Exploring co-occurrence of closely-related guild members in a fragmented landscape subject to rapid transformation

David B. Lindenmayer[1, 2], Alan Welsh[3], Wade Blanchard[1], Philip Tennant[1,2], Christine Donnelly[1], Philip Barton[1]

[1]Fenner School of Environment and Society, The Australian National University, Canberra, ACT, 0200, Australia

[2]Long-term Ecological Research Network, Fenner School of Environment and Society, The Australian National University, Canberra, ACT, 0200, Australia

[3]Centre for Mathematics and its Applications, The Australian National University, Canberra, ACT, 0200, Australia

Corresponding author: David Lindenmayer, email: david.lindenmayer@anu.edu.au phone: +61 2 6125 0654, fax: +61 2 6125 0757

Running Head: Landscape change and co-occurrence patterns

Word count: Abstract 298; Text 6199 words; Refs 58

1 **ABSTRACT**

2 Quantifying biotic responses to landscape transformation is a major research focus. Most past

3 studies have explored co-occurrence of entire communities of a given group (e.g. birds)

4 within largely intact ecosystems or over a limited time-frame. By contrast, here we use data

5 from a 15-year experimental study, to explore intra-guild co-occurrence of six closely-related

6 and functionally-similar sets of birds within 55 woodland fragments. Areas surrounding these

7 remnants are undergoing transformation from grazed paddocks to *Pinus radiata* plantations,

8 leading to a novel assemblage of forest and woodland birds. We sought to determine if the

9 occurrence of a given species in a guild influenced the occurrence of other closely-related

10 species in that guild, and through this relationship whether there was evidence of co-

11 occurrence between species.

12 After controlling for environmental and habitat variables which can affect species occurrence

13 like time since commencement of landscape transformation, patch size and vegetation type,

14 we found the occurrence of a given species was influenced by the occurrence of a closely-

15 related species in the same guild. Co-occurrence varied among bird guilds and included: **(1)**

16 positive co-occurrence in which occurrence of one species within fragments positively

17 affected the occurrence of another closely-related guild member (e.g. Eastern and Crimson

18 Rosellas); and **(2)** negative co-occurrence in which the occurrence of one species was

19 negatively associated with the occurrence of another within the same guild (e.g. Willie

20 Wagtail and Grey Fantail).

21 We also identified interactions between patch size and species recording frequency within

22 members of two guilds. For example, modelling of conditional recording frequency revealed

23 the Eastern Rosella increased with increasing recordings of the Crimson Rosella in large

24 patches, but decreased with increasing recordings of the Crimson Rosella in small patches.

25   Our results provide empirical evidence of co-occurrence among guild members and

26   underscore the complexity of biotic responses to landscape transformation.

27   **Keywords:** Co-occurrence; birds; landscape change; plantation; woodland fragments.

INTRODUCTION

The occurrence of species in human-modified landscapes can be influenced by an array of factors (Zuidema et al. 1996), many of which can be intimately inter-related (Lindenmayer and Fischer 2006). These include habitat loss (Fahrig 2003), habitat fragmentation (Collinge 2009), temporal changes in habitat suitability (Felton et al. 2003), the size of remaining patches of habitat (Hanski 1994), edge effects (Ries et al. 2004), the condition of and changes in the matrix surrounding habitat patches (Driscoll et al. 2013), and altered key ecosystem processes (Galetti et al. 2013).

Species occurrence in rapidly transforming landscapes also may be influenced by the presence and abundance of other species (Maron and Kennedy 2007, Ovaskainen and Soininen 2011, Godsoe and Harmon 2012, Mac Nally et al. 2012). This may arise because of increased aggressive interactions between species (Mac Nally et al. 2012), increased levels of parasitism (Smith et al. 2003), and disrupted mutualisms (Bascompte and Jordano 2007). However, most studies of co-occurrence focus on entire communities of a given group of organisms (e.g. birds or mammals), have not taken place in landscapes undergoing rapid transformation, and/or are conducted either at one point in time or over a limited time-frame (2-3 years) (but see Heske et al. 1994, Sebastian-Gonzalez et al. 2012). Here we take a different approach by exploring the tendency of two species to occur together (or apart), after controlling for other factors that affect the occurrence of the species. We do this using systematic bird surveys from a 15 year observational study in a rapidly transforming landscape to examine co-occurrence among sets of closely-related, morphologically-similar and functionally-similar bird species.

Our study area was characterized by 55 fragments of temperate eucalypt woodland around which the landscape was undergoing marked and ongoing transformation from grazed paddocks to stands of densely-spaced Radiata Pine (*Pinus radiata*) plantation trees. The

53 landscape is therefore a mosaic (sensu Bennett et al. 2006) of woodland patches embedded

54 within an extensive exotic plantation. In Australia, temperature eucalypt woodland

55 ecosystems are recognized as a distinctly different environment from native eucalypt forest

56 ecosystems because of differences in: **(1)** dominant tree, understorey and ground cover plants,

57 **(2)** vegetation structure (Specht and Specht 1999), and **(3)** animal biota (Lindenmayer et al.

58 2010). In earlier work, we found that some forest-associated bird species have colonised the

59 exotic Radiata Pine stands and then spilled over to also occupy adjacent woodland fragments

60 (Lindenmayer et al. 2008). As a result, the woodland fragments support a novel assemblage

61 (sensu Hobbs et al. 2006) of woodland bird and forest bird species that does not occur

62 elsewhere in the region's forests or in the region's temperate woodlands (Lindenmayer et al.

63 2008). For a number of bird guilds, the woodland species and the forest species are closely

64 related and morphologically and functionally similar (see Appendix 1). Given this, the

65 primary question which underpinned our investigation was:

66 *Is the occurrence of a given species in a guild influenced by the occurrence of another closely*

67 *related species in that guild?*

68   We recognized three possible broad kinds of co-occurrence for this study. These were:

69 **(1)** Positive co-occurrence in which the occurrence within woodland patches of one species in

70 a given guild had a positive effect on the occurrence of another closely related species in that

71 same guild. **(2)** Negative co-occurrence in which the presence of one species was negatively

72 associated with the presence of another within the same guild. And **(3)** An absence of positive

73 or negative patterns of co-occurrence. That is, where there was no evidence of significant

74 positive or negative influence of one species on the occurrence of one or more members of

75 the same guild.

76   Theory and empirical studies suggest the existence of positive co-occurrence in some

77 ecosystems but negative co-occurrence in others (Ovaskainen et al. 2010, Andersen et al.

78   2013). Positive co-occurrence might occur because functionally similar and/or closely related

79   taxa might be adapted to similar environments (Ovaskainen et al. 2010) or gain mutual

80   benefits (like enhanced foraging opportunities in mixed-species feeding flocks) (Bell 1980,

81   Sridhar et al. 2012). An additional reason for positive co-occurrence could be that a given

82   species might choose habitat using information gleaned from other species present at a

83   location (Smith and Hellman 2002, Sebastian-Gonzalez et al. 2012), particularly a species

84   that is very similar to itself (Seppänen et al. 2007). Alternatively, two or more

85   morphologically and/or functionally similar species may exhibit negative co-occurrence

86   because of competition (e.g. see Alatalo et al. 1986, Lovette and Hochacka 2006, Steen et al.

