

Shared environmental responses drive co-occurrence patterns in river bird communities

Royan, Alexander; Reynolds, S. James; Hannah, David; Prudhomme, Christel; Noble, David G.; Sadler, Jonathan

DOI:
[10.1111/ecog.01703](https://doi.org/10.1111/ecog.01703)

Document Version

Early version, also known as pre-print

Citation for published version (Harvard):

Royan, A, Reynolds, SJ, Hannah, D, Prudhomme, C, Noble, DG & Sadler, J 2015, 'Shared environmental responses drive co-occurrence patterns in river bird communities', *Ecography*, vol. 39, no. 8, pp. 733-742. <https://doi.org/10.1111/ecog.01703>

[Link to publication on Research at Birmingham portal](#)

Publisher Rights Statement:

Checked for eligibility: 27/01/2017

General rights

Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

Take down policy

While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact UBIRA@lists.bham.ac.uk providing details and we will remove access to the work immediately and investigate.

1 **Shared environmental responses drive co-occurrence**
2 **patterns in river bird communities**

3 Alexander Royan^{a*}, S James Reynolds^b, David M Hannah^a, Christel
4 Prudhomme^c, David G Noble^d, and Jonathan P Sadler^{a,b*}

5
6 ^aSchool of Geography, Earth & Environmental Sciences, College of Life &
7 Environmental Sciences, University of Birmingham, Birmingham B15 2TT, UK

8
9 ^bCentre for Ornithology, School of Biosciences, College of Life & Environmental
10 Sciences, University of Birmingham, Birmingham B15 2TT, UK

11
12 ^cCentre for Ecology and Hydrology, Wallingford OX10 8BB, UK

13
14 ^dThe British Trust for Ornithology, The Nunnery, Thetford IP24 2PU, UK

15
16 *Corresponding authors: axr196@bham.ac.uk; j.p.sadler@bham.ac.uk

17
18 Submitted to Ecography – Final accepted draft (13.5.2015)

19 **Abstract**

20

21 Positive or negative patterns of co-occurrence might imply an influence of biotic
22 interactions on community structure. However, species may co-occur simply because
23 of shared environmental responses. Here, we apply two complementary modelling
24 methodologies - a probabilistic model of significant pairwise associations and a
25 hierarchical multivariate probit regression model - to (i) attribute co-occurrence
26 patterns in 100 river bird communities to either shared environmental responses or to
27 other ecological mechanisms such as interaction with heterospecifics, and (ii) examine
28 the strength of evidence for four alternative models of community structure. Species
29 co-occurred more often than would be expected by random community assembly and
30 the species composition of bird communities was highly structured. Co-occurrence
31 patterns were primarily explained by shared environmental responses; species'
32 responses to the environmental variables were highly divergent, with both strong
33 positive and negative environmental correlations occurring. We found limited
34 evidence for behaviour-driven assemblage patterns in bird communities at a large
35 spatial scale, although statistically significant positive associations amongst some
36 species suggested the operation of facilitative mechanisms such as heterospecific
37 attraction. This lends support to an environmental filtering model of community
38 assembly as being the principle mechanism shaping river bird community structure.
39 Consequently, species interactions may be reduced to an ancillary role in some
40 avifaunal communities, meaning if shared environmental responses are not quantified
41 studies of co-occurrence may overestimate the role of species interactions in shaping
42 community structure.

43

- 44 **Key-words:** Assembly rules; Bayesian; Coexistence; Community assembly;
- 45 Community ecology; Ecohydrology; Hydroecology; River birds; Spatial analysis

46 **Introduction**

47 Species distributions are determined by a range of factors, including climate, land
48 cover, landscape barriers, dispersal ability and species interactions (MacArthur, R. H.
49 1972). Mechanistic models of community assembly predicate that the impacts of these
50 biotic and abiotic factors on the trait composition of communities manifest through
51 assembly rules (i.e. biological filters) and the ability of species to tolerate local
52 conditions (i.e. environmental filters) (Belmaker, J. and Jetz, W. 2013).

