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High-productivity vegetation is important for lessening bird declines during prolonged drought

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Abstract

1. Locations in which ecological assemblages show high resistance to climate pressures, such as drought, are likely to be important refuges for biota in changing climates. We asked whether environmental characteristics of locations were associated with the capacity of bird assemblages to withstand prolonged drought.

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2. We used a multi-species index to quantify trends in bird assemblages during a 13-year drought at >500 locations (>18,000 surveys) in the Murray-Darling Basin, south eastern Australia, using data from the Atlas of Australian Birds. We investigated whether the resistance of bird assemblages was associated with: (1) vegetation structure; (2) vegetation productivity (vegetation greenness); (3) landscape context (patch size, landscape vegetation cover); or (4) physical environment (elevation, terrain, topography, availability of surface water).
3. Vegetation productivity, measured by vegetation greenness (Normalized Difference Vegetation Index), was the only potential predictor with strong evidence of an effect, and was positively associated with the index of drought resistance. There was little evidence that variables characterising landscape context, vegetation structure or the physical environment of sites were associated with drought resistance of bird communities.
4. *Synthesis and applications.* Bird assemblages in locations with high vegetation greenness are more resistant to severe drought. Prioritizing conservation investments in areas with locally high vegetation productivity is likely to be an effective strategy for increasing the resistance of bird assemblages to extreme drought, especially in areas where mean productivity is relatively low, such as arid and semi-arid regions. Remotely sensed vegetation greenness may be a promising source of information for identifying drought refuges for birds and possibly other biota.

Keywords: birds, climate change, refuge, refugia, drought, NDVI, species resistance, vegetation productivity, vegetation greenness, habitat characteristics

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1 **Introduction**

2 Climate change is a key driver of biodiversity change (Bellard *et al.* 2012). Increases
3 in the frequency and severity of climate extremes, such as drought, heat-waves and
4 extreme weather events, may pose a greater threat to ecosystem function than gradual
5 increases in mean temperature or aridification (Parmesan, Root & Willig 2000;
6 Jentsch & Beierkuhnlein 2008). Climate extremes may have severe local effects on
7 ecosystems, and it is difficult to manage pressures of climate change at local or even
8 regional scales. Strengthening the capacity of local ecosystems to withstand climate
9 extremes such as drought ('resistance' = the maintenance of positive or stable
10 population trends, or less severe declines, compared to other locations) is likely to be
11 a key management strategy for minimizing the adverse effects of climate change on
12 biota (Nimmo *et al.* 2015).

13 Drought is occurring with increased frequency, severity and extent in many
14 parts of the world (Sheffield & Wood 2008), and poses a major threat to many
15 ecosystems (Mitchell *et al.* 2014). Drought reduces resource availability for animals,
16 including food, shelter and nesting resources and xeric climate conditions place
17 physiological pressures on individuals (Albright *et al.* 2010). Locations in which biota
18 show resistance to drought are likely to be important climate refuges. Identifying
19 environmental characteristics that affect the resistance of animal assemblages
20 contributes important information to two approaches for mitigating the effects of
21 climate extremes: (1) predicting and protecting those locations that are likely to be
22 resistant to climate extremes; and (2) identifying environmental variables that might
23 be manipulated to improve the resistance of the resident biota (Nimmo *et al.* 2015).

24 There are four main types of environmental variables that may affect the
25 resistance of animal assemblages to climate pressures by influencing abiotic and
26 microclimatic conditions or resource availability: (1) vegetation structure; (2)
27 vegetation productivity; (3) landscape context; and (4) the physical environment.

28 Locations in which vegetation is in better condition may be more likely to
29 sustain populations through climate extremes, such as drought (Mac Nally *et al.*
30 2014). Vegetation structure affects the local availability of food and nesting resources
31 and micro-refuges, which affect population vital rates (Selwood, Mac Nally &
32 Thomson 2009). Vegetation productivity may affect drought resistance of animal
33 assemblages because more-productive ecosystems have more food and habitat
34 resources and so, support more individuals and more species (Hurlbert 2004). Low-

35 productivity ecosystems, such as arid and semi-arid ecosystems, may be more
36 vulnerable to resource declines caused by low rainfall and drought (Weltzin *et al.*
37 2003, Holmgren *et al.* 2006). Analogues of vegetation productivity can be estimated
38 by remotely sensed measures of vegetation greenness, such as the Normalized
39 Difference Vegetation Index (NDVI) (Wang *et al.* 2004), which has been linked to
40 resource quality and the abundance and dynamics of many groups of animals,
41 including birds (Pettorelli *et al.* 2005; Pettorelli *et al.* 2011).

42 Landscape context may affect the ability of fauna to withstand drought,
43 especially for mobile taxa such as birds. Fragmented vegetation may be more
44 susceptible to drought-induced degradation (Bennett *et al.* 2015), while ready access
45 to food resources in the surrounding landscape may increase the capacity of animals
46 to survive hot, dry periods (Bennett *et al.* 2014). Last, the physical environment
47 consists of the abiotic elements that influence microclimatic conditions and water
48 availability of ecosystems, which can affect biotic resistance. For example, gullies
49 provide more-sheltered and more-mesic microclimates than nearby ridges, which may
50 protect individuals from climate extremes (Mac Nally, Soderquist & Tzaros 2000).
51 Ecosystems with locally low water availability (e.g., hilltop or range ridges), or
52 regionally low water availability (e.g. arid climate zones), may be particularly
53 vulnerable to drought because they are already water-limited, while wetter locations,
54 such as those with high water retention or sites in mesic climate zones may have
55 greater capacity to withstand drought (Weltzin *et al.* 2003).