87   2014), particularly when resources are limited (Newton 1998). Given the potential

88   manifestation of processes such as competition versus inter-specific attraction, we focused

89   this study on six closely-related, morphologically similar, and functionally similar guilds of

90   species to maximize the chances of detecting positive or negative co-occurrence (see Gaston

91   1996).

92   We were acutely aware that two species within a guild may co-occur in an area for

93   reasons other than the influence of one species on the other (e.g. by having similar habitat

94   requirements (Ovaskainen et al. 2010)). Therefore, a novel feature of our study was to

95   explore patterns of co-occurrence while accounting for habitat and environmental variables

96   that we believe also may influence the occurrence of particular species. These included

97   vegetation type and the time elapsed since the start of transformation of the landscape

98   surrounding the remnant woodland patches. We also recognized that the potential for the

99   occurrence of one species to affect the occurrence of another might be influenced by factors

100   like patch size. This may arise because, for example, large patches may support more

101   resources (see Zanette et al. 2000)) or more heterogeneous than small patches (Lindenmayer

102   and Fischer 2006). More resources and/or greater heterogeneity may make it possible for

103   closely related species to co-exist (Jeltsch et al. 1998) such as in large heterogeneous patches

104   but not in smaller, more homogeneous patches. Therefore, a second question we addressed in

105   this study was:

106   *If the presence of a given species is influenced by the occurrence of another closely-related*

107   *species from the same guild, does that relationship change with patch size? That is, is there*

108   *evidence of an interaction between the occurrence of a predictor species and patch size?*

109   **METHODS**

110   **Study area**

111   Our study region is called the Nanangroe area and it is 10-20 km south-east of the town

112   of Jugiong in southern New South Wales, south-eastern Australia (Fig. 1). Nanangroe lies

113   approximately 70 km north-west of Canberra (coordinates 34.9°–35.0°S and 148.4°–148.5°E,

114   altitudinal range: 250-750 m asl) and is characterised by a temperate climate (hot summers

115   and relatively cool winters). The original vegetation cover in the study area included several

116   temperate woodland vegetation types. Over 80 per cent of the vegetation cover in the study

117   area has been cleared in the past 150 years, primarily for domestic stock grazing (McKernan

118   2010). Vegetation in these heavily cleared paddocks is dominated by exotic pasture grasses

119   and isolated single trees that are the remnants of past woodland vegetation cover. Prolonged

120   periods of livestock grazing in the region meant that understorey vegetation of *Acacia* spp.

121   and other plants was largely absent from all areas of woodland in the study area. In several

122   parts of the region, an emerging pine plantation now surrounds patches of remnant woodland

123   that escaped earlier waves of land clearing. Further details of the study area can be found in

124   Lindenmayer et al. (2008).

125   **The design of the Nanangroe study**

126   In 1998, prior to commencement of landscape transformation to a pine-dominated

127   system, we randomly selected 55 of the 70 remnant woodland patches stratified by vegetation

128　class and woodland patch size. These woodland patches were exempt from clearing while

129　plantation establishment in the surrounding areas was undertaken. The 55 remnant woodland

130　patches varied in dominant vegetation type, including Yellow Box (*Eucalyptus melliodora*),

131　Red Box (*E. polyanthemos*), White Box (*E. albens*), Blakely's Red Gum (*E. blakelyi*), Apple

132　Box (*E. bridgesiana*) and Long-leaf Box (*E. goniocalyx*). In addition, there were patches

133　dominated by Red Stringybark (*E. macrorhyncha*), Broad-leaved Peppermint (*E. dives*), and

134　River Oak (*Allocasuarina cunninghamiana*).

135　　The size of the patches in our study ranged from 0.5 to 28.8 ha (median = 1.5 ha, 32

136　remnants < 2 ha) and they were typically located at least 500 m apart. Although our

137　investigation included some larger remnant patches (e.g. eight > 5 ha), numerous large

138　woodland patches were not available for study because of the extent of past land clearing for

139　agriculture and domestic livestock grazing in this part of Australia (McKernan 2010).

140　However, we note that over the past decade, in many patches, including the small patches,

141　there is strong evidence of breeding by many of the 15 species of birds we have targeted in

142　this study.

143　　Between 1997 and 2011 grazing by domestic livestock continued throughout the pine

144　plantation and the 55 patches of remnant woodland at Nanangroe. This was important to

145　ensure that grazing and landscape context effects were not confounded.

146　**Bird surveys**

147　　To survey birds, we established a permanent 200 m long transect randomly within each

148　of the 55 woodland patches. For each survey, two observers each visited three points at 0 m,

149　100 m and 200 m along the transect on different days; typically 2-4 days apart. At each point,

150　the observer recorded which species were detected in a 5 minute interval within the woodland

151　patch and within 50m of the point. The above layout of point-interval count stations within a

152　site was consistent across the study except in some of small patches where the third station

153 was placed closer than 100m to the second station. In the few instances where a portion of the

154 station's 50m radius was not confined within the woodland patch, our field protocols

155 restricted the recording of birds to only those within the patch (i.e. not in the adjacent pine

156 plantation). We completed field surveys in early November of the following years- 1999,

157 2001, 2003, 2005, 2007, 2009, and 2011. Early November is the peak breeding season in the

158 study region, when summer migrants are present and birds have established territories and

159 exhibit strong patterns of site fidelity (Lindenmayer et al. 2008). Detections were made

160 between 5.30-9.30am and were not undertaken on days of poor weather (rain, high wind, fog

161 or heavy cloud cover). The order in which particular sites were surveyed on any given day

162 was varied so that if birds were sampled, for example, late in the morning on a site on one

163 day, that site was surveyed early in a subsequent survey.

164   Bird observers with a minimum of ten years of experience completed surveys of forest

165 and woodland birds. These observers varied in their ability to detect some groups of birds but

166 Lindenmayer et al. (2009) showed that pooling counts of two or more observers at the same

167 plot point could compensate for extra variability due to observer heterogeneity. The 15

168 species we investigated in this study were readily recognizable taxa with distinctive calls.

169 Moreover, we were familiar with them from many previous studies in a range of

170 environments in south-eastern Australia (Lindenmayer et al. 2009). We therefore assumed

171 that mis-identification was low for the species in the six guilds included in this study.

172 **Bird guilds**

173   We selected six groups of birds for study using three key criteria. First, the members of

174 a group were closely related – almost always congeneric, always from the same family, and

175 always from the same dietary guild (see Appendix 1). Birds in the same group also were

176 similar in body size. Second, the six groups represented different foraging guilds, diets,

177 breeding strategies and other life history attributes. Therefore, our analyses enabled us to

178   determine if patterns of co-occurrence were consistent across groupings. A third criterion for

179   selection was that at least one member of a given set of birds was a woodland or open-

180   country species, whereas one or more of the others was a forest-associated species This

181   enabled us to explore whether there was avoidance by woodland-associated taxa of forest

182   birds in the respective groups of birds as the pine plantation stands surrounding the woodland

183   patches matured.

184   **Bird data used in statistical analyses**

185   We obtained bird species presence/absence data by pooling the six point-interval counts per

186   site for each survey year. We also examined a recording frequency index which was the

187   proportion of plots (out of a maximum of six in any given survey year) at which a given

188   species was recorded.