53 Environmental filters restrict community membership to species possessing a
54 particular set of functional traits (Petchey, O. L. et al. 2007). Conversely, a number of
55 positive (e.g. mutualisms and commensalisms), negative (e.g. competition) and
56 neutral models of species interaction may describe overlapping patterns in species
57 distributions (Araújo, M. B. and Rozenfeld, A. 2013). Such interactions may leave
58 imprints on species distributions that are detectable at large spatial scales (Baselga, A.
59 et al. 2012, Gotelli, N. J. et al. 2010, Heikkinen, R. K. et al. 2007); both positive and
60 negative interactions can be discernible across scales of hundreds of kilometres
61 (Araújo, M. B. and Rozenfeld, A. 2013). However, positive/negative associations can
62 result from species having similar/dissimilar habitat requirements as well as from
63 direct or indirect interactions (Ovaskainen, O. et al. 2010), meaning (dis)similarity in
64 habitat preference is a legitimate ecological explanation for why two species might
65 have positive (or negative) association. Consequently, disentangling the relative roles
66 of environmental and biotic factors in community assemblage processes *and*
67 understanding their link to spatial patterns in species distributions is a considerable
68 challenge and is a prominent unresolved issue in ecology (Barnagaud, J. Y. et al.
69 2014, Kraft, N. J. B. et al. 2014, MacArthur, R. and Levins, R. 1964, MacArthur, R. H.
70 1958, Peron, G. and Altwegg, R. 2015).

71 Associations between species have particularly pervasive impacts on bird
72 populations, where interspecific competition may influence the distribution, habitat
73 choice, abundance and reproduction of species (Cody, M. L. 1974), and interactions
74 between them have been detected in the distributions of species at large scales
75 (Gotelli, N. J. et al. 2010, Heikkinen, R. K. et al. 2007, Robertson, O. J. et al. 2013).
76 Community-wide patterns of spatial segregation in the Danish avifauna could not be
77 attributed to heterogeneity in the distribution of habitat or differences in habitat
78 utilisation, suggesting that the large-scale operation of species interactions (e.g.
79 interspecific territoriality and conspecific attraction) can cause behaviour-driven
80 assembly patterns (Gotelli, N. J. et al. 2010). However, it has been suggested that
81 habitat variability, disturbance regimes and food availability structure bird
82 communities at finer spatial scales, with geomorphic landforms and climatic
83 envelopes becoming more important in determining neighbourhood associations at
84 coarser scales (Börger, L. and Nudds, T. D. 2014, Gotelli, N. J. et al. 1997, Kroll, A.
85 J. et al. 2014, Mattsson, B. J. et al. 2013).

86 Considering the impact of both environmental and biotic effects, there are four
87 prevalent hypotheses that explain the distribution of heterospecifics (Mattsson, B. J. et
88 al. 2013): (1) a null hypothesis that species are distributed entirely randomly and
89 patterns of species occurrence do not conform to variability in habitat condition or the
90 distribution of heterospecifics (Hubbell, S. P. 2001); (2) the environmental filtering
91 hypothesis where community structure relates to variability in abiotic factors (e.g.
92 disturbance) with species partitioned according to abiotic constraints (Macarthur, R.
93 H. 1958). Community membership will therefore be restricted to those species
94 possessing a particular set of functional traits (Keddy, P. A. 1992, Petchey, O. L. et al.
95 2007, Weiher, E. and Keddy, P. A. 1995) and one might expect species occurrences to

96 be highly correlated with environmental variables; (3) the interspecific interaction
97 hypothesis, where species distributions are primarily influenced by the occurrence of
98 heterospecifics and species either aggregate in patches occupied by heterospecifics or
99 segregate to occupy empty patches. Individuals may cluster with heterospecifics
100 because of the benefits of group membership in terms of increased vigilance, reduced
101 predation risk and enhanced assessment of habitat quality (Ward, P. and Zahavi, A.
102 1973). Conversely, segregation may occur due to mechanisms such as competitive
103 exclusion (MacArthur, R. and Levins, R. 1967). In this interspecific interaction
104 hypothesis we would expect to find irregular distributions of species that are poorly
105 explained solely by environmental variables; (4) a pluralistic hypothesis in which
106 species not only interact and aggregate/segregate according to the distribution of
107 heterospecifics but they do so in a manner reflecting the patchiness of habitats that
108 promote fitness. These hypotheses can be termed 'surrogate hypotheses' as they are
109 assessed through an examination of patterns in data rather than by controlled
110 experimentation (Araujo, M. B. and Luoto, M. 2007) and provide a strong analytical
111 framework in macro-ecological studies where the manipulation of experimental
112 conditions is not possible (Gotelli, N. J. and McGill, B. J. 2006).

