

Long-term bird colonization and turnover in restored woodlands

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1 **Abstract**

2 The long-term effectiveness of restored areas for biodiversity is poorly known for the
3 majority of restored ecosystems worldwide. We quantified temporal changes in bird
4 occurrence in restoration plantings of different ages and geometries, and compared observed
5 patterns with a reference dataset from woodland remnants on the same farms as our plantings.

6 Over time, bird species richness remained unchanged in spring but exhibited modest
7 increases in winter. We found that wider plantings supported significantly greater bird
8 species richness in spring and winter than narrow plantings. There was no evidence of a
9 significant interaction between planting width and time.

10 We recorded major temporal changes in the occurrence of a range of individual species that
11 indicated a clear turnover of species as plantings matured. Our results further revealed
12 marked differences in individual species occurrence between plantings and woodland
13 remnants. Life-history attributes associated with temporal changes in the bird assemblage
14 were most apparent in winter survey data, and included diet, foraging and nesting patterns,
15 movement behaviour (e.g. migratory vs dispersive), and body size.

16 Differences in bird assemblages between plantings of different ages suggest that it is
17 important that farms support a range of age classes of planted woodland, if the aim is to
18 maximize the number of native bird species in restored areas. Our data also suggest that
19 changes in the bird species occupying plantings of different ages can be anticipated in a
20 broadly predictable way based on planting geometry (especially width) and key life-history
21 attributes, particularly movement patterns and habitat and diet specialisation.

22

23 **Keywords:** Vegetation restoration, remnant woodland, native birds, agricultural areas

24

25 **Introduction**

26 Millions of hectares of land worldwide are degraded (World Resources Institute 2011;
27 Stanturf et al 2014) leading to a loss of biodiversity (Clewell and Aronson 2007; Suding
28 2011). In response, billions of dollars are being spent annually by governments and
29 organisations on vegetation restoration in an effort to tackle this problem (Hajkowicz 2009;
30 Aronson and Alexander 2013; Kimball et al 2015). However, the effectiveness of restoration
31 efforts for biodiversity needs to be carefully quantified (Rey Benayas et al 2009) as it can be
32 unclear whether the biota inhabiting replanted areas is similar to that of intact areas (e.g.
33 Catterall et al 2012), or whether it is on a quite different trajectory (Wilkins et al 2003; Brady
34 and Noske 2009).

35 Species colonization of planted vegetation is a core assumption of the restoration
36 approach (Reay and Norton 1999; Barrett et al 2008; Catterall et al. 2012). But the extent to
37 which this assumption holds for real-world restoration efforts needs to be quantified
38 (Hilderbrand et al 2005; Mossman et al 2012). Indeed, the medium- to long-term
39 effectiveness for biodiversity of restored areas is often poorly documented, particularly where
40 vegetation has been deliberately replanted (but see for example Nichols and Grants 2007;
41 Pywell et al 2011; Menke et al 2015). This is a major knowledge gap as short-term responses
42 may not be a good predictor of long-term restoration success (Vesk et al 2008).

43 There is a range of other significant knowledge gaps associated with the effectiveness
44 of restored areas for biodiversity conservation. First, it remains unclear how patterns of
45 species richness and patterns of occurrence of individual species within restored areas may
46 change over time. Some ecological theories suggest that new species will be added to a
47 recovering ecosystem as time elapses since disturbance (Pulsford et al 2016) or the
48 commencement of restoration efforts (Cristescu et al 2012). Conversely, species richness in
49 restored areas may remain unchanged over time, consistent with the general findings from a

50 meta-analysis of time-series datasets on biodiversity from an array of disturbed ecosystems
51 worldwide (Dornelas et al 2014). In addition, succession theory suggests that species may
52 establish in an ecosystem when the vegetation structure and composition first meets their
53 habitat requirements (Pulsford et al. 2016). Species may then decline or be excluded when the
54 vegetation structure and composition changes and/or better-suited species outcompete them
55 (Fox et al 2003). In the case of restored areas, vegetation height, structure and plant species
56 composition may change over time (Vesk et al. 2008; Brady and Noske 2009) and this may
57 influence the occurrence of biota.

58 A second significant knowledge gap associated with the effectiveness of restored areas
59 for biodiversity concerns a paucity of information on relationships between the geometry of
60 restored areas (e.g. size, width) and temporal changes in species richness and the occurrence
61 of individual species. A range of general landscape ecology theories (e.g. island
62 biogeography theory, edge-effects theory and habitat heterogeneity theory; reviewed by
63 Lindenmayer and Fischer (2006)) suggest that larger and wider plantings should support
64 more bird species. In addition, area-sensitive species may be likely to colonize larger, wider
65 plantings more quickly than smaller and narrower plantings.