189   We made comparisons of bird taxa only within groups of similar species so the

190   interpretation of the recording frequency was the same for each species in a given group.

191   Finally, we used the same field methodology through time so the comparisons within groups

192   of similar species were meaningful.

193   **Statistical analyses**

194   We conducted our statistical analyses in a series of steps. First, we completed graphical

195   analyses to examine patterns in species occurrence and our recording frequency in relation to

196   plantation age, vegetation type and the presence and abundance of other guild member

197   species. Second, we used a univariate two-part binomial model to examine the factors

198   influencing the occurrence and conditional abundance of birds. Third, we fitted the Bayesian

199   multivariate logistic regression model of O'Brien and Dunson (2004) to determine the

200   consistency of results obtained from the univariate two-part models.

201   Welsh et al. (1996) used a two-part model to examine fauna abundance data. The first

202   component of their model estimates the probability of a species being present using binary

203   logistic regression and the second component models abundance, conditional on the animal

204   being present. The two-part model was developed using a zero-truncated Poisson or Negative

205   Binomial distribution for the second (conditional) part of the model (Welsh et al. 1996). We

206   have not measured abundance directly in this investigation, but adopt this general modelling

207   framework and substitute a truncated Binomial distribution for the second part of the model

208   to describe the recording frequency in lieu of a direct measure of abundance. We refer to the

209   second part of the model as the (mean) conditional recording frequency. The `vglm()` function

210   in the R VGAM package was used, with the second conditional part of the model fit using the

211   `posbinomial` (zero-truncated binomial) distribution family ([see Appendix 2 and Yee 2012](#)).

212   The two-part modelling approach allows for over-dispersion and both parts of the model

213   allow for serial dependence by including the lagged value of the response as an explanatory

214   variable. The lagged value is the response recorded in the previous survey two years before—

215   lagged presence for the first part of the model and lagged recording frequency for the second

216   part of the model. We used a lagged value of two years to account for the fact that our field

217   surveys were conducted two years apart.

218   A number of factors can influence species response in a complex, fragmented

219   agricultural environment. To more clearly identify the role that fellow-guild member species

220   may play in species occurrence (and through this, co-occurrence), it was advantageous to

221   include some key environmental covariates in the analysis. We fitted four types of two-part

222   binomial models which differed in their complexity or number of covariates.

223   **(1)** <u>The base model</u> included the lagged value of the response, guild member predictor

224   species, years since planting, and log patch size. The idea was that the potential explanatory

225   variables for guild member species captured positive (or negative) co-occurrence with a

226   positive coefficient (or a negative coefficient) and the years since planting captured change

227   through time as the Radiata Pine plantation surrounding the woodland patches matured. With

228   respect to the guild member predictor species term in the model, species presence is used for

229   the first (occurrence) part of the model and the recording frequency is used for the second,

230   conditional recording frequency stage. For all models, the focus was on the occurrence part of

231   the model but we also were interested to see if the conditional recording frequency revealed

232   any patterns among the species.

233   **(2)** <u>The vegetation model</u> included the same terms as the base model but also included a four

234   level factor for vegetation type which described the dominant vegetation community of the

235   remnants. The possible values for vegetation community type were: **(i)** Scribbly Gum

236   (<u>*Eucalyptus rossii*</u>)-stringybark (*E.macrorhyncha*)-silvertop ash *(E. sieberi)*; **(ii)** Swamp Gum

237   (*E. ovata*)-Snow Gum (*E. pauciflora*); **(iii)** Yellow Box (*E. melliodora*)-Blakely's Red Gum

238   (*E. blakelyi*)-River Oak (*Casuarina cunninghamiana)*; and **(iv)** a White Box (*E. albens*)

239   dominated community with associated Yellow Box and Blakely's Red Gum. Vegetation type

240   was coded to provide contrasts for each level against the baseline reference level Scribbly

241   Gum-stringybark-silvertop ash.

242   **(3)** <u>The interaction model</u> included an interaction term between guild member predictor

243   species (presence or conditional recording frequency) and log patch size in addition to the

244   terms included in the base model. And,

245   **(4)** A <u>composite model</u> which included vegetation type and the interaction terms, as well as

246   the terms included in the base model. We used the Bayesian (Schwarz) information criteria

247   (BIC) to choose between the four types of models for each bird species response (Schwarz

248   1978) (Appendix 4A).

249   For the univariate two-part models, we interpreted co-occurrence as significant

250   coefficients in paired sets of regressions within a set of guild models. For example, within a

251   guild, species B and C may have a positive effect on the probability of occurrence of the

252   response, species A. In a second, corresponding model, the probability of occurrence for

253 species B may be positively influenced by species A but not species C (*viz*: an absence of co-

254 occurrence). Here, we interpret this complementary result as evidence that species A and B

255 co-occur. The models will have one less predictor species than there are guild members: for a

256 guild with two members like the rosellas, there will be one predictor species and for the four-

257 member thornbill guild there will be three predictor species in each model. We note that the

258 second, conditional recording frequency part of the two-part model may also provide

259 evidence of co-occurrence under this interpretation, where a matching or reciprocal

260 relationship in regression coefficients is present.

261   The log patch size variable and vegetation type were of interest because occurrence and

262 recording frequency may depend on the size and dominant vegetation of a patch. As is usual

263 in transition models for longitudinal data, the lagged response variable was intended to

264 capture serial dependence and was not of interest in its own right. We examined spatial

265 dependence among sites for each response variable using variograms of the Pearson residuals

266 from each of the logistic regression models.

267   In the Bayesian multivariate logistic regression analysis, we modelled the joint

268 probability of occurrence of each species in a given guild. For each response component, we

269 fitted the lagged species occurrence indicator (as defined above for the two-part model) for

270 each species to capture the serial dependence, the years since planting of the surrounding

271 Radiata Pine plantation, and the logarithm of the patch size. Here, the co-occurrence effects

272 were obtained directly from the pairwise correlations between the different response

273 components on the logistic scale (O'Brien and Dunson 2004). For other applications of the

274 approach taken by O'Brien and Dunson (2004), see Ovaskainen et al. (2010) and Sebastian-

275 Gonzalez et al. (2012). Bayesian *P*-values (bpv) were reported to provide a measure of the

276 strength of evidence for individual terms in the model. All statistical analysis was done using

277 R (R Development Core Team 2013).

278 **RESULTS**

279   We summarize our data on the number of woodland patches occupied by each of the 15

280 species in the six guilds in each survey year in Table 1. These data highlight marked

281 interspecific differences and temporal changes in the number of occupied patches. Our

282 graphical approach revealed patterns in occurrence and recording frequency between species

283 within a guild. For example, there was increasing recording frequency of the Brown

284 Thornbill with increasing time since planting with some evidence that the rate or magnitude

285 of increase may differ among vegetation types. The frequency of recording of the Yellow-

286 rumped Thornbill appeared to decrease with increasing time since planting (Appendix 3).

