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1   **Tests of predictions associated with temporal changes in Australian bird populations**

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24   **Running Head**: Tests of predictions associated with temporal changes in bird populations

25 **ABSTRACT**

26 Global biodiversity loss is the cumulative result of local species declines. To combat

27 biodiversity loss, detailed information on the temporal trends of at-risk species at local scales

28 is needed. Here we report the results of a 13-year study of temporal change in bird occupancy

29 in one of the most heavily modified biomes worldwide; the temperate woodlands of south-

30 eastern Australia. We sought to determine if temporal changes in bird species were different

31 between three broad native vegetation types (old-growth woodland, regrowth woodland and

32 restoration plantings) and between species traits (body size, migratory status, rarity,

33 woodland dependency, or diet). We found evidence of decline for over a quarter of all bird

34 species for which we had sufficient data for detailed analysis (30 out of 108 species). In

35 contrast, only 14 species increased significantly. Temporal change of birds was linked to life-

36 history attributes, with patterns often being habitat-dependent. Nectarivores and large-bodied

37 birds declined across all vegetation types, whereas small-bodied species increased,

38 particularly in restoration plantings. Contrasting with patterns documented elsewhere,

39 resident but not migratory species declined, with this trend strongest in restoration plantings.

40 Finally, our analyses showed that, as a group, common birds tended to decline whereas rare

41 birds tended to increase, with effects for both most pronounced in restoration plantings. Our

42 results highlight the benefit of targeted restoration planting for some species, but also

43 demonstrate that many common species that have long-persisted in human-dominated

44 landscapes are experiencing severe declines.

45

46 **Keywords:** Woodland birds, south-eastern Australia, time-series data, life-history traits,

47 species declines and increases, conservation

INTRODUCTION

48

49 The earth is facing a major global extinction crisis with significant species losses forecast for

50 many groups of biota (Pimm et al. 2014; Ceballos et al. 2017). For example, data from the

51 (IUCN 2016) suggest that 13 % of the world's bird species might be facing extinction in the

52 next 50 years (Tilman et al. 2017). Global patterns of species extinction are, of course,

53 underpinned by local and regional trends in populations (e.g. Sanderson et al. 2006; Inger et

54 al. 2014), and detailed temporal studies of local and regional species are essential to

55 understand broader biodiversity changes. Such information is also critical to help better

56 determine those species in need of conservation interventions (Muir 2010) and, in turn, guide

57 associated investments in appropriate land use management such as landscape restoration

58 (Crouzeilles et al. 2016) or expanded reservation (Pringle 2017).

59 Globally, landscapes converted to agricultural land uses have suffered significant losses of

60 biodiversity (Tilman et al. 2017), including birds. The effects of agriculture on biodiversity

61 has been particularly profound in Australia (Williams and Price 2011) with Australian bird

62 biota under considerable pressure (Ford 2011). Detailed long-term studies are required to

63 determine which species are declining and/or are under threat in agriculture-dominated

64 environments. Yet, there are relatively few large-scale, long-term studies within the vast

65 majority of Australian agro-ecosystems that encompass many species (Lindenmayer et al.

66 2014). This shortfall inhibits examination of patterns of temporal change in Australian

67 avifauna, thus limiting our ability to identify species declines, or conversely, examples of

68 species recovery.

69 Here we report the results of a 13-year time series study of temporal change in bird

70 populations within the endangered temperate box gum grassy woodlands of south-eastern

71 Australia. This is an agriculture-dominated biome containing one of the most heavily

72 modified natural ecosystems globally, with more than 85% cleared or altered to create

73   grazing pastures and croplands for agriculture (Benson 2008). Yet, it maintains high

74   biodiversity value supporting over 170 bird species including more than 20 of conservation

75   concern (Lindenmayer et al. 2016b). There are long-held concerns about the status of

76   Australia's woodland birds (Ford 2011) due, in part, to substantial historical and ongoing

77   changes to their habitat. Extensive revegetation efforts through restoration plantings

78   (Lindenmayer et al. 2016a), as well as natural regeneration (Sato et al. 2016), have been

79   among the management responses to past losses of woodland cover. Native vegetation cover

80   in the Australian temperate woodland belt is now comprised of three broad structural kinds of

81   vegetation – old-growth woodlands, naturally regenerated regrowth woodland, and

82   restoration plantings. These kinds of vegetation are spatiotemporally dynamic, exhibit

83   marked differences in structure (Ikin et al. 2015) and represent different kinds of habitat for

84   distinct assemblages of birds (Lindenmayer et al. 2012a). On this basis, one of the objectives

85   of this investigation was to compare and contrast temporal changes in bird species in these

86   three broad structural vegetation types.

87   There is an increasing body of work relating patterns of landscape change to the functional

88   traits of species (Barnagaud et al. 2014). Some of this work has revealed that taxa with

89   particular kinds of attributes will respond more or less favourably over time to landscape

90   change in human-modified landscapes (e.g. Newbold et al. 2013; Lindenmayer et al. 2015).

91   We therefore tested a series of predictions about what life-history traits of species were

92   associated with temporal changes in birds. Specifically, we tested the following five

93   predictions:

94   **Prediction 1**. *That large-bodied species are more likely to decline than small-bodied species.*

95   Several studies elsewhere around the world have indicated that large-bodied species are more

96   extinction prone than small-bodied species in human-modified environments (e.g. Haddad et

97   al. 2015; Tilman et al. 2017). However, elsewhere in Australian woodlands, large-bodied

98   birds are more strongly associated with heavily modified and degraded agricultural

99   landscapes (Lindenmayer et al. 2012b) with several studies in Australia suggesting that many

100   birds of conservation concern are small-bodied taxa (Reid 1999; Montague-Drake et al.