66 A final important knowledge gap is the paucity of studies examining relationships
67 between life history attributes of biota and temporal changes in occupancy of restored areas.
68 Several studies have quantified trait-based relationships of species with the time elapsed since
69 disturbance (e.g. Langlands et al 2012). The performance filtering hypothesis (Mouillot et al
70 2012; Barnagaud et al 2014) suggests that species with particular functional traits are likely to
71 be lost or gained in landscapes undergoing change (Newbold et al 2013), including
72 intensively managed agricultural ecosystems (Tschardt et al 2008; Hanspach et al 2012).

73 To address the key knowledge gaps outlined above, here we quantify temporal changes
74 in bird species richness and the occurrence of individual species between 2002 and 2013 in

75 woodland restoration sites (hereafter termed “plantings”) in south-eastern Australia. We
76 compared these patterns with that of bird species richness and occurrence in “reference sites”
77 comprised of remnant woodland patches (hereafter termed “remnants”) surveyed at the same
78 time and on the same farms as the planting sites. Specifically, we posed the following five
79 questions:

80 Question 1. Does bird species richness in plantings change over time? Specifically, we tested
81 the hypothesis that species richness would be greatest in the oldest plantings. At the outset of
82 our investigation, we also postulated that the bird species richness of older plantings would
83 more closely approximate that of remnant (“benchmark”) sites than younger plantings.

84 Question 2. Does planting geometry influence temporal changes in bird species richness? We
85 explicitly quantified relationships between planting geometry and *changes* in various
86 measures of bird biota over time. We predicted that larger and wider plantings should be
87 characterised by faster rates of increase in species richness than narrow plantings. That is, we
88 hypothesized an interaction between planting age, planting geometry and bird species
89 richness. We also quantified relationships between birds and the geometry of woodland
90 remnants for subsequent qualitative comparison with planting geometry effects.

91 Question 3. Are there changes in the occurrence of individual bird species over time? We
92 predicted temporal changes in the occurrence of individual bird species within plantings and
93 that these changes would be influenced by temporal changes in vegetation structure. We also
94 quantified temporal patterns of change in individual bird species within patches of remnant
95 native woodland, and compared them with the temporal patterns of species occurrence in
96 plantings.

97 Question 4. Does planting geometry influence temporal changes in occurrence of individual
98 bird species? We quantified individual bird species responses to time, planting geometry, and
99 their interaction. We predicted that area-sensitive woodland bird species (Montague-Drake et

100 al. 2009) would colonize larger, wider plantings more quickly than smaller and narrower
101 plantings.

102 Question 5. Are temporal changes in species' identities within plantings linked with
103 particular kinds of life-history attributes? At the outset of our investigation, we postulated
104 that different functional groups of birds would be associated with plantings of different ages.
105 This was because of temporal changes in such features as vegetation height and structure, the
106 suitability of nesting sites, and food availability (e.g. insect prey) (Gibb and Cunningham
107 2010) – all of which can be important for birds.

108 Restoration of degraded ecosystems is a major global issue (Rey Benayas et al. 2009;
109 Suding 2011; Kimball et al. 2015). The outcomes of the long-term work that we report here
110 are important for informing decisions about restoration efforts and setting expectations for the
111 time-scale required for the return of assemblages of species.

112 **Methods**

113 *Study area*

114 Our study region was a 150 x 120 km agricultural area within the South-west Slopes region
115 of New South Wales, south-eastern Australia (Figure 1). The South-west Slopes was formerly
116 dominated by temperate native woodland (Lindenmayer et al 2010a), but has been cleared of
117 an estimated 85% of its original cover to facilitate livestock grazing and cereal cropping. As a
118 result, the South-west Slopes region has been the target of major planting programs
119 (Cunningham et al 2014).

120 We focused on 64 areas of replanted native vegetation and 33 woodland remnants on
121 27 farms in our study region. The plantings we examined were located on the same farms as
122 the benchmark woodland remnants (Figure 1). This enabled us to account for potential farm-
123 level heterogeneity effects on fauna associated with farm-level management practices such as

124 fox-baiting, chemical spraying and fertilizer application (see Barrett 2000). Attributes such as
125 patch size and shape for plantings and remnants were matched as far as practicable on farms.

126

127 ***Plantings***

128 Our 64 planted native vegetation sites were characterized by a mix of local endemic and
129 exotic Australian ground cover, understorey, and overstorey plant species. Most plants were
130 typically spaced 2 m apart, but there was not a standard set of spacing and plant species
131 composition protocols applied in revegetation efforts. The area of plantings ranged from 0.3-
132 60.3 ha, width ranged from 10-300 m, and perimeter ranged from 412-3802 m. Of the 64
133 plantings, 37 exceeded 6 years old and 22 were 10-20 years old at the start of this study
134 (2002).

