were opposing responses between the two programmes for some species, such as the Australian magpie *Cracticus tibicen*, brown treecreeper *Climacteris picumnus*, galah *Eolophus roseicapilla* and red wattlebird *Anthochaera carunculata*.

Species' resistance and resilience

For the fragment programme, of the species that declined during 1997–2004, 34% (14 of 41) of species declined even further from 2004 to 2010; for the landscape programme, of the species that declined between 2002 and 2006, 15% (12 of 82) showed further declines from 2006 to 2011. However, of those species that initially declined in the fragment (41) and landscape (82) programmes, 76% (31) and 78% (64), respectively, had net declines over the entire period. Of species that declined during the Big Dry, 20% of species for the fragment programme (8 of 41) and 35% of species for the landscape

Table 3 Summary of net changes in reporting rates in the fragment- and landscape programmes over the entire survey period (1995–1997 to 2010–2011 and 2002–2003 to 2011–2012, respectively). Species were characterized according to ecological traits relating to their vulnerability to habitat loss and fragmentation, foraging and nesting guilds, mobility, conservation concern (Radford & Bennett, 2005) and geographic distributions (Blakers *et al.*, 1984). Results for the fragment programme are shown first. ‘–’ denotes decrease; ‘0’ denotes no evidence of change; ‘+’ denotes increase (e.g. –/– = a decline in both the fragment and landscape programmes)

Classification	Class	Total	–/–	–/0	0/–	0/0	+/0	0/+	+/+	–/+	+/–
Habitat	Open-country	11	4	1	2	1	0	0	0	0	3
Habitat	Open-tolerant	26	11	3	5	3	3	1	0	0	0
Habitat	Woodland-dependent	58	26	7	5	7	3	1	2	1	6
Foraging zone	Aerial	8	6	0	1	1	0	0	0	0	0
Foraging zone	Bark	4	2	0	1	0	0	0	0	0	1
Foraging zone	Canopy	31	16	4	1	1	3	0	0	1	5
Foraging zone	Ground	46	16	6	8	8	3	1	1	0	3
Foraging zone	Low shrubs	2	0	0	1	1	0	0	0	0	0
Foraging zone	Tall shrubs	4	1	1	0	0	0	1	1	0	0
Food	Frugivore	3	1	2	0	0	0	0	0	0	0
Food	Insectivore	50	21	3	7	7	4	2	0	1	5
Food	Nectarivore	16	10	2	0	0	1	0	1	0	2
Food	Raptor/vertebrate	14	5	2	4	2	1	0	0	0	0
Food	Granivore	12	4	2	1	2	0	0	1	0	2
Nesting	N/A	1	1	0	0	0	0	0	0	0	0
Nesting	Burrow	3	2	0	0	0	0	0	0	1	0
Nesting	Ground	6	2	1	1	0	0	1	1	0	0
Nesting	Hollows	18	9	2	2	3	0	0	0	0	2
Nesting	Shrub/canopy	63	27	7	8	8	5	0	1	0	7
Nesting	Parasite	4	0	1	1	0	1	1	0	0	0
Conserv. concern	No	69	30	7	10	4	5	2	1	1	9
Conserv. concern	Yes	26	11	4	2	7	1	0	1	0	0
Mobility	Migrant	18	8	2	2	2	1	2	0	0	1
Mobility	Itinerant	13	7	2	0	1	0	0	1	0	2
Mobility	Resident	64	26	7	10	8	5	0	1	1	6
Distribution	Dry	20	9	3	2	3	1	0	0	0	2
Distribution	Mesic	7	5	1	0	0	0	0	0	0	1
Distribution	Widespread	68	27	7	10	8	5	2	2	1	6
Totals	–	95	41	11	12	11	6	2	2	1	9

programme (29 of 82) increased in the Big Wet, although 13% (1 of 8) and 59% (17 of 29) of those species declined overall (2010–2012 compared with 1997–2002). Species that had low resistance but high resilience in both programmes were the black-faced cuckoo-shrike *Coracina novaehollandiae* and jacky winter *Microeca fascians*, both of which declined in the Big Dry and then recovered or overshot their initial reporting rates in the Big Wet. The majority of resistant species that were unchanged or increased in response to the Big Dry subsequently were unchanged in the Big Wet, while 21% of resistant species in the fragment data set (Fig. 4a) and 14% in the landscape data set declined (Fig. 4b).