113 Investigation into non-random patterns of association between pairs of species
114 has largely centred on the comparison of presence/absence matrices with null models
115 (Gotelli, N. J. et al. 1997, Gotelli, N. J. et al. 2010, Ulrich, W. and Gotelli, N. J. 2010,
116 Weiher, E. et al. 1998). Analyses are based on inferences as to whether an observed
117 matrix differs from those produced by random processes or from a known ecological
118 mechanism. Investigations of these matrices have led to the analysis of empirical
119 patterns in species distributions and the development of ecological hypotheses for
120 community organisation, including the community assembly rules of Diamond, J. M.

121 (1975). However, it is not clear if it is possible to use such approaches to discriminate
122 between spatial patterns caused by species interaction and those caused by affinities
123 for particular habitats. An alternative method in modelling biotic interactions is to
124 restrict the distribution of one species by including the abundance of another as a
125 predictor alongside environmental variables (Meier, E. S. et al. 2010). However, the
126 abundance of heterospecifics could act as a surrogate for absent important
127 environmental variables (Araújo, M. B. and Luoto, M. 2007). Additionally, two-
128 species occupancy models can use species distribution data to model the probability
129 of occurrence of species pairs and show how the detection probability of either
130 species may change in the presence of the other (Richmond, O. M. W. et al. 2010).
131 This approach is well suited to the analysis of the co-occurrence of subordinate (e.g.
132 prey) species and dominant (e.g. predator) species (Robinson, Q. H. et al. 2014) but
133 has less applicability to macro-ecological studies of multiple species distributions.

134 In this study we aimed to: (a) investigate pairwise patterns in species co-
135 occurrence and partition co-occurrence into correlative responses to environmental
136 variables or potential species interactions, and (b) evaluate the evidence for the
137 operation of different community assembly processes. We applied two
138 complementary models to a large-scale dataset of river bird records for mainland
139 Great Britain, relating river bird occurrence data to variables that quantify land use
140 and long-term variability in climate and river flow. First we used the probabilistic
141 model of species co-occurrence developed by Veech, J. A. (2013) to calculate
142 significant positive, negative or random associations between species, which represent
143 all of the ways in which species can co-occur (Veech, J. A. 2014). We then compared
144 the output of the probabilistic model to that of a joint species distribution model
145 (JSDM) (Pollock, L. J. et al. 2014), which attributes co-occurrence patterns to either

146 shared environmental responses or other ecological processes (e.g. species
147 interactions) in a single integrated modelling process.

148 We addressed three specific objectives which were to: (i) examine patterns of
149 significant positive or negative co-occurrence in river bird communities across
150 mainland Great Britain; (ii) assess the strength of shared environmental responses
151 between species pairs relative to the strength of evidence for species interactions; and
152 (iii) characterise the composition of river bird communities and assess the importance
153 of species interactions in determining species distributions across different guilds.

154

155 **Material and methods**

156 *River bird data*

157 Bird survey data were obtained from the British Trust for Ornithology's (BTO's)
158 Waterways Breeding Bird Survey (WBBS), an annual large-scale national survey of
159 birds on rivers in Great Britain. Waterway locations for the WBBS are randomly
160 selected according to a stratification procedure (Marchant, J. H., Noble, D.G., Leech,
161 D.I., Freeman, S.N. 2002). First, national grid squares at 2×2 km resolution are
162 selected at random and those without a waterway are discarded. Waterways within
163 remaining squares are then identified according to the definition of any double blue
164 line, with shaded in-fill, on the OS 1:25,000 Pathfinder map series. A single waterway
165 within each square is then randomly selected, with the start and end points of the
166 survey location determined by the observer. Each year two visits are made to WBBS
167 survey locations by the same observer, one in the first half of the breeding season and
168 one in the second half; typically early April and late June, respectively. The WBBS
169 comprises transect methodology, with survey locations divided into 10 linear transects
170 of fixed 500 m length situated along one side of the waterway. The observer counts all

171 birds seen or heard within 100 m of each 500 m linear transect, with the total number
172 of transects surveyed (up to a maximum of 10) counted and recorded so that
173 heterogeneity in survey effort may be quantified and accounted for in subsequent
174 statistical analyses. As multiple visits to survey locations provide more reasonable
175 estimates of species occupancy and abundance which, in turn, reduce bias associated
176 with detection probability (McCarthy, M. A. et al. 2012), we selected WBBS survey
177 locations with a minimum of four repeated visits between 1998 and 2011 (inclusive).
178 In total, 100 WBBS locations were used, achieving wide coverage across mainland
179 Great Britain (Fig.1).