287   The use of BIC to select from our four main groups of models resulted in the base

288 model being preferred in all but a few cases (see Appendix 4A). The results of univariate

289 two-part modelling provided evidence for positive co-occurrence in five pairs of species,

290 negative co-occurrence in one pair of species, and an absence of (positive or negative) co-

291 occurrence patterns in seven pairs of species. Positive co-occurrence occurred among

292 members of three guilds – the rosellas, flycatchers, and thornbills. Conversely, we found

293 evidence of negative co-occurrence among two members of the flycatcher guild. There was

294 no discernible pattern of (positive or negative) co-occurrence for the two members of the

295 treecreeper group, nor for the two members of the whistler group.

296 *Rosellas*

297   For the rosellas, the presence/absence component of the two-part model contained

298 evidence of co-occurrence (Fig. 2), and the probability of occurrence of the Eastern Rosella

299 decreased with years since planting (p=0.019, Fig. 2). For the Eastern Rosella, we identified

300 an interaction between log patch size and recording frequency of the guild member species

301 the Crimson Rosella (p<0.002); as the recording frequency of the Crimson Rosella increased,

302 the conditional recording frequency of the Eastern Rosellas fell for small patches but

303 increased in larger patches.

304 *Flycatchers*

305   In the flycatcher group, the Willie Wagtail and the Restless Flycatcher exhibited

306 positive patterns of co-occurrence while the Willie Wagtail and the Grey Fantail showed

307 negative co-occurrence (Fig. 3).

308 *Thornbills*

309   From the presence/absence component of the two-part models, we inferred patterns of

310 co-occurrence among the Striated Thornbill and the Brown Thornbill, the Striated Thornbill

311 and the Buff-rumped Thornbill, and the Buff-rumped Thornbill and the Yellow-rumped

312 Thornbill (Fig. 4). There was a positive interaction between log patch size and the guild

313 member predictor species – the Striated Thornbill ($p<0.005$) and the Yellow-rumped

314 Thornbill ($p=0.03$). As the numbers of the Striated or Yellow-rumped Thornbill increased,

315 the conditional recording frequency of the Buff-rumped Thornbill decreased in small patches

316 but increased within large patches. There was no evidence of a reciprocal interaction for

317 either the Striated or Yellow-rumped Thornbill. We note that both the Brown Thornbill and

318 the Buff-rumped Thornbill, and the Striated Thornbill and the Yellow-rumped Thornbill

319 exhibited no evidence of co-occurrence.

320 *Honeyeaters*

321   Although the paired regression coefficients were not significant for the honeyeaters

322 (indicating co-occurrence), we found weak evidence that the probability of occurrence of the

323 White-plumed Honeyeater was reduced when the Yellow-faced Honeyeater was present

324 ($p=0.064$, Fig. 2) and that the conditional recording frequency of the Yellow-faced

325 Honeyeater decreased as the conditional recording frequency of the White-plumed

326 Honeyeater increased ($p=0.013$).

327   Results obtained from fitting Bayesian multivariate logistic regression models (as per

328   O'Brien and Dunson 2004) were broadly consistent with those from the univariate two-part

329   binomial models and are summarized in Figure 5 and supplementary material (Appendices

330   4D and 4E)

331   We have focused the reporting of our results on evidence for co-occurrence. However,

332   our modelling also indicated that the presence and/or conditional recording frequency of

333   almost all species also was significantly influenced by factors such as time since planting, log

334   patch size, vegetation type or the presence and/or conditional abundance of fellow-guild

335   member species. The full results are listed in Appendices 3B and 3C. Examination of

336   variograms of Pearson residuals revealed no substantial, systematic spatial dependence

337   among the sites in our dataset.

338   **DISCUSSION**

339   Landscape change and habitat fragmentation are major land management issues

340   worldwide and understanding their impacts on biota is critical for developing informed

341   strategies for biodiversity conservation (Lindenmayer and Fischer 2006). Similarly,

342   quantifying patterns of co-occurrence and understanding the factors that influence such

343   patterns remains one of the most enduring and controversial issues in ecology (Sfenthourakis

344   et al. 2005, Ovaskainen et al. 2010, Sridhar et al. 2012, Andersen et al. 2013, Steen et al.

345   2014). Indeed, Dammhahn and Kappeler (2008, p. 473) noted that" *Understanding the co-*

346   *occurrence of ecologically similar species remains a puzzling issue in ecology*".

347   In this study, we have examined a topic that lies at the intersection of these two

348   substantial arenas of ecological research by exploring co-occurrence among closely related

349   (intra-guild) sets of bird species in a landscape subject to major and rapid change. Our

350   primary question was: *Is the occurrence of a given species in a guild influenced by the*

351   *occurrence of another closely related species in that guild?* The answer to this question was

352 yes for some of the members of several guilds– with the results of our landscape experiment

353 indicating that, after controlling for key factors like the time elapsed since landscape

354 transformation, there were effects of the presence or recording frequency of a given species

355 on the occurrence of other, closely-related and functionally-similar species in the same guild.

356 The existence of positive or negative co-occurrence varied among some sets of species and

357 also between species within the same guild, including for those cases where three or more

358 taxa were considered.

359   An interesting result of our investigation was an interaction between patch size and

360 recording frequency for the members of two bird guilds; with the conditional recording

361 frequency of one species in a group increasing with increasing frequency of another member

362 of the guild in large patches, but decreasing with increasing frequency in small patches. Thus,

363 the answer to our second question posed at the outset of this study – *Does the influence that*

364 *one species has on the presence of another change with patch size?* – also was yes, albeit not

365 for all species. We further discuss these and other findings in the remainder of this paper.

366 **Broad kinds of co-occurrence**

367 *Positive co-occurrence patterns*

368   A key aim of our study was to explore the types of co-occurrence among species in the

369 same guild in a rapidly transforming landscape, while at the same time controlling for other

370 factors which can influence species like time since landscape transformation commenced,

371 patch size and vegetation type. This novel environmental and habitat filtering approach

372 provided evidence of positive co-occurrence in three groups – the rosellas, flycatchers and

373 thornbills. For example, the probability of occurrence of the Eastern Rosella increased

374 significantly when the Crimson Rosella was present and the reverse (i.e. reciprocal) pattern

375 also was present. That is, the probability of occurrence of both species was positively

376 influenced by the presence of the other in the respective, paired models. Similarly, the

377 probability of occurrence of the Striated Thornbill increased significantly when the Brown

378 Thornbill was present. The complementary relationship also occurred. That is, the probability

379 of occurrence of the Brown Thornbill increased significantly when the Striated Thornbill was

380 present. Similar complementary relationships to those for the Striated and Brown Thornbills

381 were found for the Striated and Buff-rumped Thornbills, and the Buff-rumped and Yellow-

382 rumped Thornbills.