56 We used a multi-species index based on trends in the occurrences of
57 drought-declining bird species to quantify the resistance of bird assemblages to a
58 prolonged drought, the 'Big Dry', at >500 locations in the Murray-Darling Basin,
59 southeastern Australia. The Big Dry (1997 – 2010), was the most severe drought in
60 the instrumental record in southeastern Australia (Verdon-Kidd & Kiem 2009) and
61 had profound effects on bird assemblages, with widespread declines in all guilds
62 (Bennett *et al.* 2014; Selwood *et al.* 2015a; Selwood *et al.* 2015b). The relative
63 resistance of bird species to the Big Dry appeared to be unrelated to species'
64 ecological, biological and life-history traits, which suggested that differences in the
65 responses of birds may be driven by extrinsic factors rather than intrinsic traits
66 (Bennett *et al.* 2014; Selwood *et al.* 2015a; Selwood *et al.* 2015b). Prolonged
67 droughts are expected to become more frequent in the region (Timbal *et al.* 2015), so
68 identifying drought refuges is vital. We focused on birds as exemplars because they

69 are highly mobile, and many species can respond to spatial variation in conditions at
70 regional scales. We investigated whether site characteristics are associated with the
71 resistance of bird assemblages to drought by relating bird-assemblage resistance to:
72 (1) vegetation structure; (2) vegetation productivity; (3) landscape context; and (4) the
73 physical environment. We expected that the following conditions would increase the
74 resistance of bird assemblages to the drought:

- 75 1. Local availability of ecological resources (measured by ground, shrub
76 and tree cover, plant species diversity and fallen timber);
- 77 2. High productivity (measured by using vegetation greenness);
- 78 3. Potential availability of resources in the surrounding landscape
79 (measured by patch size, landscape vegetation cover); and
- 80 4. Sheltered landscapes with high water availability (measured by
81 elevation, terrain, topography, surface water, distance to permanent
82 water).

83 **Materials and Methods**

84 *Bird surveys*

85 We used bird-survey data from BirdLife Australia's New Atlas of Australian Birds
86 program, specifically, from the standard 2-ha/20-min surveys, from January 1998 to
87 December 2009 in the Murray-Darling Basin (Barrett *et al.* 2003). We used sites at
88 which vegetation structure and cover data at the survey location had been recorded by
89 bird surveyors on a standard 'habitat form' (Table 1; BirdLife Australia 2012). We
90 included only those sites that were surveyed for ≥ 4 years. We considered this a
91 minimum period for detecting trends because other research in the region has detected
92 changes in bird assemblages during the Big Dry in a 4-yr period (Haslem *et al.* 2015).
93 We excluded sites that had incomplete information on site coordinates (accuracy >100
94 m), vegetation variables (see *Site characteristics*) or that had been surveyed <10
95 times. The resulting data were for 546 sites with 18,306 bird surveys (mean number
96 of surveys per site = 24.6, standard deviation = 22.8) (Fig. 1).

97 *Climate data*

98 We obtained spatial rainfall and temperature data (modeled at 500-m resolution) for
99 the survey years (Bureau of Meteorology (Australia) 2015b; Bureau of Meteorology
100 (Australia) 2015a). We calculated mean annual temperature and rainfall anomalies,
101 compared to the Australian Bureau of Meteorology's standard historic baseline of

102 1961–1990, at each site, in each year of the study using QGIS (QGIS Development
103 Team 2013).

104 *Multispecies drought-resistance index*

105 We developed a multispecies index to measure the resistance of drought-declining
106 bird assemblages at each site, which we call the ‘Drought Resistance Index’ (DRI).
107 This index resembles the multispecies indices used by Gregory *et al.* (2009) and
108 Stephens *et al.* (2016) to compile trends in groups of birds for which climate
109 suitability is either increasing or decreasing. Multispecies indices aggregate
110 information for groups of species into scalar measures. Although the absolute values
111 of multispecies indices are difficult to interpret on their own, indices are useful for
112 comparing composite trends in species in time or space in response to anthropogenic
113 pressures (Stephens *et al.* 2016).

114 The index was based on ‘drought-declining’ species. We defined these as
115 species with a mean negative temporal trend in occurrence (t_i , Table S1) during the
116 Big Dry. These trends were identified in a previous study that measured trends in the
117 occurrence of terrestrial bird species using data from > 39,000 surveys in > 28,000
118 sites in the Murray-Darling Basin (Selwood *et al.* 2015b). The widespread extent of
119 the drought meant that there were no concurrent ‘controls’ to determine whether
120 species declines were caused, or enhanced, by the drought. The spatially explicit Atlas
121 of Australian Birds commenced in 1998, so there were no comparable pre-drought
122 baselines. As such, it is possible that some of these ‘drought-declining’ species were
123 declining for reasons other than drought, such as lags caused by long-term (since the
124 mid-19th century) land-use change in the region (Ford 2011).