101   2009). On this basis, we tested whether the temporal patterns in birds of different body size in

102   our long-term study were consistent with global patterns.

103   **Prediction 2**. *That migratory species are more likely to decline than resident species.* Several

104   studies have found that migratory species are at risk of decline and extinction due to a range

105   of factors including habitat loss (including along migration routes), climate change, and

106   hunting (Runge et al. 2015; Gilroy et al. 2016). By testing this prediction, we sought to

107   determine if the temporal patterns we observed were broadly consistent with those

108   documented in other parts of the world.

109   **Prediction 3.** *That rare species are more likely to decline than common species*. Many

110   studies of extinction proneness suggest that rare species are at particular risk of decline

111   (reviewed by (reviewed by Lindenmayer and Fischer 2006)) in part due to small population

112   sizes but also because they are often habitat specialists disadvantaged by human-induced

113   landscape change (Colles et al. 2009). However, recent work in Europe found the opposite

114   effect with more common species undergoing declines (Inger et al. 2014). Given this, we

115   tested whether the patterns of temporal change we observed mirrored those quantified

116   elsewhere such as in Europe.

117   We also tested a further two predictions that relate specifically to Australian temperate

118   woodlands and particular kinds of bird species in those environments

119   **Prediction 4**. *That insectivores are more likely to decline than other dietary groups*.

120   Widespread land clearing associated with agricultural development in the temperate

121   woodland ecosystems of south-eastern Australia has been associated with changes in insect

122   populations and communities (Gibb and Cunningham 2010; Barton et al. 2016). Many of the

123   bird species in temperate woodland ecosystems are insectivores (Higgins 1991-2006) and on

124   this basis, insectivorous birds as a distinct dietary group may also be subject to greater levels

125   of change relative to birds in other broad dietary categories (see Lindenmayer et al. 2012b).

126   We therefore sought to determine if there were relationships between diet and temporal

127   patterns of change in birds and test the prediction that insectivores would be more susceptible

128   to decline than species that consume other kinds of food.

129   **Prediction 5**: *That woodland bird species are more likely to decline than open-country*

130   *species*. Land-clearing removed large areas of temperate woodland vegetation leaving

131   remnant woodland patches and "open-country" cleared paddocks and croplands which now

132   comprise 70-85% of the land area in this region (Cunningham et al. 2014). The terrestrial bird

133   species inhabiting our study region can be broadly classified as being woodland associated or

134   open-country associated (i.e. not associated with woodland). Given the predominance of

135   cleared areas in our study, we predicted a temporal decline in woodland-associated species

136   and an increase in open-country species. Earlier work in a comparable landscape made long-

137   term predictions of bird occurrence based on the availability of woodland versus cleared

138   pasture environments and habitat selection for open-country and woodland habitats (Fischer

139   et al. 2010). This study provided an opportunity to test those earlier predictions.

140   **METHODS**

141   *Study area*

142   Our study region was an 18,000 km^2 agricultural area within the South-west Slopes region of

143   New South Wales, south-eastern Australia (Figure 1). The South-west Slopes region was

144   formerly dominated by temperate native woodland, but has been cleared of an estimated 85

145   % of its original cover to facilitate livestock grazing and cereal cropping (Benson 2008). In

146   response to conservation concerns, the region has been the target of major restoration

147   planting programs (Cunningham et al 2014). There has also been significant natural

148   regeneration of temperate woodlands over the past 10 years in our study region (Sato et al.

149   2016). Thus, there are three broad structural kinds of woodland vegetation cover: actively

150   replanted or restored woodland (termed restoration plantings), naturally regenerated

151   woodland (termed regrowth woodland), and old-growth woodland. Our study comprised 203

152   sites, including 65 restoration plantings, 66 patches of regrowth woodland, and 72 patches of

153   old-growth woodland. Importantly, different assemblages of birds are associated with these

154   different kinds of woodland habitats (Lindenmayer et al. 2012a), and it was therefore

155   appropriate to explore temporal trends in relation to these three broad kinds of vegetation

156   cover.

157   Restoration plantings were areas of planted native vegetation characterized by a mix of local

158   endemic and exotic ground cover, understorey and overstorey plant species. Woody plants

159   were typically spaced 2 m apart, but there was not a standard set of spacing and plant species

160   composition protocols applied in revegetation efforts. All restoration plantings were at least

161   seven years old at the start of this investigation in 2002, and many were 10-20 years old.

162   Restoration plantings were established to mitigate problems associated with soil erosion

163   and/or salinity, and provide on-farm habitat for wildlife (Lindenmayer et al. 2016a).

164   Regrowth woodland refers to existing living trees recovering after disturbance by fire,

165   clearing or both; or regeneration of trees from seeds germinating after being dropped by

166   overstorey trees. Old-growth woodland was dominated by large old scattered trees was

167   typically 200 or more years old.

168   For the analyses reported here, we focused on a size range of patches of old-growth

169   woodland, regrowth woodland, and restoration plantings that were broadly similar to avoid

170   the potential for confounding between patch size and vegetation type. Within-group

171 variability in patch attributes (size, shape, aspect etc.) exceeded between group variation (Ikin

172 et al. 2015). Notably, differences in key attributes such as stand height and stem density

173 between the three broad vegetation types were much greater than within-group variability

174 (Ikin et al. 2015; Lindenmayer et al. 2016a).

175 In addition to vegetation type, we used satellite data to calculate a measure of the extent (ha)

176 of native vegetation (termed "vegetation extent) in an area of 500m radius around the

177 centroid of the permanent transect established at each site. The mean value was 5.0 ha and the

178 median value was 2.25 ha, with values ranging from 0 (19% of the values) to 53 ha. The

179 amount of surrounding vegetation was slightly lower around plantings (mean = 3.6 ha) than

180 regrowth (mean = 4.7 ha) and old growth woodland (mean 6.6 ha).