383 Several factors may explain the positive co-occurrence patterns that we observed in this

384 study. In the case of the thornbills, earlier studies of this group have shown that several

385 species of thornbills often form mixed feeding flocks (Bell 1980). Sridhar et al. (2012)

386 showed in an analysis of a global dataset that positive patterns co-occurrence can arise among

387 bird species which share similar taxonomy, body size and foraging methods. This may occur

388 because of co-operative benefits like the discovery of food resources or recognition of alarm

389 calls – that result from being a member of such kinds of flocks, especially when there is a

390 high level of similarly among species (Sridhar et al. 2012). Notably, other studies have found

391 that among some species such as breeding waterbirds, there is heterospecific attraction

392 leading to positive co-occurrence (Ovaskainen et al. 2010). Such patterns may arise because

393 of calling behaviour that alerts another species to the presence of predators or the location of

394 high quality habitat (Catchpole and Slater 1995, Smith and Hellman 2002). An additional or

395 alternative explanation for positive co-occurrence could be that a given species might choose

396 habitat using information gleaned from other species present at a location (Smith and

397 Hellman 2002, Sebastian-Gonzalez et al. 2012). This is particularly true for a species that is

398 very similar to itself (Seppänen et al. 2007) as occurs for many of the intra-guild members

399 examined in this investigation. However, a novel feature of our study was to explore patterns

400 of co-occurrence while accounting for habitat and environmental variables. This was

401 important as two species within a guild may co-occur because of similar habitat requirements

402   (Ovaskainen et al. 2010) and thus we attempted to account for this prior to exploring the

403   influence of one or more intra-guild members on another guild member. *Negative co-*

404   *occurrence patterns*

405   We recorded negative co-occurrence among two species in the flycatcher guild. We

406   found that after accounting for log patch size and years since planting, the probability of

407   occurrence of the Grey Fantail declined when the Willie Wagtail was present. The reciprocal

408   relationship also occurred in which (after accounting for other explanatory variables), the

409   occurrence of the Willie Wagtail declined when the Grey Fantail was present. Both these

410   species can be relatively aggressive and are known to attack other birds and this may explain

411   the negative co-occurrence or avoidance patterns we observed in this study. Notably, such

412   relationships were not observed with the third member of the flycatcher guild – the Restless

413   Flycatcher, suggesting asymmetrical co-occurrence patterns among group members

414   reinforced by the positive co-occurrence inferred from the model between the Willie Wagtail

415   and Restless Flycatcher. The Willie Wagtail and Restless Flycatcher are typically woodland

416   birds whereas the Grey Fantail is generally a forest-associated species. Indeed, the Willie

417   Wagtail and the Restless Flycatcher are common co-inhabitants of remnants of temperate

418   eucalypt woodland throughout large parts of inland eastern Australia. Conversely, it is

419   possible that the development of the novel ecosystem in the Nanangroe area has led to an

420   aggressive woodland species (the Willie Wagtail) avoiding an aggressive forest species (the

421   Grey Fantail).

422   There was weak evidence that the probability of occurrence of the White-plumed

423   Honeyeater was reduced when the Yellow-faced Honeyeater was present and that the

424   conditional recording frequency of the Yellow-faced Honeyeater decreased as the conditional

425   recording frequency of the White-plumed Honeyeater increased. These two species have

426   similar habitat, nesting and dietary requirements and it is possible that the negative

19

427 relationships in conditional abundance and occurrence (Fig. 2) reflects competition between

428 them. Notably, other authors have identified negative associations between the Yellow-faced

429 and White-plumed Honeyeaters (Kinross and Nicol 2008), although unlike this investigation,

430 they did not account for the effects of other important habitat-related factors such as

431 vegetation type that can influence occurrence.

432   We suggest that because we have controlled for factors like vegetation type in our

433 study, then the negative intra-guild co-occurrence patterns we observed are likely to be driven

434 by competition and resource availability. Transformation of the Nanangroe landscape has

435 altered the matrix around the remnants, and likely then altered the resources available to

436 species within the patches (Driscoll et al. 2013). This leads to altered competitive dynamics

437 among similar species, leading to "winners and losers" and in turn, changes in the bird

438 community over time to produce the novel assemblages (sensu Hobbs et al. 2013) observed

439 in the Nanangroe landscape (Lindenmayer et al. 2008).

440 **Patch size effects**

441   Our analyses revealed a significant interaction between log patch size and conditional

442 recording frequency for the Eastern Rosella and the Buff-rumped Thornbill with respective

443 guild members. In both cases, the patterns of increasing conditional recording frequency that

444 were accompanied by increasing recording frequency of guild member species in large

445 patches of woodland surrounded by maturing pine stands were reversed in small patches. The

446 reasons for these patch size effects remain unclear. However, at the outset of this study, we

447 postulated (see Question 2) that interactions between patch size and occurrence and/or

448 recording frequency patterns may occur because large patches may be more resource rich

449 and/or more heterogeneous than small patches. This may make it possible for closely-related

450 species to influence each other in small (less resource rich and more homogeneous) patches

451 but not in larger, more heterogeneous and more resource-rich patches. This postulate would

452 be consistent with work by authors such as Jeltsch et al. (1998) who have found that fine-

453 scale habitat heterogeneity can facilitate co-existence. Similarly, competition between species

454 might be particularly pronounced when resources are limited (Ford 1979, Newton 1998). On

455 this basis, a key future research task will be to carefully measure the structural and floristic

456 variability of the woodland patches in our study area and determine if larger patches are in

457 fact more heterogeneous than small patches. Such work, together with additional studies of

458 the habitat requirements of bird species, would aim to determine if measures of micro-

459 heterogeneity can help explain patterns of occurrence and/or recording frequency.

460   Some of the temperate woodland patches in our investigation were smaller (< 1 ha)

461 than the territory size of individuals of the species we examined. Given this, it is possible

462 these birds were using resources from multiple woodland patches or used such patches as

463 stepping stones (see Fischer and Lindenmayer 2002). Such spatially dispersed multiple patch

464 use may have provided opportunities for species within the same guild to co-occur.

465 Conversely, patterns of negative co-occurrence observed for some members of particular

466 guilds still imply that apparently competitively inferior species are using small patches less

467 often, including as stepping stones to other patches.

468 **Conservation implications**

469   Plantation forestry is increasingly recognised as a major driver of landscape change

470 around the worldwide (Felton et al. 2010, Hulvey et al. 2013). Many plantations are being

471 established in areas where patches of original native vegetation cover are retained (Bauhus et

472 al. 2010). This study has revealed that these retained patches support some key elements of

473 biota, but changes in the surrounding matrix can lead to significant changes in biodiversity,

474 including the development of novel assemblages (Lindenmayer et al. 2008). After controlling

475 for factors like time since plantation establishment and vegetation type, our results indicated

476 that the occurrence and abundance of a particular species in rapid transforming plantation

477   landscapes can be influenced by the occurrence and abundance of other closely-related and

478   functionally-similar species. Surprisingly, the majority of co-occurrence patterns were

479   positive, suggesting that novel assemblages of typically forest and woodland-associated birds

480   may promote the development of behaviours like mixed feeding flocks that might otherwise

481   not have occurred. However, because some of the observed co-occurrence patterns were

482   contingent upon patch size, we have identified potential "winners and losers" resulting from

483   plantation-generated landscape transformation. For example, the competitively inferior

484   Eastern Rosella (relative to the Crimson Rosella) and Buff-rumped Thornbill (relative to the

485   Striated and Yellow-rumped Thornbills) are likely losers in small patches of woodland

486   embedded within the maturing plantation-dominated landscape. From a conservation

487   perspective, this may, in turn, lead to elevated local and region extinction risks that are not

488   due to localised changes in habitat, but rather localised changes in competition among similar

489   species (within the same guild) as reflected by patch size mediated effects on co-occurrence

490   patterns. Such patch size mediated effects have significant implications for plantation design.