180 We used data for 19 bird species which were selected because they are largely
181 ubiquitous across riverine landscapes in Great Britain and sufficiently characterised
182 diversity in river bird communities (Royan, A. et al. 2013, Royan, A. et al. 2014).
183 Additionally, these species also possess an array of ecological traits, which provides
184 the opportunity to study a broad range of responses to the environmental variables and
185 interaction with heterospecifics (Newbold, T. et al. 2014, Vandewalle, M. et al. 2010),
186 whilst the relationship between their distribution in Great Britain and key
187 environmental variables is well characterised (Royan, A. et al. 2013, Vaughan, I. P. et
188 al. 2007). Our response variable was defined as the presence/absence of a bird species
189 at each of the 100 locations. Because waterbird distributions may shift across years
190 (Lehikoinen, A. et al. 2013), river bird occurrence data could potentially be influenced
191 by the date of survey. Occurrence data were, therefore, combined across visits to the
192 survey locations, whereby a species was recorded as present if it was observed during
193 surveys at any time between 1998 and 2011 (the presence/absence matrix is provided
194 in Table A1).

195 *Environmental data*

196 Bird distributions can be influenced by a range of environmental factors, including
197 heterogeneity in land use and habitat (Luck, G. W. et al. 2013), variability in climate
198 (Renwick, A. R. et al. 2012) and, in the case of river birds, variability in river flows
199 (Royan, A. et al. 2013). We therefore paired river bird occurrence data with variables
200 that quantify each of these environmental factors (Table 1).

201 Annual river flow data for the period 1998 to 2011 were obtained from the
202 National River Flow Archive (NRFA), organised by the Centre for Ecology and
203 Hydrology (CEH). River flow variables were calculated using long-term averages
204 between 1998 and 2011 (inclusive) and characterised variability around average, high
205 and low flows in the UK and were defined *a priori* according to (Royan, A. et al.
206 2013). To ensure the relevance of flow variables to the river bird data, all 100 WBBS
207 survey locations were situated within 10 km of a river flow gauging station. We also
208 ensured that there were no major tributary inflows or anthropogenic barriers located
209 between station-survey pairings.

210 Land use data were produced by the CEH as part of the Countryside Survey
211 2000 and were derived from the satellite-generated Land Cover Map 2000
212 (LCM2000) with a resolution of 50 m. Land use variables quantified the percentage of
213 the riverine catchment comprising woodland, arable, urban, heathland and grassland
214 habitats. Climate data for each survey location were obtained from the UKCP09
215 gridded observation datasets at 5×5 km resolution at monthly timescales and climate
216 variables were calculated using data between January 1998 and December 2011
217 (inclusive). Further details on how these data were derived can be found on the UK
218 Met Office website
219 (<http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/index.html>).
220 We calculated mean breeding season temperature ($^{\circ}\text{C}$) and total breeding season

221 rainfall (mm), with the breeding season defined as April to July (inclusive). We chose
222 to use climate variables calculated during the breeding season rather than annual or
223 winter variables as they have been shown to be better predictors of bird distributions
224 in Great Britain (Renwick, A. R. et al. 2012).

225 *Modelling procedure*

226 Initially, we used the probabilistic modelling approach developed by Veech, J.
227 A. (2013) to investigate statistically significant pairwise patterns in species co-
228 occurrence. The model calculates the expected frequency of co-occurrence between
229 each pair of species based on the distribution of one species being independent of the
230 second one. It then compares the expected frequency to the observed frequency and
231 returns the probability that a lower or higher value of co-occurrence could have been
232 obtained by chance. The probabilities can be interpreted as p values as the model
233 classifies species pairs into categories of significant positive, negative or random
234 association based upon an alpha threshold of 0.05.