135 We completed detailed surveys of vegetation structure and composition in the plantings
136 including the total number of stems, canopy depth and height, and the percentage cover in the
137 understorey, midstorey and overstorey. We measured these variables in three 20 x 20 m plots
138 at 0, 100 and 200 m points along a permanent transect at each site on three occasions: 2002
139 (at the establishment of the study), 2008 and 2013. To obtain a site-level description of the
140 vegetation features, we aggregated plot-level data to the site level. We defined understorey,
141 midstorey and overstorey based on height; the overstorey was vegetation exceeding 10 meters
142 in height, midstorey was 2-10 m in height, and understorey was woody vegetation less than 2
143 m in height.

144 ***Woodland remnants as benchmark sites***

145 We compared the avifauna of plantings against 33 temperate eucalypt woodland remnants
146 dominated by the following tree species: white box (*Eucalyptus albens*), yellow box (*E.*
147 *melliodora*), Blakely's red gum (*E. blakelyi*), grey box (*E. microcarpa*), red stringybark (*E.*
148 *macrorhyncha*), mugga ironbark (*E. sideroxylon*) and red box (*E. polyanthemos*). Remnant

149 size ranged from 0.5–53.8 ha, width from 20–480 m, and perimeter from 603–3797 m. Other
150 attributes of these remnants are summarized by Montague-Drake et al. (2009).

151 *Bird surveys*

152 We gathered bird data using repeated five-minute point interval counts at 0 m, 100 m and 200
153 m along the fixed transect at each site. We completed winter and spring surveys because the
154 assemblages of birds can be markedly different at these times, with winter latitudinal and
155 altitudinal migrants (e.g. the flame robin; see Online Resource 1 for scientific names) absent
156 in spring when latitudinal migrants (e.g. restless flycatcher) are present. For plantings, we
157 completed spring counts at 39 sites in 2002, 46 in 2004, and 64 in 2006, 2008, 2009 and
158 2011, and 60 in 2013. This resulted in a total of 401 site-by-year observations (hereafter
159 termed “surveys”). For winter surveys of plantings, we completed counts at 46 sites in 2004,
160 and 64 in 2007, 2008 and 2011, and 60 in 2013, giving 298 surveys. Our bird data for the
161 remnants were based on surveys completed in spring at 29 sites in 2002, 33 in 2004, 2006,
162 2008, 2009, 2011, and 32 in 2013, giving 226 site-by-year observations (viz: surveys). In
163 winter, there were 33 sites in 2004, 2007, 2008, 2011 and 32 in 2013, giving 164 surveys.
164 The number of sites surveyed in any given year varied depending upon access to farms and
165 paddock conditions. The total dataset for our study comprised 1089 surveys and 6534 point
166 counts.

167 For each point-interval count in plantings and remnants, an observer recorded all bird
168 species seen or heard within the site and the detection of each individual bird was assigned to
169 one of several distance categories from the centre of a plot; 0-25 m, 25-50 m and > 50 m. We
170 restricted our analyses to detections made within 50 m of the centre of a field plot point. In
171 any given year and season, a site was surveyed by two observers on different days. We did
172 not undertake surveys during poor weather (rain, high wind, fog or heavy cloud cover). We
173 observed these protocols to reduce the effects of observer heterogeneity and day effects

174 (Lindenmayer et al 2009). We elected not to complete detectability/occupancy analyses in
175 our study of individual species for a range of key reasons. Most importantly, past detailed
176 statistical analyses on the topic of detection/occupancy (e.g. Welsh et al 2013) suggests that
177 the current statistical methods for detection/occupancy may not improve model fit and in
178 some cases can make the outcomes worse. Moreover, it is currently not possible to determine
179 when detection occupancy improves model fit and when it does not (Welsh et al 2015).

180 *Bird life-history analyses*

181 We collated data on bird species traits to address Question 5 on links between temporal
182 changes in species' identities within plantings linked with particular kinds of life-history
183 attributes. We summarized data on life-history (habitat, diet, foraging substrate, movement,
184 social system, nesting and mating behaviour, and reproductive output), and morphological
185 (body mass and relative wing length) traits (see Online Resource 2) (Handbook of Australian
186 and New Zealand Birds 1990-2006; BirdLife Australia 2014). These traits are thought to
187 reflect the ability of species to respond to environmental change (Luck et al 2012). For
188 analysis of winter data, we excluded four traits that are most applicable to the spring breeding
189 season; nest type, nest height, mating behaviour and reproductive output.

190 *Statistical analyses*

191 To assess whether time since planting was a proxy for change in vegetation structure in
192 plantings, we modelled eight vegetation measures (Table 1), fitting a linear effect of time
193 since planting using the generalized linear mixed model facilities of GenStat (VSNi 2013).
194 We included a random effect of site nested within farm to take account of the repeated
195 measurements at each site. For count and percentage measurements, we used a negative
196 binomial distribution with a log link function because there was substantial over-dispersion in
197 the data.