Ecological traits

There were few relationships between resistance or resilience and ecological characteristics such as primary habitat, foraging zone, feeding or nesting guild, broad distribution or level of conservation concern (Table 3, Fig. S1 in Supporting Information). During the Big Dry, trends for nectarivores were more negative on average than trends for other feeding guilds (Table 3, Fig. S1). Net trends over the whole period tended to be more negative for species of conservation concern (Fig. S1). There were no consistent trait effects related to resilience (Fig. S1).

DISCUSSION

Predicting how a biota will respond to the increased frequency and intensity of climatic extremes that are projected to occur with climate change is contingent upon an understanding of the species' resistance and resilience to such events. Birds in the much modified box and ironbark ecosystem generally displayed poor resistance to protracted drought, the Big Dry, and poor resilience during the Big Wet. By the end of the Big Dry, there was a 42–62% reduction in the reporting rates of diurnal land-bird species in the region, but only about a quarter of species subsequently recovered during the Big Wet. Declines were on-going for 76–78% of species with low resistance to the Big Dry because these species were still in decline after the release of the drought pressure when compared to their initial reporting rates. Species' resistances and resiliences were weakly related, and declines were not strongly related to species' traits.

Diminished resistance and resilience

Which factors are likely to have led to the low levels of both resistance and resilience of the avifauna to the Big Dry? First, although the drought broke, many of its effects persisted. Bennett *et al.* (2013) documented a drought-induced decline