125 Each species was given a weighting such that highly drought-declining species
126 contributed more heavily to the DRI. We calculated the weight w_i for species i as:

$$w_i = \frac{(|t_i| - \min(|t_S|))}{(\text{range}(|t_S|))},$$

127 where: t_i is a species’ overall trend during the Big Dry [from Selwood *et al.* (2015b);
128 Supplementary Table S1] and S is the list of drought-declining species, including all
129 species with a mean negative trend, regardless of the statistical magnitude of t_i (i.e.,
130 the posterior probability that $t_i < 0$).

131 For each site j , we estimated temporal trends for each species i for the Big Dry
132 period. The model was $\text{probit}(p_{i,j}) = \alpha_0 + X_{i,j} \times \text{year}$, where: $p_{i,j}$ is the probability of
133 observing species i at site j in a single survey; α_0 is the intercept; and $X_{i,j}$ is the

134 temporal trend parameter, with *year* ranging from 1 (1998) to 12 (2009). We assumed
135 all trends were linear (Selwood *et al.* 2015b). Site trends were fitted using the *glm*
136 function in R (R Core Team 2015).

137 The DRI was calculated as the mean of $w_i \times X_{i,j}$ for all drought-declining species
138 at each site *j*, giving a composite indicator of species' trends at that site weighted by
139 species' drought sensitivities, independently of species richness. Larger values of the
140 DRI indicated greater drought resistance of drought-declining species. To be included
141 in the analysis, a site had to have had a minimum of ten surveys in the survey period,
142 and species had to have had at least two records.

143 To provide a measure of uncertainty in the DRI values, we generated 1000
144 bootstrapped samples of $\sum_{i=1}^n w_i \times X_{i,j}$ for each site, with replacement, from the set
145 of species present at site *j* (*n* = number of species present at site *j*) using the package
146 'boot' (Canty & Ripley 2015) in R. The standard deviation for each site was
147 calculated from the 1000 samples, and the precision calculated for the DRI of each
148 site. We tested for spatial dependence in the DRI with Moran's *I* using the 'ncf'
149 package (Bjornstad 2016) in R.

150

151 *Site characteristics*

152 1. Vegetation structure

153 We estimated vegetation structure from data recorded in Habitat forms of the New Atlas
154 of Australian Birds program (Table 1; BirdLife Australia 2012). Variables included
155 estimated cover and diversity of small shrubs, tall shrubs, trees and ground cover and the
156 amount of fallen timber (Table 1). While other variables were included on the Habitat
157 form, we included only variables that had near-complete data for all sites (< 10 sites
158 [1.8%] missing information for each variable) to maximize the number of sites included
159 in the analysis. The cover and diversity of tall and small shrubs were correlated ($r > 0.70$)
160 so we excluded all but small shrub cover because it was most highly correlated with all
161 three other shrub variables.

162 2. Vegetation productivity

163 We extracted the mean annual Normalized Difference Vegetation Index (NDVI) using
164 site coordinates to obtain an estimate of the average vegetation productivity of a site
165 (Table 1). The NDVI is strongly related to vegetation productivity, and links between
166 NDVI and the fraction of absorbed photosynthetic active radiation intercepted are
167 well documented (Pettoelli *et al.* 2005).

168 3. Landscape context

169 We measured the percentage cover of native vegetation to indicate resource availability in
170 the surrounding landscape for each site using 'raster' (Hijmans & van Etten 2013) in R
171 (Table 1). We used a 500-m radius because this scale previously has been shown to be a
172 good predictor of bird species response in the study region (Thomson *et al.* 2009). The
173 area of vegetation patches in which sites were located was obtained from Atlas of
174 Australian Birds Habitat forms (Table 1).

175 4. Physical environment

176 We used spatial information on elevation, topographic wetness index, frequency of
177 surface water presence, and distance to permanent water sources using site
178 coordinates and information on site terrain from habitat forms (Table 1) to
179 characterize the physical environment of sites. We obtained the mean annual aridity
180 of sites, but this was highly correlated with NDVI ($r = -0.79$), so we excluded it from
181 the analysis (Table 1). We included NDVI rather than aridity because we believed
182 that NDVI would be more directly linked to bird responses than aridity because NDVI
183 links vegetation productivity and hence probable resource availability to climate
184 (Pettorelli *et al.* 2005).

185

186 *Statistical analysis*

187 We used three approaches, which have differing capabilities, to investigate the
188 potential relationships between the DRI and environmental characteristics. First, we
189 used the flexibility of Bayesian multiple regression (BMR) to propagate the
190 uncertainties in the DRI and to accommodate possible spatial dependencies by
191 employing regional random effects. We used Bayesian model averaging (BMA) to
192 evaluate which variables were important predictors of the DRI. BMA is a useful way
193 to incorporate model-selection uncertainty (which predictors should be included?)
194 into inference and prediction in ecological models (Wintle *et al.* 2003). Last, we used
195 hierarchical partitioning to estimate the individual explanatory power of the predictors
196 identified in the BMR and BMA. For all approaches, we standardized (mean = 0,
197 standard deviation = 1) the predictors to make the ranges of all predictors comparable
198 and to assist in model convergence. The distributions of the retained predictors were
199 near normally or near uniformly distributed. All pairwise-correlations for retained
200 continuous predictors were ≤ 0.55 .