198 To address Question 1 about temporal changes in species richness, we modelled species
199 richness for planted and remnant sites, again using negative binomial regression with a linear
200 effect of time since planting on the log scale. We included a random effect of site nested
201 within farm, a fixed effect of calendar time (defined as the number of years since 2002 when
202 the first measurements were made), and a fixed effect representing the type of site (remnant
203 or planting). For remnant sites, we set time since planting to zero; there was no loss of
204 generality because of the latter fixed effect. We fitted models of the change in species
205 richness associated with increasing length of time since planting, adjusting for any effect of
206 calendar time, which was estimated from planted and remnant sites together. For planted
207 sites, we fitted a time trend for bird species richness with time since planting.

208 Question 2 explored relationships between temporal changes in bird species richness
209 and planting geometry (width, length, area and perimeter). For width effects, we examined
210 the smallest average dimension of the planting and remnant sites. We modelled the effect of
211 width first as a linear trend, then explored non-linearity using a four-dimensional smooth (a
212 generalized linear additive model with a smoothing spline) and as a two-level factor with
213 boundaries suggested by the smooth line. We also examined other available measurements of
214 geometry (length, area and perimeter).

215 Question 3 examined temporal changes in individual species in plantings. We focussed
216 on species observed in $> 10\%$ of the surveys completed in spring or winter; we excluded
217 other species as we deemed there were insufficient data on them to facilitate detailed
218 statistical analyses. We defined a factor by grouping surveys into three approximately equal-
219 sized groups by time since planting: < 8 , $8-16$, and > 16 years. For winter and spring
220 separately, we fitted a generalized linear mixed model for occurrence of each species in
221 planted sites and in remnant sites. The model included random effects to account for repeated
222 measurements on sites within farms, and a fixed effect of the three-level factor representing

223 time since planting, fitted on the logistic scale (using the GLMM procedure of GenStat). We
224 included fixed effects for calendar time and type of site (remnant or planting), and without
225 loss of generality set “time since planting” as zero for remnant sites. We investigated the
226 trends in time further for individual species with the largest effects evident from the previous
227 analysis, by fitting a linear trend (on the logit scale) to the relationship with time since
228 planting as a continuous variable. We fitted models of the change in occurrence of each
229 species associated with increasing length of time since planting, adjusting for any effect of
230 calendar time, which was estimated from planted and remnant sites together.

231 We also explored changes in the composition of the whole bird assemblage over time
232 using multivariate ordination. We used principal coordinate analysis based on an among-site
233 similarity matrix derived from bird species presence-absence data, and using the Jaccard
234 similarity metric. However, we found that the best coordinate identified by this method
235 accounted for less than 5% of the variation in our data, and the next best 3%. We also
236 employed Correspondence Analyses (Greenacre 2007) as an alternative method to explore
237 the patterns of community composition but the largest root accounted for only 2.9% of the
238 variation in our data in spring and 3.5% in winter. We therefore concluded these approaches
239 did not lead to any useful characterization of changes in bird assemblage composition. We
240 instead focused on quantifying temporal changes in the occurrence of individual bird species.

241 Question 4 focused on relationships between temporal changes in the occurrence of
242 individual bird species and planting geometry. Here we employed the same statistical
243 approaches as those used to answer Question 2 but focused on individual species occurrence
244 rather than overall species richness (see above).

245 To address Question 5 concerning the links between life-history attributes and
246 plantings, we divided bird species into two groups for each of eleven different species traits.
247 These traits were habitat type (open country vs woodland), diet, foraging strategy, movement,

248 social system, nest type, nest height, mating system, reproductive output, body mass, relative
249 wing length (see Online Resource 2). We modelled species richness within each trait group,
250 as for total species richness, fitting the fixed effect of time since planting and the random
251 effects of site nested within farm. As most of the life-history variables were categorical, we
252 adopted a parsimonious approach to our analyses based on dichotomies between groups of
253 categories within a given life-history variable rather than attempting to construct linear
254 effects. We assessed each attribute in turn, ignoring the other attributes because of potential
255 confounding between traits (e.g. larger bodied birds tend to have more eggs). Thus, we did
256 not include all the traits in the same model.

257 All p-values stated in the results are derived from Wald tests applied to the relevant
258 generalized linear mixed model.

259 **Results**

260 We recorded 146 bird species in spring and 119 in winter (yielding 151 species in total; see
261 Online Resource 1). Of these, 109 species in spring (84 species in winter) were common to
262 plantings and remnants, with an additional 12 (8) in remnants and 25(27) in plantings. Many
263 species were seen rarely: 80 in spring and 95 in winter were observed in less than 1% of the
264 627 (462) site-year surveys; 31 species (23) were observed in more than 10% of the surveys.