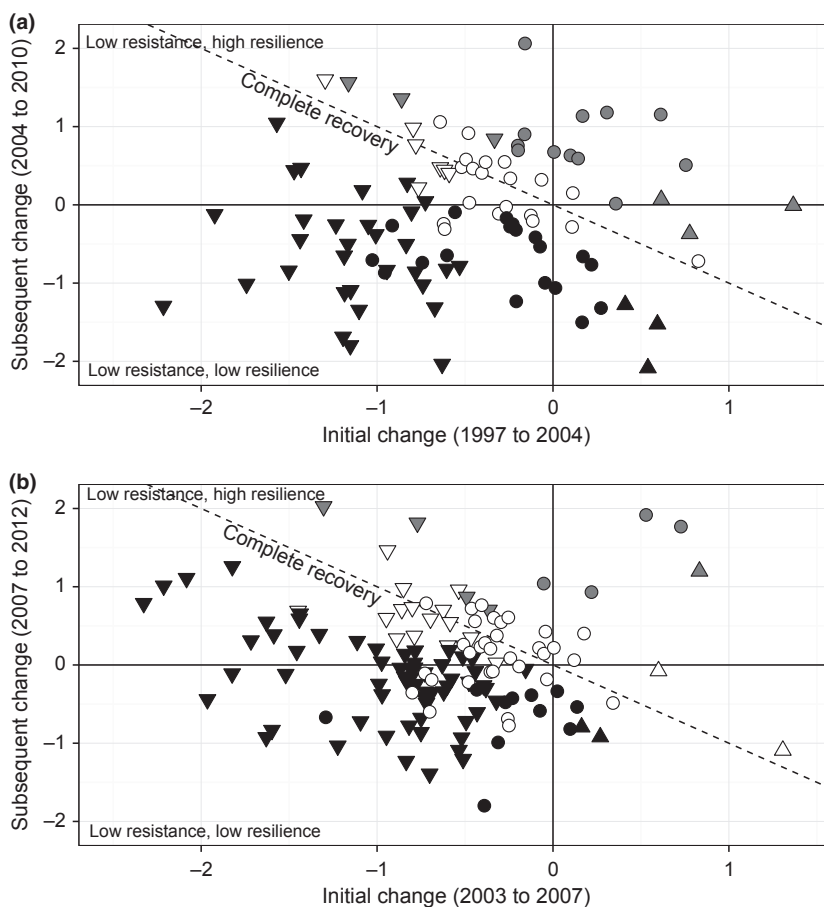


Figure 4 Comparison of species-level coefficients for two time periods in both the fragment (a) and landscape (b) survey programmes. Conceptually, if recovery were complete all species would fall along the dashed 'one-to-one' line. Downward triangles show species that – declined from first to second period (with > 90% certainty); upward triangles – increased from first to second period (with > 90% certainty); circles – no substantial difference between first and second period (< 90%); black – substantially lower in third survey period than first (90% certainty); grey – substantially higher in third survey period than first (90% certainty); open – no substantial difference between first and third period (< 90%).

in vegetation, including the deterioration of many resources exploited by birds. The extensive loss of canopy, litter and shrub cover in the drought (Bennett *et al.*, 2013) is a decline in habitat quality for many species. The regeneration of many of these vegetation attributes may take years or even decades (Vesk *et al.*, 2008), so that birds' recoveries, if any, from drought are likely to be delayed.

Second, climate change may amplify pressures on species in much modified regions. Fragments of native vegetation in human-dominated landscapes are interspersed with tracts of land largely unsuitable for woodland birds and movements between populations of species that depend on native vegetation are impeded (Opdam & Wascher, 2004). Elevated water and heat stress associated with fragmented vegetation may increase physiological stresses on birds (McAlpine *et al.*, 2009), leading to increased mortality (McKechnie & Wolf, 2010) or reduced recruitment (Stevenson & Bryant, 2000).

Third, clearance of native vegetation is biased towards more productive parts of the landscape (Etter *et al.*, 2006). Consequently, larger remnants in the region occur on less fertile, drier soils (ECC, 2001). More productive parts of the landscape are likely to be pivotal in providing opportunities for resistance for birds by reducing the impacts of heat stress, water loss and food availability; and resilience, by acting as refuges for *in situ* survival and, therefore, recovery (Mackey *et al.*, 2012).

Last, recovery may be on-going and we may have captured only the beginnings. Our surveys monitored avifauna during the first year of the drought-breaking rains (the fragment surveys), and 1–2 years after the drought broke (the landscape surveys). Several breeding seasons may be required to reverse the long-term declines associated with the Big Dry. Despite a full breeding season having passed before surveys commenced in the landscape programme, recovery was modest and similar to that of the fragment programme. Declines for many species were continuing. Given the predicted increase in the frequency of prolonged drought (Cai *et al.*, 2014), interrupted by shorter, more intense periods of precipitation (IPCC, 2013), and the low reproductive rates of many Australian passerines (Yom-Tov, 1987), it will be of great concern if species do not have time to fully recover before the start of the next extended dry period. Another El Niño drought in south-eastern Australia is predicted for 2014 (Ludescher *et al.*, 2014). Therefore, on-going surveys to determine future trajectories of recovery or decline are crucial.

Resistance vs. resilience

The relationship between resistance and resilience indicates the degree to which species can recover following the release of a pressure. A strong inverse one-to-one relationship between resistance and resilience would occur if species-level recovery were complete. That is, species that declined the most – those having lowest resistance – need to be the same species that 'bounce back' fastest, indicative

of high resilience. We found little evidence for such a relationship.

The lack of a strong relationship between resistance and resilience perhaps is unsurprising given the limited period for recovery post-drought (a maximum of two breeding seasons between the drought breaking and avifauna surveys). The ability to bounce back over a short-time interval is dependent on high reproductive rates, particularly for species with low resistance, because their recovery must outpace other species for a strong negative relationship to be realized. Australian birds, particularly passerines, typically have low reproductive rates (Yom-Tov, 1987), so that recovery may take considerable time. However, even in taxonomic groups with the biological potential for rapid reproductive responses, such a bounce back during the Big Wet failed to materialize (e.g. anuran amphibians; Mac Nally *et al.*, 2014). A large proportion of bird species in our study showed no signs of recovery, and many continued to decline.