491   This is because they highlight the need to ensure the retention and subsequent maintenance of

492   large patches of remnant vegetation during plantation establishment (reviewed by

493   Lindenmayer and Hobbs 2004) and thereby avoid elevated levels of competition between

494   closely related species within small patches.

495   We argue that a better understanding of associations between species is important to

496   prevent problems like inter-linked extinctions (Saterberg et al. 2013) such as those of

497   particular species which result from losses of co-dependent or closely associated species

498   (sometimes termed co-extinction cascades; Koh et al. 2004, Bascompte 2009). This is also

499   useful to improve the ability to quantify the effects of landscape transformation and habitat

500   fragmentation on biota (Meyer and Kalko 2008) as well as better predict the potential

501   distributions of species (Elmendorf and Moore 2008), including species distribution patterns

502   in human-modified environments (Lindenmayer and Fischer 2006). Finally, we suggest that

503   the kind of work reported here is important as many studies recognize the need to conserve

504   not only species themselves, but also the associations among species as these are also critical

505   in the functioning and assembly of ecological communities (Bascompte and Jordano 2007,

506   Tylianakis et al. 2010).

507   **Concluding remarks**

508   We found that after controlling for factors like time since landscape change, vegetation

509   type and other factors, the occurrence and abundance of a particular species in landscapes

510   undergoing rapid transformation can be influenced by the occurrence and recording

511   frequency of other closely-related and functionally-similar species. Co-occurrence can be

512   either positive or negative and may also vary between different groups of species, even

513   within a given guild. Co-occurrence also can be influenced by factors like patch size,

514   sometimes in quite unanticipated ways. Together, our findings underscore the complexity of

515   biotic responses to rapid large-scale landscape transformations, like plantation expansion, and

516   indicate that some responses can be unexpected.

526   **REFERENCES**

527 Alatalo, R. V., et al. 1986. Interspecific competition and niche changes in tits (*Parus* spp.),

528 evaluation of nonexperimental data. - Am. Nat. 127: 819-834.

529 Andersen, A. N., et al. 2013. Limited niche differentiation within remarkable co-occurrence

530 of congeneric species: *Monomorium* ants in the Australian seasonal tropics. - Austral Ecol.

531 38: 557-567.

532 Bascompte, J. 2009. Disentangling the web of life. - Science 325: 416-419.

533 Bascompte, J. and Jordano, P. 2007. Plant-animal mutualistic networks: the architecture of

534 biodiversity. - Annu. Rev. Ecol. Evol. Syst. 38: 567-593.

535 Bauhus, J., et al. 2010. Ecosystem Goods and Services from Plantation Forests. - Earthscan.

536 Bell, H. L. 1980. Composition and Seasonality of Mixed-Species Feeding Flocks of

537 Insectivorous Birds in the Australian Capital Territory. - Emu 80: 227-232.

538 Bennett, A. F., et al. 2006. Properties of land mosaics: Implications for nature conservation in

539 agricultural landscapes. - Biol. Conserv. 133: 250-264.

540 Catchpole, C. K. and Slater, P. J. 1995. Bird Song. Biological Themes and Variations. -

541 Cambridge University Press.

542 Collinge, S. K. 2009. Ecology of Fragmented Landscapes. - The John Hopkins University

543 Press.

544 Dammhahn, M. and Kappeler, P. M. 2008. Small-scale coexistence of two mouse lemur

545 species (*Microcebus berthae* and *M. murinus*) within a homogeneous competitive

546 environment. - Oecologia 157: 473-483.

547 Driscoll, D. A., et al. 2013. Conceptual domain of the matrix in fragmented landscapes. -

548 Trends Ecol. Evol. 28: 605-613.

549 Elmendorf, S. C. and Moore, K. A. 2008. Use of community-composition data to predict the

550 fecundity and abundance of species. - Conserv. Biol. 22: 1523-1532.

551   Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. - Annu. Rev. Ecol. Evol.

552   Syst. 34: 487-515.

553   Felton, A., et al. 2010. A meta-analysis of fauna and flora species richness and abundance in

554   plantations and pasture lands. - Biol. Conserv. 143: 545-554.

555   Felton, A. M., et al. 2003. Orangutan population density, forest structure and fruit availability

556   in hand-logged and unlogged peat swamp forests in West Kalimantan, Indonesia. - Biol.

557   Conserv. 114: 91-101.

558   Fischer, J. and Lindenmayer, D. B. 2002. The conservation value of paddock trees for birds

559   in a variegated landscape in southern New South Wales. 2. Paddock trees as stepping stones.

560   - Biodiv. Conserv. 11: 833-849.

561   Ford, H. A. 1979. Interspecific competition in Australian honeyeaters - depletion of common

562   resources. - Aust. J. Ecol. 4: 145-164.

563   Galetti, M., et al. 2013. Functional extinction of birds drives rapid evolutionary changes in

564   seed size. - Science 340: 1086-1090.

565   Gaston, K. 1996. Biodiversity: A Biology of Numbers and Difference. - Blackwell Science.

566   Godsoe, W. and Harmon, L. J. 2012. How do species interactions affect species distribution

567   models? - Ecography 35: 1-10.

568   Hanski, I. 1994. Patch occupancy dynamics in fragmented landscapes. - Trends Ecol. Evol. 9:

569   131-135.

570   Heske, E. J., et al. 1994. Long-term experimental study of a Chihuahuan Desert Rodent

571   community: 13 years of competition. - Ecology 75: 438-445.

572   Hobbs, R. J., et al. (eds). 2013. Novel Ecosystems: Intervening in the New World Order. -

573   Wiley.

574   Hobbs, R. J., et al. 2006. Novel ecosystems: theoretical and management aspects of the new

575   ecological world order. - Glob. Ecol. Biogeogr. 15: 1-7.

576 Hulvey, K. B., et al. 2013. Benefits of tree mixes in carbon plantings. - Nature Climate

577 Change 3: 869-874.

578 Jeltsch, F., et al. 1998. Modelling the impact of small-scale heterogeneities on tree-grass

579 coexistence in semiarid savannas. - J. Ecol. 86: 780–793.

580 Kinross, C. and Nicol, H. 2008. Responses of birds to the characteristics of farm windbreaks

581 in central New South Wales, Australia. - Emu 108: 139-152.

582 Koh, L. P., et al. 2004. Ecological correlates of extinction proneness in tropical butterflies. -

583 Conserv. Biol. 18: 1571-1578.

584 Lindenmayer, D. B. and Hobbs, R. J. 2004. Fauna conservation in Australian plantation

585 forests - a review. - Biol. Conserv. 119: 151-168.

586 Lindenmayer, D. B. and Fischer, J. 2006. Habitat Fragmentation and Landscape Change. -

587 Island Press.

588 Lindenmayer, D. B., et al. 2009. Do observer differences in bird detection affect inferences

589 from large-scale ecological studies? - Emu 109: 100-106.

590 Lindenmayer, D. B., et al. (eds). 2010. Temperate Woodland Conservation and Management.

591 - CSIRO Publishing.