181 ***Bird surveys***

182 We completed all bird surveys in spring; however, due to farm access and other logistical

183 restrictions, not all sites could be surveyed in all survey years. For restoration plantings, we

184 completed counts at 39 sites in 2002, 46 in 2004, and 65 in 2006, 2008, 2009 and 2011, 61 in

185 2013, and 58 in 2015. This resulted in a total of 464 site-by-year observations (hereafter

186 termed "surveys"). For old-growth woodland, we surveyed 68 sites in 2002, 72 in 2004,

187 2006, 2008 and 2009, 70 in 2011, and 69 in 2013 and 2015, giving 564 site-by-year surveys.

188 For regrowth woodland, we surveyed 61 sites in 2002, 66 in 2004, 2006, 2008 and 2009, 64

189 in 2011, 61 in 2013 and 60 in 2015, giving 510 site-by-year surveys.

190 We gathered bird data using repeated five-minute point-interval counts (*sensu* Pyke and

191 Recher 1983) at 0 m, 100 m and 200 m along a fixed transect at each site. Bird species seen

192 or heard within 50 m of each point were recorded. Detections >50 m from the count point

193 were not included in our analyses. In any given year and season, each site was surveyed by at

194 least two observers on different days, giving a minimum of six point-interval counts in each

195   survey. We conducted surveys for up to four hours from dawn on a given day. We did not

196   undertake surveys during poor weather (rain, high wind, fog, or heavy cloud cover). A site

197   surveyed early in the morning on the first day of counts was surveyed later in the morning on

198   second day of counts. These protocols reduced the effects of observer heterogeneity, time of

199   day, and day of survey effects (Lindenmayer et al. 2009). The total dataset for our study

200   comprised 9377 point counts.

201   ***Bird life history and other attributes***

202   We constructed an extensive database of life history attributes for all birds recorded in our

203   study region over the past 13 years. Body mass, movement, habitat (open-country versus

204   woodland) and dietary data were derived from compilations of bird biology and ecology

205   published in various ornithological monographs (see Luck et al. 2012). Birds identified as

206   those of conservation concern followed (Reid 1999; Montague-Drake et al. 2009).

207   We assigned each bird species to one of two categories of movement status: migrants (68

208   species) and residents (40 species). Resident species were those which did not undertake

209   large-scale movement, including latitudinal migration, elevational migration or nomadic

210   movements. We used body mass as a proxy for size, which we analysed as a continuous

211   variable, which we log-transformed (base e) in all models. However, we present our results at

212   three representative size categories: small ($\bar{x}$ =12 g, range 6-25 g, n = 46 species, e.g. Striated

213   Pardalote); medium ($\bar{x}$ =55 g, range 26-114 g, n=34 species, e.g. Brown Songlark); and large

214   ($\bar{x}$ =245 g, range 118-790 g, n=28 species, e.g. Australian Hobby): 28 species. We

215   categorised species based on habitat preferences as either a 'woodland' species (those birds

216   associated only with, or mostly with woodland) or 'open-country' species (remaining birds

217   that do not have any preference for woodland habitat). Recent research has determined that

218   this classification does represent an ecological meaningful grouping, and 'woodland birds'

219   are not simply a collection of species united by shared traits (Fraser et al. 2017). We defined

220 rare species as those with less than 1 % occurrence on average in the 2002 and 2004 surveys

221 (n=57), moderately common species as those with 1-10 % occurrence on average (n=35), and

222 common species as those with 10 % or more occurrence on average (n=15). Finally, we

223 assigned birds to one of four broad diet categories: those that primarily consumed **(1)**

224 invertebrates, **(2)** nectar, **(3)** seeds, and **(4)** vertebrates. We acknowledge that many species in

225 categories 2, 3 and 4 supplement their diet with invertebrates.

226 We checked the correlation between the four trait variables we investigated, and found that

227 no correlation was greater than 0.42 in magnitude (Appendix Table 1), with the exception of

228 a correlation of 0.56 between the linear effect of body size and the contrast between birds that

229 consume vertebrates.

230 ***Statistical analyses***

231 We recorded a total of 177 individual species over the 13-year duration of this study. Of

232 these, 22 were waterbirds and were excluded from the study. A further 47 species were

233 excluded because there were insufficient detections to facilitate robust statistical analyses.

234 We tested our five predictions using data from the 108 individual bird species detected in at

235 least four of the eight survey years (Appendix 1).

236 We took a two-stage approach to our analysis. We began by investigating individual species

237 trajectories over time, accounting for differences in occurrence between our three broad

238 vegetation types. We followed this by a set of assemblage-wide analyses to investigate the

239 association between species traits, site-level covariates (i.e. patch type) and time.

240 We used generalized linear mixed models (GLMMs) in GenStat (Release 18.1) for both sets

241 of analysis. Our response variable for all analyses was the proportion of times each species

242 was observed at a site (out of a possible 6 point counts) in each survey year. All models were

243 fit using a binomial distribution with over-dispersion (Wedderburn 1974) and the logit link

244   function (Cunningham et al. 2014). For presentation purposes, we summarized the effects of

245   interest using predictions adjusted for all the other variables in the model (Lane and Nelder

246   1982): specifically, predictions were calculated at the mean values of continuous variables

247   (such as body mass), and averages were calculated over the predictions at each level of

248   categorical variables (such as diet), with equal weights for each level.