235 We further analysed co-occurrence patterns using the JSMD developed by
236 Pollock, L. J. et al. (2014). This hierarchical modelling approach attributes co-
237 occurrence patterns to shared environmental responses and residual patterns of co-
238 occurrence and so can be used to investigate the mechanisms that influence the
239 structure and dynamics of species assemblages. For instance, evidence of strong
240 environmental correlation would support the hypothesis for the operation of
241 environmental filtering assembly mechanisms. Weak environmental correlation and
242 strong residual correlation would lend support to the interspecific interaction
243 hypothesis, although one cannot completely discount the possibility of some influence
244 of unmeasured habitat relationships (Börger, L. and Nudds, T. D. 2014). Evidence of
245 strong environmental correlation and also a broad range of residual correlation would

246 provide evidence for a pluralistic hypothesis of community organisation. The null
247 hypothesis of random community organisation would be supported if no significant
248 positive or negative pairwise associations were detected.

249 Full details of the JsDM can be found in Pollock, L. J. et al. (2014) but below
250 we summarise this approach in brief. Co-occurrence patterns were modelled using a
251 hierarchical probit regression model in which the linear environmental predictors
252 were related to a binary response variable using a latent variable formulation. The
253 probability of occurrence of each species at a site is determined by the mean of a
254 normal distribution (the latent variable), assuming a standard deviation of one,
255 whereby species are modelled as being present when the distribution mean is greater
256 than zero and modelled as absent when less than zero. Associations amongst species
257 are modelled by changing the locations of the latent multivariate normal distribution
258 and probabilities of co-occurrence by changing the correlations of the latent
259 distribution. The number of species being modelled determines the number of
260 dimensions of the multivariate normal distribution. The means of the normal
261 distribution were modelled using regression equations and a matrix of regression
262 coefficients. To relate species occurrences to the environmental variables, we
263 calculated the coefficients by fitting a Bayesian implementation of a binomial
264 generalized linear model (Gelman, A., Yu-Sung, S., Yajima, M., Hill, J., Pittau, M.G.,
265 Kerman, J., Zheng, T., Dorie, V. 2014), specifying a logit link function and a Cauchy
266 prior distribution for the coefficients to prevent coefficient inflation from complete
267 separation of occurrences across predictor variables (a common problem in logistic
268 regression) (Gelman, A. et al. 2008). Residual correlation is controlled by a matrix of
269 correlation coefficients in the latent distribution between species. This was calculated
270 by re-scaling the variance/covariance matrix of the multivariate normal distribution by

271 dividing the terms by the corresponding standard deviations and defining with an
272 inverse-Wishart prior. A second correlation matrix was also calculated to account for
273 the component of between-species correlation that is due to shared environmental
274 responses. The model estimates posterior distributions for four parameters:
275 correlations between species due to the environment, the residual correlation between
276 species, regression coefficients, and the predicted probability of occurrence of a
277 species at each site.

278 The model was fitted using the Markov Chain Monte Carlo Bayesian software
279 JAGS v3.4.0 in R v3.0.2 via R2jags v0.03-11 (Plummer, M. 2014). We ran five
280 chains for 100,000 iterations with the first 10,000 discarded as burn-in and the
281 remaining samples thinned by a factor of 10 such that 9,000 samples were retained for
282 analysis. We used vague normal priors for all model parameters (mean = 0, standard
283 deviation = 1).

284 We characterised the composition of river bird communities by converting the
285 matrix of species occurrences across the 100 river locations into a binary dissimilarity
286 matrix and by then using hierarchical cluster analysis, with Ward's clustering, to
287 create a dendrogram that illustrates the clustering of species occurrences. Non-
288 parametric analysis of variance tests (Kruskal-Wallis Rank Sum) were used to
289 investigate differences in the distribution of residual correlations between species
290 within each guild identified by clustering.

291 **Results**

292 Probabilistic modelling of species co-occurrence revealed instances of positive
293 (species co-occur significantly more frequently than expected), negative (species co-
294 occur significantly less frequently than expected) and random species associations
295 (observed frequency of co-occurrence does not significantly depart from expected).

296 Positive associations were more common than negative associations (Fig. 2). Because
297 the geographic range of all 19 species encompasses the whole of Great Britain, all 100
298 locations were used in the analysis of 171 species pairs; 42% of species associations
299 were positive, 11% were negative, and 47% were random. This indicates that the
300 species composition of bird communities largely followed non-random patterns of
301 community assembly, although random co-occurrence patterns were prevalent.