592 Lindenmayer, D. B., et al. 2008. Temporal changes in vertebrates during landscape

593 transformation: a large-scale "natural experiment". - Ecol. Monogr. 78: 567-590.

594 Lovette, I. J. and Hochacka, W. M. 2006. Simultaneous effects of phylogenetic niche

595 conservatism and competition on avian community structure. - Ecology 87: S14-S28.

596 Mac Nally, R., et al. 2012. Despotic, high-impact species and the subcontinental scale control

597 of avian assemblage structure. - Ecology 93: 668-678.

598 Maron, M. and Kennedy, S. 2007. Roads, fire and aggressive competitors: Determinants of

599 bird distribution in subtropical production forests. - Forest Ecol. Manag. 240: 24-31.

600 McKernan, M. 2010. The Valley. A Story from the Heart of the Land. - Allen and Unwin.

601   Meyer, C. F. and Kalko, E. K. 2008. Bat assemblages on Neotropical land-bridge islands:

602   nested subsets and null model analyses of species co-occurrence patterns. - Divers. Distrib.

603   14: 644-654.

604   Newton, I. 1998. Population Limitation in Birds. - Academic Press.

605   O'Brien, S. M. and Dunson, D. B. 2004. Bayesian multivariate logistic regression. -

606   Biometrics 60: 739–746.

607   Ovaskainen, O. and Soininen, J. 2011. Making more out of sparse data: hierarchical modeling

608   of species communities. - Ecology 92: 289-295.

609   Ovaskainen, O., et al. 2010. Modeling species co-occurrence by multivariate logistic

610   regression generates new hypotheses on fungal interactions. - Ecology 91: 2514–2521.

611   R Development Core Team. 2013. R: A Language and Environment for Statistical

612   Computing. R Foundation for Statistical Computing, Vienna, Austria.

613   Ries, L., et al. 2004. Ecological responses to habitat edges: Mechanisms, models, and

614   variability explained. - Annu. Rev. Ecol. Evol. Syst. 35: 491-522.

615   Saterberg, T., et al. 2013. High frequency of functional extinctions in ecological networks. -

616   Nature 499: 468-470.

617   Schwarz, G. E. 1978. Estimating the dimension of a model. - Ann. Stat. 6: 461-464.

618   Sebastian-Gonzalez, E., et al. 2012. Testing the heterospecific attraction hypothesis with

619   time-series data on species co-occurrence. - Proc. Roy. Soc. Lond. B 277: 2983-2990.

620   Seppänen, J. T., et al. 2007. Social information use is a process across time, space, and

621   ecology, reaching heterospecifics. - Ecology 88: 1622-1633.

622   Sfenthourakis, S., et al. 2005. Species co-occurrence: the case of congeneric species and a

623   causal approach to patterns of species associations. - Glob. Ecol. Biogeogr. 15: 39-49.

624   Smith, J. N. and Hellman, J. J. 2002. Population persistence in fragmented landscapes. -

625   Trends Ecol. Evol. 17: 397-399.

626   Smith, J. N., et al. 2003. How do Brown-headed Cowbirds (*Molothrus ater*) cause nest

627   failures in Song Sparrows (*Melospiza melodia)*? A removal experiment. - Auk 120: 772-783.

628   Specht, R. L. and Specht, A. 1999. Australian plant communities. Dynamics of structure,

629   growth and biodiversity. - Oxford University Press.

630   Sridhar, H., et al. 2012. Positive relationships between association strength and phenotypic

631   similarity characterize the assembly of mixed-species bird flocks worldwide. - Am. Nat. 180:

632   777-790.

633   Steen, D. A., et al. 2014. Snake co-occurrence patterns are best explained by habitat and

634   hypothezied effects of interspecific interactions. - J. Anim. Ecol. 83: 286-295.

635   Tylianakis, J. M., et al. 2010. Conservation of species interaction networks. - Biol. Conserv.

636   143: 2270-2279.

637   Welsh, A. H., et al. 1996. Modelling the abundance of rare species: statistical models for

638   counts with extra zeros. - Ecol. Model. 88: 297-308.

639   Zanette, L., et al. 2000. Food shortage in small fragments: evidence from an area- sensitive

640   passerine. - Ecology 81: 1654-1666.

641   Zuidema, P. A., et al. 1996. Forest fragmentation and biodiversity: the case for intermediate-

642   sized reserves. - Environ. Conserv. 2: 290-297.

643

644

645

646   **Table 1.** Number of detections of each bird species in each year. The values in a given cell

647   correspond to the number of eucalypt woodland remnants (out of 55) in which a particular

648   species was recorded in a given year. Note that including a lagged value of the response

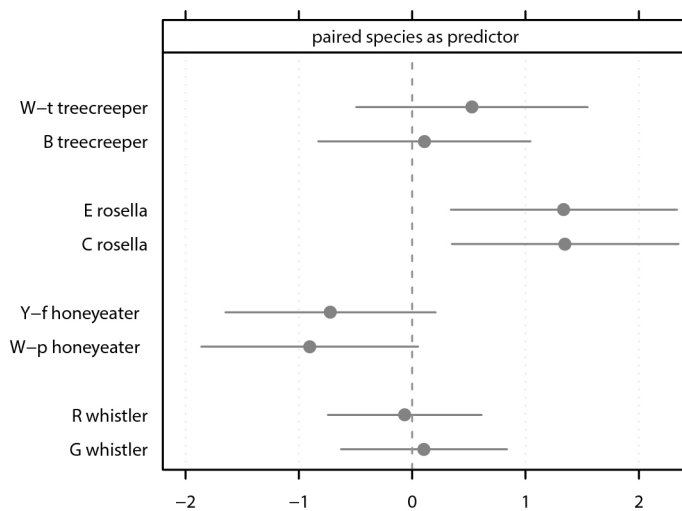649   resulted in data from 1998 and 2000 not being incorporated in the statistical modelling.

650

Species/ Year	1999	2001	2003	2005	2007	2009	2011
Brown Thornbill	19	16	20	31	45	49	51
Yellow-rumped Thornbill	13	11	7	6	6	10	7
Buff-rumped Thornbill	7	6	11	9	10	14	11
Striated Thornbill	12	13	11	25	24	26	36
Brown Treecreeper	8	5	4	3	5	3	3
White-throated Treecreeper	22	19	28	28	23	26	28
Crimson Rosella	27	32	35	33	39	42	41
Eastern Rosella	8	8	6	9	4	3	8
Golden Whistler	0	4	7	11	11	16	16
Rufous Whistler	29	29	40	41	39	43	42
White-plumed Honeyeater	18	28	15	15	15	9	3
Yellow-faced Honeyeater	30	36	43	54	53	51	55
Grey Fantail	32	41	40	48	49	54	55
Willie Wagtail	15	17	16	13	6	12	4

Restless Flycatcher	4	8	3	1	4	2	3

651

652

653   **Figure 1.** Location map of Nanangroe study site

654

655

656   **Figure 2.** Regression co-efficient estimates for guild member species as predictor from the

657   occurrence part of the two-part model. Estimates are presented in pairs where the response

658   species is listed in the left-hand margin with the 'paired species' included as an indicator

659   variable. Co-occurrence is inferred from the model where there are significant 'matching'