201

202 *Statistical analysis 1: Bayesian multiple regression*

203 The BMR model was fitted using JAGS (Plummer 2003) and the R2jags interface in
204 R (Su & Yajima 2015). The model was:

$$DRI_i \sim N(z_i, \sigma_{DRI_i}^2); z_i \sim N(\mu_i, \sigma^2); \mu_i = \alpha + \sum_{j=1}^P \beta_j X_{ij} + \rho_{R(i)}.$$
$$\alpha \sim N(0, \sigma^2 = 4); \beta_j \sim N(0, \sigma_\beta^2); \sigma, \sigma_\beta \sim U(0, 0.2).$$

205 Here, DRI_i is the estimated value for site i , with variance $\sigma_{DRI_i}^2$. z_i is the value of DRI
206 with uncertainty (bootstrapped precision) propagated, and is modeled as a function of
207 the mean μ_i and variance σ^2 . μ_i is a function on the intercept α [prior: $N(0, \sigma^2 =$
208 $4)$] and a linear combination of regression coefficients (β_j) and P site-specific
209 predictor values (X_{ij}). The β_j values have exchangeable priors with mean 0 and
210 variance σ_β^2 . Regional random effects (river catchments, derived from Geoscience
211 Australia 1997), $\rho_{R(i)}$, have exchangeable priors with mean 0 and variance σ_ρ^2 , where
212 $\sigma_\rho \sim U(0, 0.2)$.

213 Model fit was assessed using posterior predictive assessment (Gelman, Meng
214 & Stern 1996), which assesses measure of fit (PPfit) between the observed and fitted
215 values (sum of absolute deviations). The model is regarded as being plausible if 0.05
216 $< \text{PPfit} < 0.95$. We made inferences on the importance of predictors by measuring the
217 posterior probability distributions (PPD) of the β_j : if < 0.1 of the PPD for β_j were > 0 ,
218 then the predictor is regarded as having a negative association with the response; if $>$
219 0.9 of the PPD for β_j were > 0 , then the predictor is regarded as having a positive
220 association with the response (Kass & Raftery 1995).

221 *Statistical analysis 2: Bayesian model averaging*

222 We used Bayesian model averaging (BMA) to estimate the relationships between DRI
223 and the predictors. The software used, `bic.glm` in the BMA package (Raftery *et al.*
224 2015) in R, fits generalized linear models using the 'leaps and bounds' algorithm and
225 the Bayesian information criterion (BIC) approximation to Bayes factors (Hoeting *et*
226 *al.* 1999). `bic.glm` cannot propagate uncertainties in the response or handle spatial
227 random effects. We assumed a Gaussian errors model, which was checked and
228 supported by post-fitting assessments. We used the posterior probability that a
229 variable had a non-zero coefficient [$\text{Pr}(\text{inc})$] as a measure of the influence of that
230 variable on the DRI. We considered values of $\text{Pr}(\text{inc}) > 0.75$ to be strong evidence

231 that a given predictor variable influenced the DRI (Viallefont, Raftery & Richardson
232 2001).

233 *Statistical analysis 3: Hierarchical partitioning*

234 The two approaches above are useful for identifying potentially influential predictors
235 but do not provide a break-down of ‘explained variation’, so we used the hier.part
236 package in R (Walsh & Mac Nally 2003) to estimate the individual explanatory power
237 of the predictors identified in the BMR and the BMA. hier.part also cannot propagate
238 uncertainties in the response or handle spatial random effects.

239

240 **Results**

241 *Climate*

242 Annual rainfall was below average at most sites (median site anomaly < 0) for 10 of
243 the 13 years of the Big Dry (Fig 2a). The mean cumulative rainfall anomaly of sites
244 for the study period was –882 mm relative to the baseline average for 1961–1990.

245 Mean annual temperature was consistently above average at most sites (median site
246 anomaly > 0) for all of the Big Dry (Fig. 2b).

247 *Drought resistance*

248 Eighty-nine species were identified as drought-declining. The number of drought-
249 declining species recorded at each site, and hence, the number of species contributing
250 to a site’s DRI, ranged from 2–50, with a mean of 17.3 and standard deviation of 8.0.
251 The majority of species had weightings <0.200, with the mean weighting being 0.167
252 (Supplementary Fig. S1, Table S1). The distribution of site values of DRI was near
253 normal (Fig. S2), ranging from –0.027 to 0.021, with a mean of –0.001 and standard
254 deviation of 0.005. There was little evidence for spatial autocorrelation in the DRI
255 (Fig. S3).

256 *Relationships between the DRI and predictors*

257 The model fitted the data well for the BMR (PPfit = 0.42). The regression parameters
258 for four predictors were substantially different from 0, with DRI being associated
259 positively with NDVI and negatively with ground cover spread (clumped vs not
260 clumped), landscape cover, and small shrub cover (Table 2). The results for the BMA
261 identified only one important [Pr(Inc) > 0.75] predictor, NDVI (Table 2, Fig. 3). The
262 other three predictors identified from the BMR showed very little evidence of being
263 important (Pr(Inc) < 0.10, Table 2). The results of the hierarchical partitioning were
264 consistent with the BMA outcomes; NDVI had the majority of independent

265 explanatory power (Table 2). Given the strong relationship between DRI and
266 vegetation productivity (NDVI), we tested whether species weightings in the DRI
267 were related to their affinity to arid (i.e., low productivity) areas (from Selwood *et al.*
268 2017), but there was no significant relationship ($R^2 < 0.01$, Fig. S4).