Ecological traits

The resistance of species to the Big Dry had little relationship to species' ecological traits. These results differ from other studies documenting change in avifaunas due to drought (Albright *et al.*, 2010a; Jiguet *et al.*, 2011) and heat (Julliard *et al.*, 2004), which reported greater trait-specific differences. That the Big Dry was an interacting ramp (temperature) and press (low rainfall) event of unprecedented severity in the instrumental records suggests that resistance may be a function not only of a species' ecological traits but also of the intensity and type of the pressure. The lack of a strong trait signature in the declines points to a common, widespread mechanism, or that traits mediate responses in a more complex way (e.g. only in some environments or for some resources).

One trait that was related to resistance was diet. We found a greater reduction in nectarivore species during the drought, which coincided with much-reduced flowering, with complete failure of flowering in some years (Mac Nally *et al.*, 2009). The Big Wet of 2010–2011 appeared to induce substantial eucalypt flowering in the study region (Bennett *et al.*, 2014a), but the nectarivores did not show disproportionately higher resilience. Resource tracking by highly mobile nectarivores still incurs energetic costs, foregone breeding opportunities and greater mortality (Mac Nally *et al.*, 2009). Therefore, even highly mobile species may reach a condition in which recruitment in increasingly rare wet years is unlikely to 'repay' the accumulated costs associated with the more frequent dry years, resulting in on-going decline.

Management implications

To improve the long-term viability of the region's avifauna, conservation management actions should be targeted at improving ecosystem resistance and resilience. Vegetation degradation was greater in smaller forest fragments than in

larger remnants during the Big Dry (see Bennett *et al.*, 2013), which has been linked to avifaunal declines (J.M. Bennett, R.H. Clarke, G.F.B. Horrocks, J.R. Thomson & R. Mac Nally, unpublished data) and reduced avian recruitment (Bennett *et al.*, 2014b). Increasing the extent of tree cover regionally and particularly on fertile soils may improve the capacity of existing remnants to act as refugia where species can survive severe drought. Increasing habitat area and reducing degradation may limit colonization by hyperaggressive spatially dominant birds, such as the noisy miner (Bennett *et al.*, 2014a), which has been linked to reductions in bird diversity across eastern Australia (Mac Nally *et al.* 2012).

GLOBAL IMPLICATIONS

Climate change and increases in the frequency and intensity of extreme events may induce widespread biodiversity loss through the degradation of habitats, which may exacerbate pressures associated with land-use change due to greater heat and water stress in much modified landscapes (McAlpine *et al.*, 2009). Differences between species' resistance to extreme climatic events and their resilience during intermittent periods of more benign climatic conditions may reshape assemblages. Rapid variations in climate are expected to alter assemblages to consist of greater numbers of generalized species that are less reliant on extensive areas of native vegetation, though our results indicate that even species with these characteristics are not necessarily immune to the effects of more severe climatic extremes. Increases in the duration and frequency of severe drought events may favour the few resistant species that are able to monopolize booms and busts in resources.

Even under the more optimistic greenhouse-gas emissions scenarios, which are unlikely, the frequency and intensity of climatic extremes will increase in many regions of the world (IPCC, 2013). There is evidence of increases in the frequency of precipitation extremes in North America, Europe, southern Africa and Asia (Knapp *et al.*, 2008). Our system is a model for other regions undergoing rapid variations in climate. Extreme climatic events may produce some of the most dramatic effects on populations and may render populations less resistant to other pressures (e.g. invasive species) (Mantyka-Pringle *et al.*, 2012).

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SUPPORTING INFORMATION

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

Figure S1 Boxplots showing the sum of species reporting rate responses within guilds between the early and later stages of the Big Dry, between the later stages of the Big Dry and the Big Wet, and between the early stages of the Big Dry and the Big Wet.

BIOSKETCHES

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