249   For our analysis of individual species trajectories, we first fitted a GLMM for each species

250   that included a fixed effect of time (linear on the logit scale) and a random effect of site, and

251   then added fixed effects of broad vegetation type and its interaction with time (see

252   Appendices 1 and 3).

253   For our analysis of trait responses to environment, we included all species in a single model,

254   and allowed for the different relative occurrences of species by including random effects for

255   species and site, assuming Normal distributions for the variation of mean percentage

256   occurrence on the logit scale. We fitted fixed effects for broad vegetation type and time

257   (again linear on the logit scale); for four trait variables: migratory vs resident species, body

258   size, woodland versus open-country, and invertebrate vs nectar vs seed vs vertebrate diets.

259   We also allowed interactions between vegetation types, time and each of the trait variables

260   (but no interactions between trait variables), summarized as follows:

261   Logit(% presence) = time * vegetation type* (migratory status + body size + habitat)

262   We fitted a separate model to investigate the interaction of rareness of species with other

263   variables: this included the effects listed above plus the effect of rareness, but excluding the

264   effects of the remaining trait variables:

265   Logit(% presence) = time * vegetation type* frequency class

266   As part of preliminary data analyses, we fitted a model that included vegetation extent

267   corresponding to the amount of native vegetation surrounding each site. We found no

268   significant interaction between vegetation extent and broad vegetation type, between

269   vegetation extent and time, or vegetation extent and both time and broad vegetation type. In

270   addition, the inclusion of vegetation extent made no significant difference to the model with

271   life history traits. On this basis, and to facilitate presentation of the most parsimonious

272   models, we elected to exclude vegetation extent from subsequent statistical analyses.

273   We did not conduct detectability/occupancy analyses for a number of reasons. Most

274   importantly, past analyses on the topic of detection/occupancy (e.g. Welsh et al. 2013)

275   suggest that the current statistical methods for detection/occupancy may not improve model

276   fit and in some cases can make the outcomes worse. Moreover, it is currently not possible to

277   determine when detection occupancy analysis improves model fit and when it does not

278   (Welsh et al. 2015).

279   **RESULTS**

280   ***Temporal trajectories***

281   Averaged over all three vegetation types, our analyses revealed a significant decline ($P <$

282   0.05) in 30 species and a significant increase in 14 species between 2002 and 2015 (Figure 2).

283   Below we provide examples of birds that decreased and increased, first for those of

284   conservation concern, then common species, and finally exotic taxa. We present deviance

285   statistics that reflect measures of model fit in Appendix 4

286   Of the 30 species that exhibited a statistically significant decline, four are of conservation

287   concern (Dusky Woodswallow *Artamus cyanopterus* [Supplementary Figure 1a], Eastern

288   Robin *Eopsaltria australis*, Black-chinned Honeyeater *Melithreptus gularis* and Masked

289   Woodswallow *Artamus personatus*), eight are common (> 10% occurrence on average

290   during the first two years of surveys) (White-plumed Honeyeater *Lichenostomus penicillatus*

291   [Supplementary Figure 1b], Crested Pigeon *Ocyphaps lophotes*, Red-rumped Parrot

292 *Psephotus haematonotus*, Striated Pardalote *Pardalotus striatus*, Magpie Lark *Grallina*

293 *cyanoleuca*, Noisy Miner *Manorina melanocephala*, Galah *Eolophus roseicapilla*, and Grey

294 Shrike-thrush *Colluricincla harmonica*) and three are exotic species (House Sparrow *Passer*

295 *domesticus*, Common Blackbird *Turdus merula* and European Goldfinch *Carduelis*

296 *carduelis*). Of the 14 species that significantly increased, three are of conservation concern

297 (Diamond Firetail *Stagonopleura guttata* ,[Supplementary Figure 1c], Rufous Whistler

298 *Pachycephala rufiventris* and White-winged Triller *Lalage tricolor*) and two were considered

299 common (Superb Fairy-wren *Malurus cyaneus* and Rufous Songlark *Megalurus mathewsi*)

300 (Figure 2).

301 ***Differences in trajectory between broad vegetation types***

302 We found that 94 species were characterized by similar temporal trends in occurrence across

303 all three vegetation types (Appendix 1, with graphs shown in Appendix 3). There were,

304 however, species that exhibited different temporal responses across vegetation type; these

305 typically related to temporal declines or increases in restoration plantings relative to regrowth

306 or old-growth. For example, the Diamond Firetail declined in restoration plantings but

307 increased in old-growth and regrowth, respectively. The White-browed Babbler

308 (*Pomatostomus superciliosus*) and White-winged Chough (*Corcorax melanorhamphos*)

309 increased in restoration plantings but declined in old-growth and regrowth, respectively.

310 Examples of species which declined most in restoration plantings compared to the other two

311 vegetation types included the White-plumed Honeyeater (*Lichenostomus penicillatus*) and

312 Willie Wagtail (*Rhipidura leucophrys*).

313 ***Prediction 1: Did large birds decline more than small birds?***

314 Averaged over time, we found that small-bodied birds were approximately twice as common

315 in restoration plantings relative to regrowth and old-growth woodland, whereas the opposite

316 was true for large birds (Figure 3). The interactions between vegetation type and the linear

317   and quadratic effects of bird size were both statistically significant (P < 0.001, see Appendix

318   4; the fitted quadratic effects are shown in Appendix 5). The occurrence of large and

319   medium-sized birds decreased over time in all growth types, whereas the occurrence of small

320   birds increased in old-growth and regrowth, and to a lesser extent in plantings. The

321   interactions between the linear effect of time and the linear and quadratic effects of bird size

322   were significant (P < 0.001), and the three-way interaction involving vegetation type and the

323   linear effect of time was also significant (P = 0.04; see Appendix 4).

324   *Prediction 2: Did migratory species decline more than resident species?*

325   Our analyses revealed that, initially, migratory species were less prevalent than residents, but

326   resident species declined over time, especially in restoration plantings (Fig.5b). The

327   interactions of movement status both with time and with growth type were significant (P <

328   0.001; see Appendix 4).