265 The plantings were characterized by temporal changes in vegetation attributes. Of the
266 eight vegetation measures investigated, we identified a significant increase in half of them
267 (Table 1). For example, canopy height increased by 0.38 m per year on average, compared to
268 a mean height of 10 m. The percentage overstorey cover also increased over time, but not in
269 the mid- or understorey. All of these increases were approximately linear over the 30-year
270 range of our dataset (on the log scale for count or proportion measurements), except for
271 canopy depth, which plateaued after about 15 years. These variables were, of course, inter-

272 correlated. Given these results, we considered that time since planting was a reasonable and
273 statistically robust proxy for change in vegetation structure in plantings.

274 ***Question 1. Does bird species richness in plantings change over time?***

275 In remnants, mean bird species richness was 12.6 in spring (s.d. 4.7) and 9.5 in winter (s.d.
276 3.4). In plantings, values for mean bird species richness were 12.7 in spring (s.d. 4.5) and
277 10.1 in winter (s.d. 4.0). One site was planted 40 years before our first surveys, whereas the
278 next oldest was 16 years. Averaging over years, this older site supported ~6 more species
279 both in spring and winter than the mean over the other sites. We excluded this outlier to avoid
280 a single site dominating the results.

281 We found no evidence of change in species richness with calendar time in spring or
282 winter ($p > 0.81$). There was evidence of an increase in species richness in winter with time
283 since planting, 1.3% per year on average (95% CI 0.1–2.6%), but no equivalent change in
284 spring ($p = 0.22$) (Figure 2; see Online Resource 3 for detailed results). This estimated rate of
285 increase in winter starting from, for example, 10 species, would give one extra species after
286 seven years, and seven extra after 40 years, if the trend were extrapolated.

287 ***Question 2: Do planting attributes influence temporal changes in bird species richness?***

288 We found a positive linear relationship between bird species richness and planting width in
289 spring ($p < 0.001$) and winter ($p = 0.04$); there was no significant similar relationship for
290 remnant sites ($p = 0.21$). Fitting a four-dimensional smooth curve provided evidence that the
291 slope of the relationships in spring decreased to a plateau at about 75 m planting width; in
292 winter there was no evidence of a nonlinear effect with width (Figure 3). Figure 6 in Online
293 Resource 4 shows the smooth curves fitted for remnant sites. We therefore summarized the
294 effect of width by fitting a three-level factor discriminating between narrow (<25 m),
295 intermediate (25–75 m) and wide (>75 m) plantings instead of the linear effect. In spring,
296 wide plantings supported, on average, 18% greater bird species richness than narrow ones

297 (95% confidence interval 3–39%, $p=0.02$); in winter the average increase was 16% (1–36%,
298 $p=0.04$). There was no significant interaction between planting width and planting time
299 ($p>0.70$).

300 Of the other plot measurements, only area had a significant relationship with species
301 richness ($p=0.02$), and that was not as strong as the relationship between width and species
302 richness. There was a strong positive correlation of area with width ($r=0.61$, $p<0.001$).

303 ***Question 3. Are there changes in the occurrence of particular individual species over time?***

304 We quantified the mean occurrence of each bird species in planted sites, tabulated into three
305 groups according to time since planting (*viz.*: < 8, 8–16, and > 16 years) (Figure 4; detailed
306 results are presented in Online Resource 3). In spring, the largest change with increasing time
307 since planting was the increase in occurrence of the red wattlebird, which occurred at 22% of
308 sites planted less than eight years before, rising to 51% of sites planted longer than 16 years
309 before ($p=0.007$). Other species whose occurrence in plantings increased significantly over
310 time were the white-winged chough (6 to 27%, $p=0.004$), weebill (7% to 24%, $p=0.03$) and
311 the yellow thornbill (8% to 25%, $p=0.02$). Conversely, the occurrence of the striated
312 pardalote decreased from 65% to 39% ($p=0.01$), as did the willie wagtail (89% to 68%,
313 $p=0.01$).

314 In winter, the occurrence of the red wattlebird increased significantly with time since
315 planting, from 23% to 53% across the duration of our study ($p=0.006$). There also were
316 significant increases of the grey fantail (2% to 38%, $p<0.001$), yellow thornbill (7% to 37%,
317 $p=0.002$) and superb fairy-wren (41% to 79%, $p=0.01$), and a decrease in the crested pigeon
318 (53% to 32%, $p=0.05$).

319 In comparison to the plantings, the largest changes in species in remnants over calendar
320 time (grouped as 2002-6, 2007-9 and 2011-13) were decreases in occurrence of the striated

321 pardalote and red-rumped parrot in winter, and of the noisy miner in spring (all highly
322 significant, $p=0.001$; Figure 5).