269

270 **Discussion**

271 The most important site characteristic related to the resistance of bird assemblages
272 was vegetation productivity, indicated by vegetation greenness, with assemblages in
273 more-productive sites having greater resistance to prolonged drought. There was little
274 evidence that vegetation structural characteristics or landscape context affected the
275 resistance of bird assemblages, and measures of the physical environment showed no
276 association with the index of drought resistance.

277 Vegetation greenness, measured by NDVI, has been used successfully to estimate
278 resource quality, abundance and dynamics for many groups of animals, including
279 birds (Pettorelli *et al.* 2005; Pettorelli *et al.* 2011). It is likely that greener sites, with
280 more productive vegetation, had more resources that enabled bird populations to
281 persist, or decline less, in the face of the Big Dry, including food (seeds, fruit, nectar,
282 invertebrates), nesting materials, shelter and breeding substrates (Hurlbert 2004;
283 Berry, Mackey & Brown 2007). Although we did not find effects of gullies or water
284 availability *per se* on the DRI, these variables might be important at local scales
285 where relatively greater water availability and topographic sheltering may create
286 'ecosystem greenspots' (Mackey *et al.* 2012).

287 Vegetation productivity declines with aridity (Roderick, Berry & Noble 2000),
288 so aridity may be an important governor of bird-assemblage resistance to drought as a
289 driver of vegetation productivity. Arid ecosystems are more sensitive to declines in
290 rainfall (Weltzin *et al.* 2003), so higher aridity (and so, lower productivity) sites may
291 have experienced greater absolute or proportional declines in productivity during the
292 Big Dry, which could explain the reduced resistance in low-productivity landscapes.
293 The aridifying conditions of drought may have caused local extirpations at sites
294 located at the edge of species' climate-suitable distributions (Selwood *et al.* 2017). It
295 is also possible that the positive relationship between DRI and NDVI was influenced
296 by movement of birds from arid, low-productivity landscapes to more-productive
297 mesic regions, although we note that species that occur in arid areas of the Murray-
298 Darling Basin are no more likely to be nomadic than species that occur in more mesic

299 regions (Selwood *et al.* 2017). Arid zone birds did not experience larger regional
300 declines than other species, that is, arid zone species were not highly influential on the
301 DRI (Fig. S4), so it is unlikely that the intrinsic traits of birds that inhabit low-
302 productivity regions had an unduly large influence on the relationship between DRI
303 and NDVI.

304 Vegetation structure, landscape context and the physical environment
305 appeared to have little influence on the drought resistance of bird assemblages. The
306 variables that we used from the Atlas program (all vegetation structure variables,
307 patch size and terrain), were designed to be coarse, ordinal measures based on visual
308 estimates by volunteer bird observers (Table 1). These measures may not have been
309 sensitive enough to detect differences in habitat structure that affect bird responses
310 and there may have been much variability in the visual estimation methods used by
311 the bird observers and in the interpretation of the vegetation structural variables
312 recorded on the habitat forms. More-detailed and consistently measured aspects of
313 vegetation structure might reveal other relationships with bird resistance, which have
314 been documented elsewhere (Bennett *et al.* 2015). Similarly, finer measures of the
315 physical landscape derived from high-resolution elevation models may better
316 characterize the microclimate conditions of sites than the variables used here (Bennie
317 *et al.* 2008).

318

319 *Synthesis and applications*

320 Bird assemblages in locations with high vegetation productivity are more resistant to
321 severe drought. This suggests that prioritizing conservation investments in high-
322 productivity ecosystems might maximize the collective persistence of drought-
323 sensitive bird species. Sites with locally high vegetation greenness are likely to be
324 particularly important, especially in regions where mean productivity is relatively
325 low, such as arid and semi-arid regions. Vegetation greenness is higher at sites that
326 are topographically sheltered and that have more reliable water availability, such as
327 run-on areas (sites of more concentrated or reliable surface or subsurface water flow),
328 gullies, floodplains and riparian zones (Mackey *et al.* 2012; Selwood *et al.* 2016).
329 Protecting these sites, maintaining their vegetation productivity and condition through
330 the provision of environmental water (Horner *et al.* 2016), and engaging in ecological
331 restoration are likely to enhance the resistance of bird assemblages to the more-
332 frequent and severe droughts that are projected for this and other southern Australian

333 regions.