302 The output of the JSDM revealed that these pairwise associations could be
303 largely attributed to shared environmental responses. Species' responses to the
304 environmental variables were highly divergent, with both strong positive and negative
305 (e.g. $R > 0.7$ and $R < -0.7$) environmental correlations occurring (Fig. 3). The range
306 of residual correlation, however, was comparatively narrower and tended to be
307 positive. The strength of environmental correlation was considerably greater than that
308 of residual correlation (Fig. 4); where both environmental and residual correlation
309 were positive ($n = 110$), environmental correlation was stronger (i.e. closer to 1) in 83
310 of the pairwise associations, and where both environmental and residual correlations
311 were negative ($n = 23$), environmental correlation was stronger (i.e. closer to -1) in 20
312 of the pairwise associations.

313 Hierarchical cluster analysis revealed that the communities can be
314 decomposed into three guilds, whereby species within each guild were likely to co-
315 occur due to similar environmental tolerances (Fig. 5). Species within each guild
316 displayed similar characteristics for foraging habitat and resource acquisition. These
317 were species that forage on fast-flowing rivers (i.e. common sandpiper [*Calidris*
318 *hypoleucos*], white-throated dipper [*Cinclus cinclus*], common merganser [*Mergus*
319 *merganser*], grey wagtail [*Motacilla cinerea*]), those that forage on large, slow-
320 flowing rivers (i.e. Eurasian coot [*Fulica atra*], great cormorant [*Phalacrocorax*

321 *carbo*], great crested grebe [*Podiceps cristatus*], common kingfisher [*Alcedo atthis*],
322 common moorhen [*Gallinula chloropus*], mute swan [*Cygnus olor*], Eurasian reed
323 warbler [*Acrocephalus scirpaceus*], sedge warbler [*A. schoenobaenus*], western
324 yellow wagtail [*Motacilla flava*]), and species that forage at riparian margins across a
325 range of rivers (i.e. northern lapwing [*Vanellus vanellus*], Eurasian oystercatcher
326 [*Haematopus ostralegus*], common redshank [*Tringa totanus*], common reed bunting
327 [*Emberiza schoeniclus*], white wagtail [*Motacilla alba*], and sand martin [*Riparia*
328 *riparia*]). Further analysis of the residual correlation between species within these
329 guilds revealed additional complexities in species covariance patterns. Residual
330 correlation was significantly higher between species within the riparian guild than
331 between species within the slow-flowing guilds (Kruskal-Wallis: $\chi^2 = 15.70$, $p <$
332 0.001) (Fig. 6).

333

334 **Discussion**

335 The diversity and complexity of abiotic and biotic factors that influence species
336 distributions present considerable challenges in the exploration of alternative
337 community assembly processes. The processes themselves may be too difficult and
338 complex to monitor directly and so inference is limited to indirect approaches, such as
339 the analysis of co-occurrence (Ovaskainen, O. et al. 2010) and the testing of surrogate
340 hypotheses (Araújo, M. B. and Luoto, M. 2007). Species interactions affect the
341 distribution of many bird species (Cody, M. L. 1974). However, the importance of
342 interactions between species in structuring bird communities at macro-ecological
343 scales is hotly debated in the ecological literature (Araújo, M. B. and Luoto, M. 2007,
344 Araújo, M. B. and Rozenfeld, A. 2013, Gotelli, N. J. et al. 2010, Heikkinen, R. K. et
345 al. 2007, Kroll, A. J. et al. 2014, Meier, E. S. et al. 2010, Ovaskainen, O. et al. 2010).

346 Here, we analysed co-occurrence in river bird communities across Great
347 Britain and assessed the degree to which patterns could be attributed to shared
348 environmental responses. This allowed us to test alternative community assembly
349 hypotheses: a null hypothesis of random assembly, environmental filtering,
350 interspecific interaction, and a pluralistic model of assembly. However, our discussion
351 is not limited to mechanistic models of community assembly but we also consider the
352 influence of the filtering of species from regional species pools on community
353 structure. We found that species co-occurred more often than random and that co-
354 occurrence patterns were primarily explained by shared environmental responses.
355 Species co-occurrences were strongly related to the environmental predictor variables,
356 whilst residual correlation was comparatively weak. These findings suggest that
357 environmental filtering is the dominant mechanism operating to structure river bird
358 assemblages and that interspecific interaction is reduced to an ancillary role.