329   *Prediction 3: Did common birds decline more than rare birds?*

330   We found that common species declined over time, especially in plantings (Fig. 5c), whereas

331   rare species increased over time, also particularly in plantings. The interactions between

332   occurrence categories and time and between occurrence categories and vegetation type were

333   significant (P < 0.001). The interaction with time and vegetation type was also significant (P

334   = 0.002).

335   *Prediction 4: Did insectivorous birds decline more than birds with other diets?*

336   Birds with predominantly invertebrate diets were characterised by a declining trend over time

337   in plantings, but not in old-growth or regrowth (Figure 5d). Nectarivores declined in all

338   growth types, with occurrence nearly halved from 2002 to 2015 in restoration plantings.

339   There was no evidence of change over time for granivores nor for carnivores except in

340   plantings where occurrence halved over the 13-year period of our study. The interactions

341 between time and diet and between growth type and diet were both significant (P < 0.001)

342 (see Appendix 4), but the three-factor interaction was not significant (P = 0.87).

343 ***Prediction 5: Did woodland birds decline more than open-country birds?***

344 We found that the interaction between habitat preference and time was not significant (P =

345 0.25) (see Appendix 4), although there was an indication that open-country birds declined

346 over time (Figure 3). Woodland birds were less prevalent on average than open-country birds

347 throughout the 13 years of our study (Figure 3), but they were more prevalent in regrowth

348 sites than in old-growth or plantings. The interaction between habitat preference and growth

349 type was significant (P < 0.001), but the three-variable interaction was not significant (P =

350 0.66).

351 **DISCUSSION**

352 We sought to quantify temporal patterns of change in birds in one of the world's most heavily

353 cleared and modified ecosystems, Australia's temperate woodlands (Fischer et al. 2009) and,

354 in doing so, test predictions about life-history attributes associated with species trajectories in

355 this ecosystem. Our analyses contained evidence of a significant decline in 30 species (over a

356 quarter of those analyzed). However, temporal changes in occurrence were not consistent

357 across bird biota as we found evidence of positive changes in a small number of species,

358 including species of conservation concern and some rarer species. Some patterns we

359 documented were not consistent with predictions derived from patterns uncovered for

360 particular kinds of bird species (e.g. migratory versus resident taxa) elsewhere around the

361 world (e.g. Both et al. 2010; Runge et al. 2015; Gilroy et al. 2016). In the remainder of this

362 paper we discuss the overall temporal trends we identified and then explore associations

363 between those trends and life history attributes that featured in the predictions we tested. We

364   conclude with commentary on the conservation and land-management implications of our

365   empirical study.

Overall temporal changes

367   Much has been written about the major losses of biodiversity at both a global and population

368   level (e.g. Ceballos et al. 2017; Tilman et al. 2017). For the intensively monitored ecosystem

369   in the study reported here, we found that the majority of species (64 of 108) showed no

370   evidence of significant change over the 13 years of this investigation, illustrating the relative

371   stability of these bird populations. However, there was also evidence of a significant decline

372   in 30 species, more than double the number of significantly increasing bird species (14

373   species). Declining species included not only species of conservation concern (such as the

374   Dusky Woodswallow, Eastern Yellow Robin, Black-chinned Honeyeater and Masked

375   Woodswallow) but also many common species that are likely, because of their abundance, to

376   play key role in ecosystem functions such as pollination and insect pest control. Declines in

377   such common species may have serious consequences for the long-term integrity of

378   temperate woodland ecosystems.

379   The reasons for the significant decline in many bird species remain unclear, as our study was

380   not the kind of targeted experiment required to determine causation (Caughley and Gunn

381   1996). The variety of species exhibiting declines suggest there may be multiple drivers of the

382   observed patterns of change. A wide range of functional types of species exhibited declines

383   including (among others) those that were large-bodied, residents, and nectar feeders. Patterns

384   of declines often differed among vegetation types and included both birds of conservation

385   concern as well as common species. For example, the hyper-aggressive and overabundant

386   Noisy Miner was one common species which declined significantly over the duration of this

387   study without any direct management (such as culling). This decline could have positive

388   outcomes for the smaller-bodied bird species that Noisy Miners exclude from woodland they

389   occupy (Mac Nally et al. 2012). In addition, our empirical analyses contained evidence of

390   significant declines in three exotic species, the Common Blackbird, the House Sparrow and

391   the Goldfinch. Species such as the House Sparrow have declined in other parts of the world

392   (Vincent 2005) with the use of pesticides being one explanation for population reduction

393   (Hallmann et al. 2014). However, if the effects of pesticides were a key driver then we would

394   anticipate a range of native species with broadly similar diets to the House Sparrow and

395   Goldfinch (e.g. the Diamond Firetail) to have declined, which they did not. Another possible

396   explanation for the large number of declines we quantified is the effect of the Millennium

397   Drought which spanned the middle periods of this study (van Dijk et al. 2013). Several earlier

398   studies have revealed that many bird species have either not recovered or continued to decline

399   after the Millennium Drought (Bennett et al. 2014; Selwood et al. 2015). Similarly, some bird

400   species in our study did not recover during the marked wet period following the drought,

401   possibly as a result of extinction debts following extensive past clearing (Nimmo et al. 2016).

402   We suggest that a longer period of monitoring than the 13 year duration of this study may be

403   required for some bird species to recover following the Millennium Drought and, in turn,

404   obtain a clearer picture of long-term trends in occurrence in different types of woodland.

405   Declines in many bird species also do not appear to be associated with a loss in habitat and

406   vegetation cover because the area of plantings and natural regeneration has increased

407   significantly in our study region over the past decade (Cunningham et al. 2014).