334 The generality of indices such as DRI is both an advantage and a limitation
335 because the needs of individual species may be overlooked. We suggest that applying
336 management actions to increase the DRI should not be done in isolation; monitoring
337 trends in component species, and employing management techniques that consider the
338 diversity of bird communities will be vital for ensuring the persistence of a
339 representative avifauna. An exclusive focus on preserving high-productivity sites may
340 result in the neglect of a substantial portion of the avifauna, especially if this approach
341 is employed at large spatial scales. Vegetation greenness is strongly correlated with
342 aridity, so although concentrating conservation resources on less-arid sites probably
343 would result in a higher average DRI, such an approach would likely favor
344 conservation of mesic avifauna at the expense of the conservation of arid and semi-
345 arid avifauna. Vegetation greenness has been used to identify ‘ecosystem greenspots’,
346 locations that may function as drought refuges, by maintaining relatively high
347 vegetation productivity (Mackey *et al.* 2012). Our findings suggest that vegetation
348 greenness may identify drought-resistant refuges for birds. Models that link remotely
349 sensed vegetation data to ground measurements of vegetation are potentially useful
350 for explaining animal responses to climate changes and for forecasting the effects of
351 future climate scenarios (Lada *et al.* 2014; Mac Nally *et al.* 2014). More-detailed
352 studies into the relationships between animal responses to drought, vegetation
353 greenness (including its temporal variability) and other site characteristics are likely
354 to be useful identifying locations that are critical for supporting resistant animal
355 assemblages.

356

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363

364

365 **Author contributions**

366

367 KS and RM conceived the study, KS and RM analysed the data, KS wrote the
368 manuscript with contributions from RM, RC and MM.

369

370 **Data accessibility**

371 Data available from the Dryad Digital repository. DOI:doi:10.5061/dryad.13p0s
372 (Selwood et al. 2017)

373

374 **Supporting Information**

375

376 Table S1: Drought-declining species trends in the Murray-Darling Basin during
377 the Big Dry

378

379 Figure S1: Histogram of species weights (w_i) for all species used to calculate the
380 drought resistance index

381

382 Figure S2: Histogram of drought resistance index values for the set of study sites.

383

384 Figure S3: Spatial correlogram of drought resistance index

385

386 Figure S4: Plot of species weights (w_i) in the drought resistance index against
387 their affinity with arid locations

388

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Table 1. Site characteristics tested as potential predictors of drought resistance in drought-declining bird assemblages. Asterisks indicate that information was obtained from the Atlas of Living Australia (2015), ‘^’ indicates variables that were excluded from analysis due to high correlation with other variables ($r > 0.70$).

| Variable categories | Site characteristic | Description | Source |
|-----------------------------|--|--|---|
| <i>Vegetation structure</i> | | | |
| | Small shrub cover (shrubs 0.5–2 m) | 0 = absent, 1 = some, 2 = many | Habitat forms (BirdLife Australia 2012) |
| | Small shrub diversity [^] | 0 = absent, 1 = one species, 2 = two or three species, 3 = > three species | Habitat forms |
| | Small shrub type | Categorical: exotic or native | Habitat forms |
| | Tall shrub cover (shrubs 2–8 m) [^] | 0 = absent, 1 = some, 2 = many | Habitat forms |
| | Tall shrub diversity [^] | 0 = 0 species, 1 = 1 species, 2 = 2–3 species, 3 = >3 species | Habitat forms |
| | Tree cover (trees > 8 m) | 0 = absent, 1 = some, 2 = many | Habitat forms |
| | Tree diversity | 0 = 0 species, 1 = 1 species, 2 = 2–3 species, 3 = >3 species | Habitat forms |
| | Ground cover | 0 = mostly bare, 1 = partly covered with grass/herbs, 2 = mostly covered | Habitat forms |
| | Ground cover spread (if present) | Classified as clumped / unclumped | Habitat forms |

| | | | |
|------------------------------------|--|---|--|
| | Fallen timber (fallen trees or branches > 2 m) | 0 = 0 pieces, 1 = 1–5 pieces, 2 = 6–15 pieces, 3 = >15 pieces | Habitat forms |
| <i>Vegetation productivity</i> | Vegetation greenness (NDVI)* | Mean annual Normalized Difference Vegetation Index for 2001–2006 | Bureau of Rural Sciences (Australia) (2007); Carroll et al. (2004) |
| <i>Landscape context</i> | Landscape cover | Percentage cover of native vegetation within a 500 m radius | Department of the Environment (2014) |
| | Patch size | Size of discrete vegetation patch that site is located within: 1 = <3 ha, 2 = 3– 10 ha, 3 = 11–30 ha, 4 = 31–100 ha, 5 = 101–400 ha, 6 = >400 ha | Habitat forms |
| <i>Physical environment</i> | Elevation* | m above sea level (log transformed) | Geoscience Australia (2001) |
| | Topographic wetness index* | $\ln(a/\tan B)$ where a is the upslope per unit contour length and B is the local slope | Williams (2010) |
| | Surface water* | Percentage of observations 1987–2014 of water from satellite imagery | Geoscience Australia (2015) |
| | Terrain | Gully or other (flat, slope, | Habitat forms |

| | | |
|------------------------------|--|-----------------|
| Distance to permanent water* | ridge) Euclidean distance to permanent natural water features | Williams (2010) |
| Aridity**^ | Annual mean aridity index | CSIRO (2010) |

Table 2 Summary of outcomes from the three analyses of the relationship between DRI and the predictor variables. PPD = posterior probability distribution, Pr(Inc) = probability inclusion in best models, PPfit = posterior predictive assessment fit, SD = standard deviation.