660   terms for the predictor species variable within a guild member pair (e.g. rosellas).
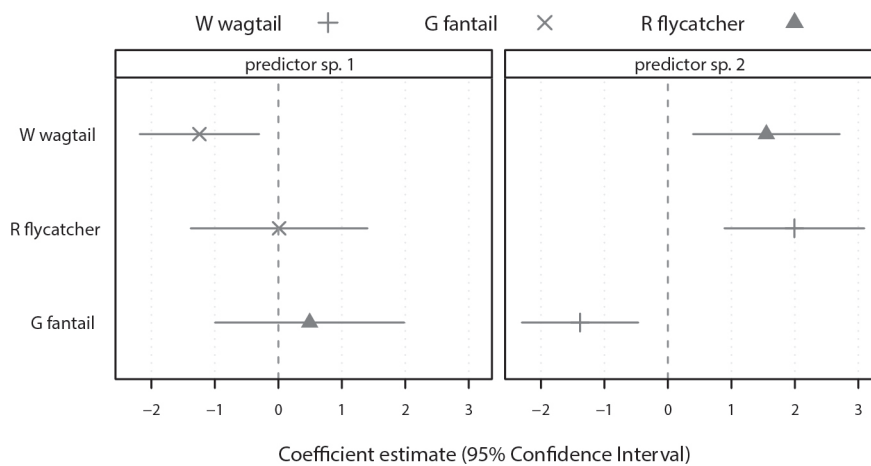
661
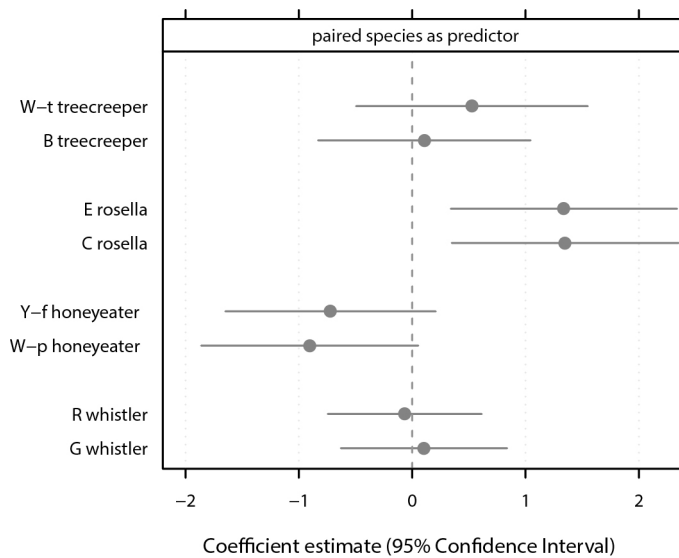
Figure 3. Flycatcher regression coefficient estimates for guild member species as predictors for the occurrence part of the two-part model. With three guild member species there are two predictor species in each model. For example, negative co-occurrence or avoidance is inferred between the wagtail and the restless flycatcher due to reciprocal, significant negative terms for the predictor species variable for these two species.
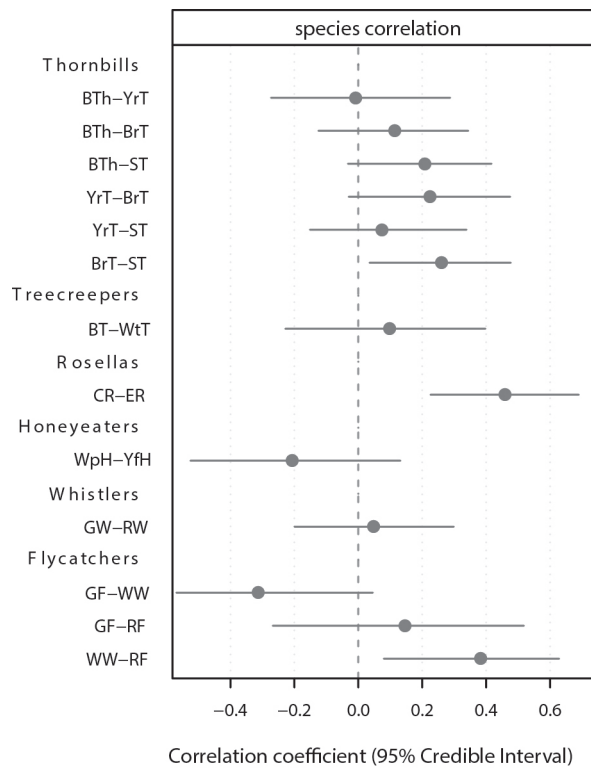
674   **Figure 4.** Thornbill regression coefficient estimates for guild member species as predictors

675   for the occurrence part of the two-part model. Each model has the occurrence of three guild

676   member species as predictors. For example, positive co-occurrence is inferred between the

677   Brown and Striated thornbills.

678   Coefficient estimate (95% Confidence Interval)
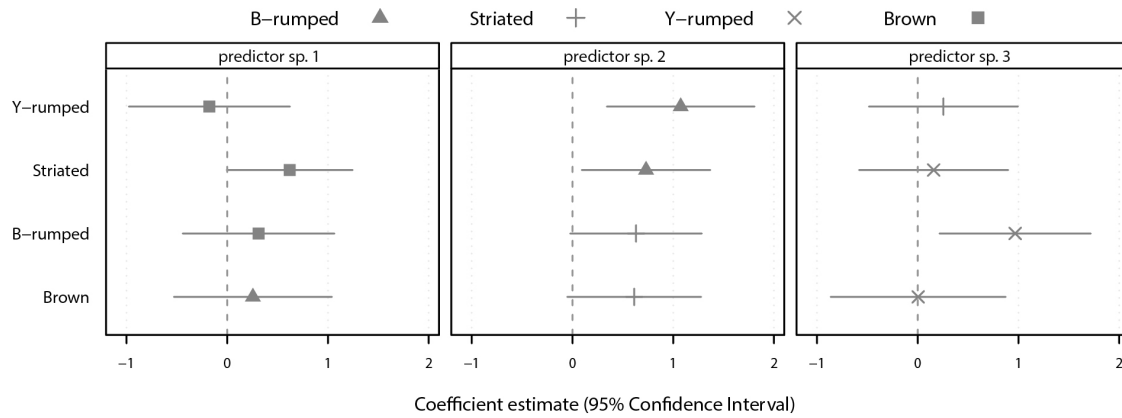
679

680   **Figure 5.** Correlation between paired species for the Bayesian multivariate logistic regression

681   models. Six models were fitted – one for each guild. Comparing the outcome of Bayesian

682   multivariate logistic regression modelling with the univariate two-part models showed that

683   the results were largely consistent between the two kinds of data analysis.

species correlation

Thornbills	
BTh–YrT	
BTh–BrT	
BTh–ST	
YrT–BrT	
YrT–ST	
BrT–ST	
Treecreepers	
BT–WtT	
Rosellas	
CR–ER	
Honeyeaters	
WpH–YfH	
Whistlers	
GW–RW	
Flycatchers	
GF–WW	
GF–RF	
WW–RF	

−0.4 −0.2 0.0 0.2 0.4 0.6

684

Correlation coefficient (95% Credible Interval)