408   We found evidence for significant increase in some species of conservation concern: the

409   Diamond Firetail, Rufous Whistler and White-winged Triller (Appendix 1). Other species,

410   such as the Grey-crowned Babbler (*Pomatostomus temporalis)*, showed substantial increases

411   but high levels of year-to-year variation in detection that may have masked evidence of

412   statistically significant temporal trends in our study (Appendix 1). Elsewhere, positive

413   temporal responses in the Grey-crowned Babbler appear to be associated with revegetation

414   programs (e.g. Robinson 2006). Both the Grey-crowned Babbler and the Rufous Whistler

415   often occupy restoration plantings and regrowth, whereas the Noisy Miner is mostly absent

416   from these areas (Lindenmayer et al. 2012a). The area of restoration plantings and natural

417   regrowth have increased substantially over the past decade in our study region (Cunningham

418   et al. 2014) as well as other agricultural regions in south-eastern Australia (Geddes et al.

419   2011). The expansion of these vegetation types over time may explain some of the temporal

420   changes in bird species occurrence that we have quantified.

421   Earlier work in agricultural landscapes relatively close to our study region (see Fischer et al.

422   2010) included predictions of future occurrence of 27 bird species based on models of the

423   tree-based habitat requirements of species and projected future patterns of tree cover. Our

424   study area supports these same bird taxa and our data provide an independent, albeit crude,

425   "test" of the accuracy of those predictions, at least in the short term. Fischer et al. (in 2010)

426   predicted that 24 of 27 species would decline and of these, 11 in this study also exhibited a

427   significant decline. We found no significant trend for a further 10 of the species predicted by

428   (Fischer et al. 2010) to decline, although it is possible that with a longer time series, evidence

429   of greater congruence between the number of species predicted to decline and those actually

430   declining might be found. Contrary to predictions by (Fischer et al. 2010), we found that

431   three of the 24 species increased (Grey Fantail *Rhipidura albiscapa,* Mistletoebird *Dicaeum*

432   *hirundinaceum* and Rufous Whistler), all of which are strongly associated with restoration

433   plantings (see Lindenmayer et al. 2010; Appendix 1), highlighting the value of strategically

434   revegetating areas for some elements of bird biota. (Fischer et al. 2010) also predicted a

435   future increase in three species, for which we found evidence of an increase in one (the

436   Rufous Songlark), no change for another, and a decline in a third (the Welcome Swallow

437   *Hirundo neoxena*). The Welcome Swallow is strongly associated with human infrastructure

438   such as buildings and farms dams and the reasons for its decline remain unclear.

439 ***Test of prediction 1: That large-bodied species are more likely to decline than smaller-***

440 ***bodied species.***

441 Consistent with our prediction at the outset of this study, large-bodied birds declined over

442 time and across all vegetation types, but particularly in old-growth and regrowth. Large-

443 bodied species typically have larger territories than small species (Schoener 1968) and may

444 require more habitat to survive thereby making them vulnerable to decline in areas

445 extensively modified by agriculture (Haddad et al. 2015). An alternative explanation might be

446 that large birds favour highly modified open-country environments (see Lindenmayer et al.

447 2012b) and they may be disadvantaged by the densely stocked vegetation characteristic of

448 regrowth woodland and restoration plantings. However, this does not account for the

449 temporal declines we found for typically open old-growth woodlands. Therefore, the reasons

450 for the decline in large bodied birds remain unclear. Tilman et al. (2017) highlighted the

451 elevated risks faced by large-bodied birds in a range of regions globally, to which the

452 temperate woodland region of south-eastern Australia might also now be added.

453 In contrast to the decline in large birds, we found evidence that small-bodied bird species

454 increased over time and in all broad vegetation types. Small-bodied bird species were

455 particularly prevalent in restoration plantings, consistent with the landscape texture

456 hypothesis (Fischer et al. 2008), which predicts that small-bodied species will benefit from

457 densely spaced trees that characterize restoration plantings and provide a greater array of

458 nesting and foraging niches for these species whilst at the same time providing protection

459 from predators. The general increase in the amount of plantings in the landscape (where small

460 birds are more prevalent) may have assisted small birds in colonizing old growth and

461 regrowth woodland. Again, this result highlights the value of targeted restoration plantings

462 for small-bodied birds.

463 ***Test of prediction 2: That migratory species are more likely to decline than resident***

464 ***species.***

465 Contrary to our initial expectations, resident – but not migratory species – declined over time

466 with the most pronounced decline being in restoration plantings. This result was particularly

467 surprising given studies elsewhere around the world which suggest that migratory species are

468 at increased risk of decline and extinction (Both et al. 2010; Runge et al. 2015; Gilroy et al.

469 2016). The reasons for our findings remain unclear, but previous work has suggested that

470 migratory species are more likely to colonize restoration plantings over time (Lindenmayer et

471 al. 2016a) and it is possible that this, in turn, displaces resident birds as such restored areas

472 mature over time. The habitat suitability for resident birds may also decline as restoration

473 plantings mature. Irrespective of the underlying reasons for our findings, they suggest a need

474 to ensure that the conservation status (and thereby subsequent targeted management) of

475 resident and not just migratory species is carefully examined.

476 ***Test of prediction 3: That rare species are more likely to decline than common species.***

477 We found that, as a group, common species of birds declined, whereas rare species increased;

478 however, there were inter-specific differences in these trends. These findings are broadly

479 consistent with those from work on birds in Europe which also reported declines in common

480 species (Inger et al. 2014). The decline of common taxa is important given the key ecological

481 roles abundant taxa play in ecosystems (Gaston 2010; Winfree et al. 2015) including

482 pollination and insect pest control. Evidence of temporal change was especially pronounced

483 in restoration plantings (e.g. the White-plumed Honeyeater; see Supplementary Figure 2),

484 highlighting the high level of dynamism in bird populations in these actively revegetated

485 environments.