| Quantity | Ground cover spread | NDVI | Landscape cover | Small shrub cover |
|--|-----------------------|----------------------|-----------------------|-------------------|
| <i>Bayesian multiple regression (PPfit = 0.42)</i> | | | | |
| PPD | 0.07 | 0.99 | 0.03 | 0.03 |
| Estimate | -0.0002 | 0.0005 | -0.0004 | -0.0003 |
| SD | 0.0002 | 0.0002 | 0.0002 | 0.0002 |
| <i>Bayesian model averaging</i> | | | | |
| Pr(Inc) | 4 | 100 | 8 | 0 |
| Estimate | -1.1×10^{-5} | 1.1×10^{-3} | -3.1×10^{-5} | 0 |
| SD | 7.6×10^{-4} | 2.6×10^{-4} | 1.27×10^{-4} | - |
| <i>Hierarchical partitioning</i> | | | | |
| Independent % | 6 | 79 | 15 | <1 |

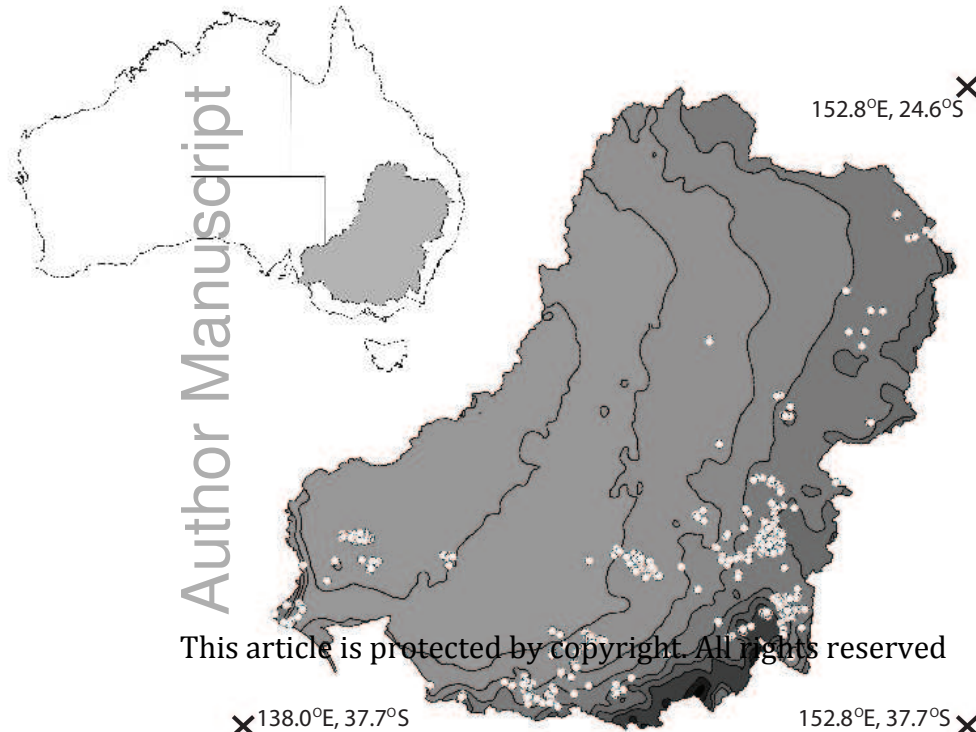
Figure legends

Figure 1. The study region of the Murray-Darling Basin, Australia (shaded grey, top left). Study sites are denoted by white circles on the enlarged map, with bands indicating long-term mean annual rainfall increasing from west (200–300 mm rainband) to east in 100-mm intervals.

Figure 2. Climate anomalies for the study sites over the Big Dry, (a) deviation of mean annual temperature from long-term average (1961–1990) in °C, and (b) deviation of total annual precipitation from long-term average in mm.