323 To investigate changes in individual species in more detail, we selected the species with
324 the largest effects identified above, three species in spring and four in winter, and fitted linear
325 trends with both calendar time and time since planting (the same explanatory model as for
326 species richness in Question 1). There was no evidence of a trend with calendar time ($p>0.20$)
327 for any of the three species in spring. The trends with time since planting were substantial
328 (first three panels of Figure 7 in Online Resource 5), but statistically significant only for the
329 red wattlebird ($p=0.02$). In winter for the red wattlebird, there was again no apparent trend
330 with calendar time ($p>0.20$), but a significant increase with time since planting ($p<0.001$; first
331 panel of Figure 8 of Online Resource 5). However, for the other three species (second to
332 fourth panels of Figure 8 of Online Resource 5), the apparent increase with time since
333 planting (Figure 4) appears to be a result of an overall trend with calendar time (significant in
334 all cases, $p<0.01$); none of the three trends with time since planting (actually negative, after
335 adjusting for the effect of calendar time) was significantly different from zero ($p>0.20$).
336 Figures 9 and 10 in Online Resource 5 show the effects of calendar time similar to those for
337 time since planting in Figures 7 and 8.

338 ***Question 4: Do planting attributes influence temporal changes in occurrence of individual***
339 ***bird species?***

340 We identified significant planting width effects for only one individual species, the grey
341 fantail. Its odds of occurrence in winter were 3.0 times greater in wide ($> 75\text{m}$) plantings than
342 in narrow ($< 25\text{m}$) plantings (95% CI 1.3–6.9, $p=0.01$).

343 ***Question 5. Are temporal changes in species' identities within plantings linked with***
344 ***particular kinds of life-history attributes?***

345 We divided bird species into two classes for each of 11 species traits (Table 2). Examining
346 species richness of these classes in spring revealed a significant positive effect of time since
347 planting for species with “co-operative” mating behaviours. Richness of these species
348 increased on average by 2.8% per annum (95% CI: -0.1 to 5.6%) (Table 2). In comparison,
349 time since planting had a significant negative effect on species with high reproductive output
350 (clutch size multiplied by number of broods per season). Richness of these species decreased
351 on average by -0.9% per annum (95% CI: -1.8 to 0%).

352 In winter, time since planting had a significant positive effect on species that (1) are
353 associated with woodland habitat, (2) feed primarily on invertebrates, (3) forage in the
354 understorey or canopy, (4) are migratory or dispersive, (5) commonly occur in small groups,
355 (6) have low mass, and (7) have long relative wing lengths (Table 2). Increases ranged from
356 1.7% per annum for long relative wing length to 4.3% for species associated with woodland
357 habitat.

358 Investigating so many effects (18 groupings) is likely to lead to one or two significant
359 effects by chance, but it is clear that many of the traits are associated with an increase in
360 richness in winter (and, of course, these effects are inter-correlated). For instance, the
361 estimate of 4.3% increase per year for woodland species corresponded to a doubling in
362 species richness in 17 years after planting. However, the mean migratory species richness in
363 winter was only 2.3, so that doubling would increase the mean to 4.6 woodland migratory
364 species in that time.

365

366 **Discussion**

367 *Temporal changes in species richness and the occurrence of individual species*

368 We observed limited increases in bird species richness in plantings over time, and this was
369 only in winter and not in spring. Even in winter, the accumulation of species was relatively

370 modest with one additional species per seven years of planting maturation. The paucity of
371 marked temporal increases in bird species richness associated with increased planting age
372 was consistent with the strong evidence we obtained for significant temporal changes in the
373 occurrence of individual species in plantings. That is, gains in species were largely countered
374 by losses of other species over time and this was reflected in limited changes in overall
375 species richness.

376 We identified few differences in temporal changes in bird species richness between
377 remnants and plantings. In contrast, there were major differences in the occurrence of
378 individual bird species. Based on individual species responses, it remains unclear whether the
379 trajectory of post-establishment recovery of replanted areas will approach that of remnant
380 woodland “reference” sites or whether it is on another trajectory altogether (see also Wilkins
381 et al. 2003; Brady and Noske 2009). We are, however, acutely aware that our study has been
382 underway for 12 years and it may take much longer before bird assemblages in plantings
383 become similar to those typical of remnant woodlands.

384 The mechanisms underlying the temporal patterns of bird species richness and
385 individual species occurrence in plantings remain unclear. However, it is possible that
386 changes in vegetation structure altered the habitat suitability for particular species of birds
387 and this, in turn, was a factor underpinning temporal changes in individual species
388 occurrence. There is a large literature on relationships between bird diversity and habitat
389 structure ([MacArthur and MacArthur 1961](#)) ([Morrison et al 2006](#)) (Barton et al 2014). Other
390 factors associated with time, like the chance that dispersing birds will locate and settle in
391 plantings (Barrett et al. 2008) also may have influenced our findings for bird species richness,
392 although limited (if any) temporal increases in species richness suggest that new arrivals may
393 displace earlier colonists.