486   ***Test of prediction 4: That insectivores are more likely to decline than species with other***

487   ***kinds of diet.***

488   We found little evidence of temporal changes in insectivores relative to birds that consume

489   other kinds of food resources, despite vegetation type differences in the occurrence of birds

490   with different diets. This was an encouraging result given suggestions by other researchers

491   (e.g. Ford et al. 2001) that many at-risk species are insectivores and susceptible to decline.

492   The reasons for the paucity of evidence for a decline in insectivores remains unclear.

493   However, it is possible that the additional areas of regrowth and restoration plantings in our

494   study area may provide habitat for insect biota (Gibb and Cunningham 2010; Barton et al.

495   2016) that are, in turn, food for insectivorous bird species, thereby limiting population

496   declines.

497   Nectar-feeding species exhibited the most pronounced declines in our study, with the

498   strongest effects in restoration plantings. Such results are perplexing given that our 13-year

499   study spanned both very dry and very wet periods when temporal changes in food would be

500   expected to occur and, more recently would be anticipated to have recovered.

501   ***Test of prediction 5: That woodland bird species are more likely to decline than open-***

502   ***country species.***

503   We found no evidence to support the prediction of a stronger decline in woodland birds

504   relative to open-country birds. Indeed, there was an indication that open-country birds

505   declined over time but the interaction between habitat preference and time was not

506   significant. The (albeit non-significant) trend for a decline in open-country species may be

507   associated with the increase in area over the past decade (see Cunningham et al. 2014) of

508   vegetation that is generally not habitat for these birds such as patches of natural regeneration

509   and restoration plantings. Notably, woodland birds were less prevalent than open-country

510   birds despite old-growth woodland, regrowth woodland and restoration plantings (but not

511   paddocks, croplands and other cleared areas) being targeted in our field studies. Areas of

512   native vegetation cover varies from 3-30% of the landscape cover in our study region

513   (Cunningham et al. 2014). Therefore, open areas dominate these landscapes and this may

514   explain the greater prevalence of open-country birds in our study.

515   **MANAGEMENT IMPLICATIONS AND GENERAL CONCLUSIONS**

516   Documenting temporal patterns of change in biota is critical to many key aspects of

517   conservation biology and ecology. This includes providing an overall assessment of the status

518   of biodiversity (e.g. Ceballos et al. 2017; Tilman et al. 2017) and identifying those species

519   (and broader functional groups of species) that require additional management interventions

520   such as additional habitat restoration (Crouzeilles et al. 2016) or expanded habitat protection

521   (Pringle 2017). We found that almost twice as many species have declined as have increased

522   over the past 13 years in the temperate woodlands of south-eastern Australia, one of the most

523   heavily cleared and modified biomes globally. These findings suggest that the temperate

524   woodland bird biota is at risk of becoming highly depauperate relative to what it was even

525   just a few decades ago, despite significant restoration efforts in large parts of the biome,

526   including the region where this study was focused. Other researchers (e.g. Garnett et al. 2011)

527   have suggested that species of conservation concern, like those we identified as being in

528   significant decline in this study, need targeted management. Hence, our results are important

529   as they allow a focus of management effort on species that are truly undergoing significant

530   decline. However, we also found compelling evidence for significant declines in some

531   common species, some of which are likely to play critical roles in ecosystem processes. We

532   suggest these species also need concerted conservation efforts, not only to prevent them from

533   becoming uncommon and eventually conservation management-dependent, but also because

534   their declines may represent future risks to key ecosystem processes mediated by formerly

535   abundant bird taxa (see Winfree et al. 2015).

536   Our analyses contained evidence of significant differences in temporal trajectories of bird

537   species between old-growth woodlands relative to restoration plantings and natural regrowth.

538   Indeed, restoration plantings were characterized by significant declines in nectar-feeders,

539   large birds, common birds and residents but also significant increases in small birds and rare

540   species. Such temporal patterns results suggest that restoration plantings in particular are

541   highly dynamic environments in which marked changes in the functional groups of birds can

542   take place within relatively short periods of time.

543   This underscores the importance of a suite of land management strategies that result not only

544   in the deliberate replanting programs to actively restore woodlands (Lindenmayer et al.

545   2016a) but also in the maintenance of seemingly more stable environments such as existing

546   old-growth woodland remnants as well as regrowth woodland.

547   **ACKNOWLEDGEMENTS**

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705 **FIGURES**

706 **Figure 1. Map of the study region.**
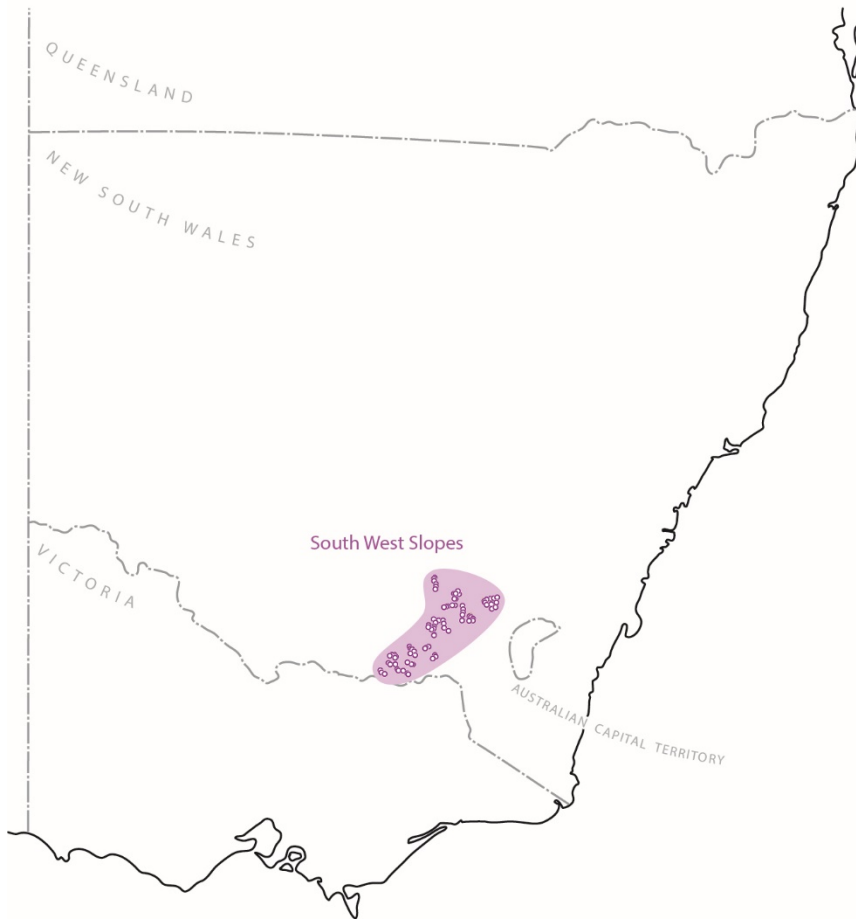
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708