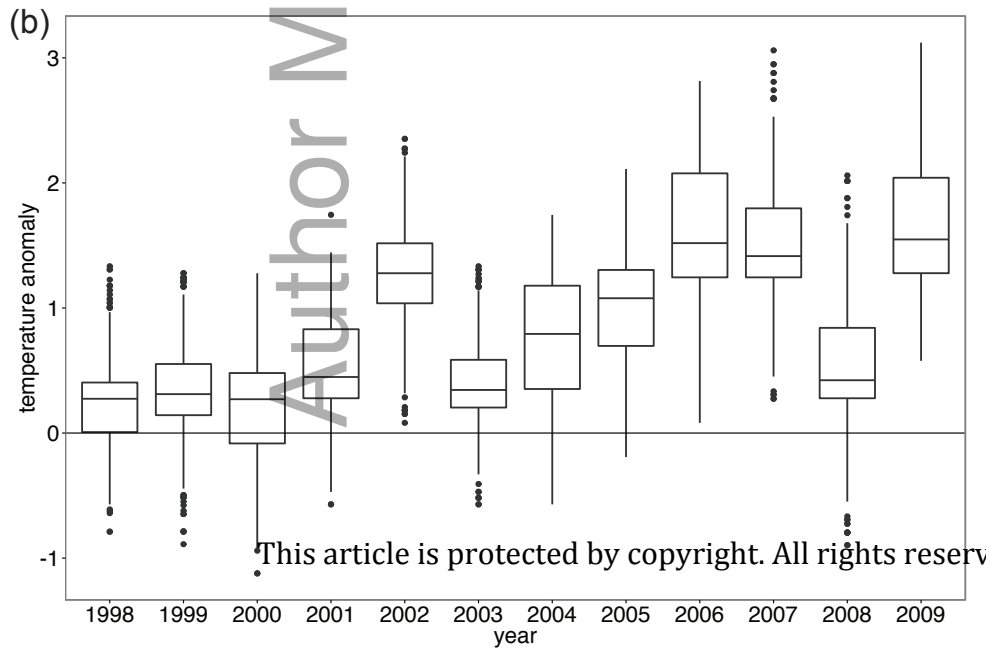
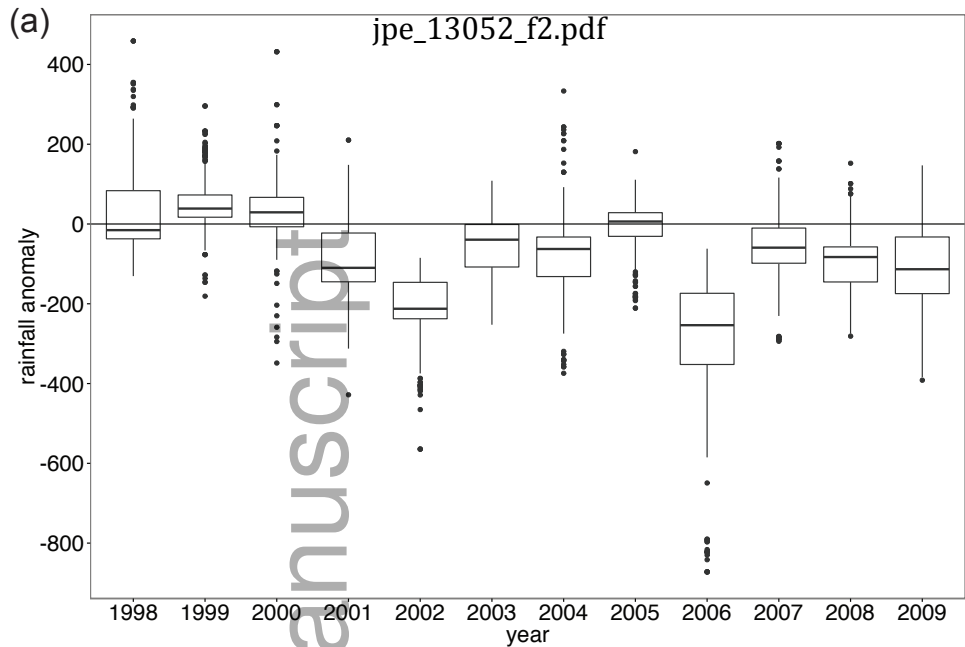
Figure 3. Plot of the drought resistance index (DRI) against the most important predictor, vegetation greenness (NDVI). Regression lines and lower and upper 95% confidence intervals are shown.

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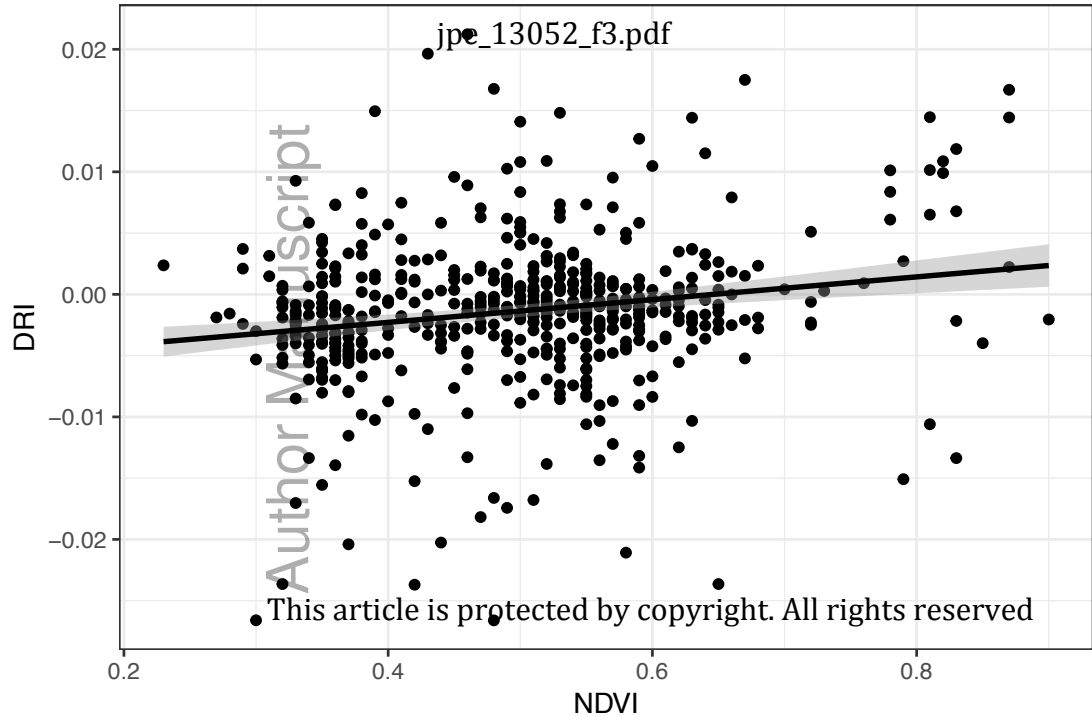


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