394 We uncovered strong evidence of marked temporal change in the occurrence of
395 particular bird species in plantings, the various ordination techniques we employed provided
396 no compelling evidence for simple combinations of species that characterized plantings of
397 different ages. Dominant axes or roots from these analyses explained only a small amount of
398 variation in our data. Large variation in bird species occurrence between sites and within sites
399 over time may explain the paucity of community composition effects.

400 Finally, a key caveat associated with this study is that our focus was on a single (albeit
401 species-rich) group. It is unclear whether our results for birds will be an accurate reflection of
402 the temporal responses of other groups such as invertebrates (Gibb and Cunningham 2010) or
403 reptiles (Cunningham et al 2007). Therefore, assessing the overall effectiveness of restoration
404 efforts should entail analyses of a range of taxa beyond a single group such as birds.

405 *Planting geometry and bird responses*

406 Our analyses indicated that of the various measures of planting geometry we examined, width
407 had the strongest effects on bird species richness; overall, wider plantings tended to support
408 significantly more bird species than narrow ones. This result was expected as it generally
409 conforms to predictions from landscape ecology theory with wider plantings expected to have
410 more interior vs edge habitat suitable for animal occupancy of sites (Lindenmayer and Hobbs
411 2007; Collinge 2009). However, only one species (the grey fantail) exhibited a significant
412 planting width effect, suggesting the majority of bird taxa are tolerant of edge environments
413 typical of most plantings in the agricultural environments in this study. This is broadly
414 congruent with other findings from this investigation indicating there were no significant
415 relationships between bird species richness and the width of woodland remnants (i.e. our so-
416 called “benchmark” sites). Finally, we found no statistical support for our hypothesized
417 response at the outset of this study that wider plantings should be characterised by faster rates
418 of increase in species richness than narrow plantings. This result may be related to the fact

419 that there was only relatively limited temporal change in overall bird species richness and
420 such effects therefore spanned plantings of a range of widths; *viz*: those that were narrow,
421 intermediate and wide.

422 ***Planting age and bird life-history attributes***

423 We found evidence that changes in the identity of birds occupying plantings of different age
424 can be anticipated in a broadly predictable way based on key life-history attributes,
425 particularly movement patterns and habitat and diet specialisation. For example, the
426 occurrence of woodland-associated species, insectivores, understorey and canopy foragers,
427 highly mobile (migratory and those with long relative wing lengths) species, solitary or
428 paired birds, and arboreal cup-nesters with low reproductive output.

429 Some of the bird life history responses were generally expected, such as the increase
430 in woodland-associated bird species with increasing planting age. Other responses may be
431 broadly linked with temporal changes in vegetation structure of plantings (see Table 1) and,
432 in turn, the suitability of nesting sites for some species (see Beruldsen 2003), as well as the
433 suitability of foraging substrates via changes in invertebrate assemblages associated with
434 plantings of different ages (Gibb and Cunningham 2010) (and hence prey for avian
435 insectivores). Migratory species were also more likely to increase in occurrence in older
436 plantings. Many migratory species in Australia (including winter migrants) often return to the
437 same areas year after year (Handbook of Australian and New Zealand Birds 1990-2006) and
438 these species are especially vulnerable to environmental change in their wintering habitat
439 (Runge et al 2014). It may therefore be some years after a planting has been established for
440 the offspring of such species to find revegetated areas.

441 ***Implications for management and biodiversity conservation***

442 We found that replanted areas of different ages supported different species of birds. Some
443 species associated with young plantings may drop out of restored ecosystems if new plantings

444 are not continuously added over time. We therefore suggest that plantings of a range of ages
445 will be needed on a farm to provide a range of suitable habitats for different native bird
446 species. However, our findings also suggest there is value in ensuring there are long
447 established plantings on farms. This is because such plantings will continue to accumulate
448 species over time (in winter).

449 A general recommendation for woodland restoration in Australia (and elsewhere) has
450 been to promote the establishment of wider areas of planted vegetation (Munro and
451 Lindenmayer 2011). Our results generally support these recommendations as wider plantings
452 support significantly greater levels of bird species richness than narrow plantings. However,
453 narrow plantings are clearly not without value as indicated by the fact that we identified only
454 one individual species that was sensitive to the effects of planting width.

455 Finally, we found strong evidence to suggest that the avifauna of plantings is markedly
456 different from that of remnants, even many years after planting establishment. It remains
457 unclear when (or even if) the bird fauna of plantings may begin to resemble that of woodland
458 remnants. Such differences underscore the value of maintaining different broad structural
459 kinds of vegetation on a farm to provide suitable habitat for a suite of native bird species.

460

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637 **Figure 1** Map of the study region in which plantings and remnants were surveyed for birds
638 between 2002 and 2013. The circular insets show plantings and remnants on two of the
639 surveyed farms.

640 **Figure 2** Fitted models for changes in bird species richness against time since planting, in
641 winter and spring separately, and observed richness at all sites and years excluding the single
642 site where the planting was more than 40 years old. The thick line shows the fitted trend with
643 time since planting, and the thin line the mean richness in remnants.