709 **Figure 2. Summary of individual species model results: estimated average percentage**

710 **change per year in odds of occurrence and 95% confidence interval, averaged over**

711 **growth types, and grouped by frequency of occurrence. Changes that are significantly**

712 **different from zero are shown in black. Bold names indicate species of conservation**

713 **concern, while * indicate exotic species. Birds are grouped by overall frequency of**

714 **occurrence (see text).**
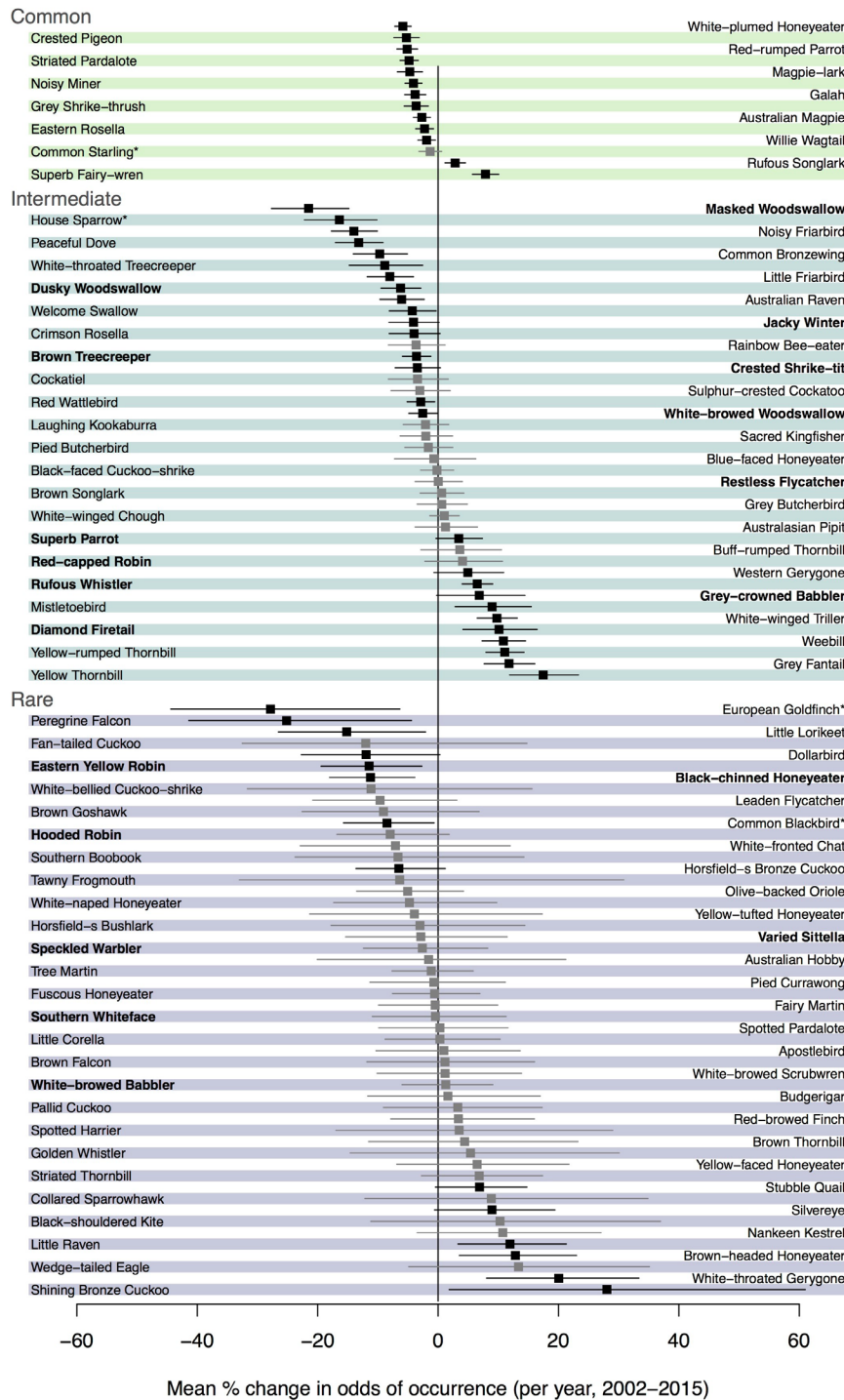
715

716 **Figure 3. Results from trait models: fitted mean % occurrence for 2002 and 2015 and**

717 **for each vegetation type, for body size, migratory status, frequency, diet and habitat**

718 **preference, with 95% confidence limits.**

719