644 **Figure 3** Smoothing splines (with 4 d.f.) fitted for the effect of width of plantings on species
645 richness in spring and winter separately.

646 **Figure 4** Changes in occurrence of individual bird species in relation to time since planting,
647 for spring and winter separately. The length of the bars indicate the size of the change and the
648 colour of the bars show the direction of the change. Red bars show species that have
649 increased with time since planting (minimum % occurrence in the <8 years time period and
650 maximum % occurrence in the >16 years period). Blue bars show species that have declined
651 with time since planting (minimum % occurrence in >16 years' period and maximum %
652 occurrence in the <8 years period). Semi-purple bars show species that have increased then
653 declined (red and purple) or declined then increased (blue and purple). The black cross-bars
654 indicated % occurrence in the 8-16 years time period. Whiskers represent standard errors of
655 the end-points of each bar. Species names are shown in Online Resource 1.

656 **Figure 5** Changes in occurrence of woodland remnant bird species with an occurrence > 10%
657 of surveys across three groups defined by calendar time in spring and winter separately. (See
658 Figure 4 for further explanation).

659 **Table 1.** Vegetation measurements investigated for changes since time since planting. The
 660 estimates are the mean value across all years and average increases per year over the 30-year
 661 range (excluding the outlying oldest site); the counts and percentages were analysed on the
 662 log scale, so estimates are average percentage increases per year, relative to the previous
 663 year.

Measurement	Mean and SD	Estimate and 95% CI
Canopy height	9.9 m (4.1)	0.38 m (0.30, 0.46)
Canopy depth	7.7 m (3.3)	0.14 m (0.06, 0.22)
No. stems/ha	935 (993)	2.9% (-0.5, 5.3)
Basal count	6.9 (4.6)	6.0% (4.2, 7.9)
% Overstorey cover	16 (22)	17% (11, 24)
% Midstorey cover	26 (25)	0.0% (-3.7, 3.7)
% Understorey cover	3.0 (4.1)	-0.3% (-4.6, 4.2)
% Bare earth	13 (17)	-2.1% (-6.3, 2.3)

664

665 **Table 2.** Species attributes investigated for changes with time since planting. Estimates are
 666 the average percentage changes per year in species richness of each class, with 95%
 667 confidence limits. Four of the attributes were not investigated in winter, as nesting and
 668 breeding behaviour was not considered relevant in that season.

Attribute	Class	Spring		Winter	
		Estimate and 95% CI	P-value	Estimate and 95% CI	P-value
Habitat	Open country	-0.8 (-1.8, 0.2)	0.12	-1.0 (-2.4, 0.3)	0.14
	Woodland	0.3 (-1.2, 1.8)	0.74	4.3 (2.4, 6.1)	<0.001
Diet	Invertebrates	-0.2 (-1.4, 1.0)	0.78	2.7 (1.2, 4.2)	<0.001
	Other	-0.7 (-1.6, 0.3)	0.18	0.1 (-1.2, 1.4)	0.89
Foraging	Understorey or canopy	-0.6 (-1.9, 0.8)	0.42	4.0 (2.4, 5.6)	<0.001
	Other	-0.3 (-1.2, 0.7)	0.55	-1.2 (-2.6, 0.1)	0.08
Movement	Sedentary	-0.7 (-1.6, 0.2)	0.14	-0.2 (-1.3, 1.0)	0.79
	Migratory or dispersive	-0.2 (-1.3, 1.0)	0.76	3.9 (2.3, 5.4)	<0.001
Social system	Small groups	-0.1 (-1.3, 1.1)	0.87	2.6 (1.2, 3.9)	<0.001
	Large groups	-0.8 (-1.7, 0.2)	0.11	0.2 (-0.9, 1.4)	0.68
Nest type	Cup	-0.7 (-1.8, 0.4)	0.23		
	Other	-0.4 (-1.4, 0.6)	0.43		
Nest height	< 4m	0.4 (-1.4, 2.2)	0.67		
	>4 m	-0.7 (-1.6, 0.3)	0.17		
Mating behaviour	Co-operative	2.8 (0.1, 5.6)	0.04		

	Other	-0.7 (-1.6, 0.2)	0.13		
Repro. output	Low	0.7 (-0.8, 2.3)	0.36		
	High	-0.9 (-1.8, 0.0)	0.05		
Mass	Low	-0.6 (-1.9, 0.7)	0.36	2.6 (0.9, 4.4)	0.002
	High	-0.3 (-1.4, 0.8)	0.63	0.1 (-1.3, 1.6)	0.86
Relative wing length	Short	-0.8 (-2.1, 0.4)	0.18	0.7 (-1.1, 2.5)	0.47
	Long	-0.3 (-1.3, 0.7)	0.55	1.7 (0.6, 2.7)	0.002

Figure 1