359 Whilst our results corroborate the findings of some studies in suggesting that
360 species interactions are of secondary importance relative to habitat structure and
361 resource availability (Börger, L. and Nudds, T. D. 2014, Gotelli, N. J. et al. 1997,
362 Kroll, A. J. et al. 2014, Mattsson, B. J. et al. 2013, Petchey, O. L. et al. 2007), they
363 contrast markedly with others (Gotelli, N. J. et al. 2010, Heikkinen, R. K. et al. 2007,
364 Robertson, O. J. et al. 2013, Sebastian-Gonzalez, E. et al. 2010). One reason for this
365 might be that we focussed on bird communities on riverine systems which are highly
366 dynamic, disturbance-prone environments in which river flow is the dominant driver
367 of changes in ecosystem structure (Junk, W. J. et al. 1989). High levels of
368 environmental disturbance result in rapid turnover of biota through flow-induced
369 spatial and temporal heterogeneities in the prevalence of key foraging and breeding
370 habitats (Ward, J. V. et al. 2002). Perturbations in aquatic-riparian food webs also

371 cause irregularity in ecological processes such as production and biotic interactions
372 (Ledger, M. E. et al. 2012). Heterogeneity in external factors such as land-cover
373 complexity and the availability of foraging habitat also exerts strong formative
374 pressure on the structure of bird communities (Devictor, V. et al. 2007, Mattsson, B. J.
375 et al. 2013, Robertson, O. J. et al. 2013). Consequently, in riverine systems the
376 influence of abiotic factors in constraining bird species distributions is likely to be
377 strengthened, with species interactions such as competitive filtering reduced to a
378 minor role. Moreover, it is plausible that those species with the greatest exposure to
379 abiotic disturbance are the least likely to be connected to other species in the
380 community and so are less influenced in distribution by interspecific interaction
381 (Araujo, M. B. et al. 2011). Evidence from bird communities indicates that when
382 species richness is depressed by disturbance, abiotic constraints are more important
383 than species interactions in structuring species assemblages (Belmaker, J. et al. 2012).

384 However, the predictive performance of the JSMD varied between bird
385 foraging guilds, with residual correlation most positive amongst riparian species. It
386 may be the case that a few species in the community have close links to others in the
387 community network with most species poorly connected to others, with a tendency for
388 individualistic behaviour and partitioning (Araújo, M. B. et al. 2011). This perhaps
389 indicates a reduced impact of environmental filtering and an enhanced influence of
390 species interactions on riparian species distributions. Therefore, a pluralistic model of
391 community organisation may be more appropriate for some avian taxa. Riparian
392 species such as the common redshank, Eurasian oystercatcher and northern lapwing
393 forage in ephemeral patches of habitat. It is plausible that competition amongst these
394 functionally similar species for transitory food resources is likely and that this would
395 lead to segregation (MacArthur, R. and Levins, R. 1967). Yet, co-occurrence between

396 these species was observed to be positive, suggesting the operation of an alternative
397 model of interspecific interaction such as heterospecific attraction. However, positive
398 residual correlation could also be caused by an unmeasured variable for habitat
399 quality which might influence species distributions. It is possible that the habitat, river
400 flow and climate variables used to model species distributions did not fully capture
401 variability in ephemeral habitat patches, which are utilised by species such as the
402 Eurasian oystercatcher and northern lapwing. It is also possible that an enhanced
403 influence of interspecific interaction might have been detected by using abundance
404 rather than presence data as there is some evidence that mechanisms underlying
405 abundance variations occur at community scales where species interaction is greatest
406 (Boulangeat, I. et al. 2012).

407 Heterospecific attraction can lead to positive patterns of co-occurrence as
408 species preferentially select patches of habitat already occupied by heterospecifics,
409 whereby individuals may use the presence of other species as an indicator of patch
410 quality (Monkkonen, M. et al. 1990). Such patterns have previously been observed in
411 some waterbird species including riparian waders (Sebastian-Gonzalez, E. et al.
412 2010). Facilitative processes like heterospecific attraction are thought to be more
413 prevalent in disturbed environments by increasing the average fitness of individuals of
414 a species that could not survive in isolation (Villarreal-Barajas, T. and Martorell, C.
415 2009). However, this requires intraspecific to be stronger than interspecific
416 competition, allowing for niche partitioning (MacArthur, R. and Levins, R. 1967), or
417 for resources to be sufficiently abundant that competitive exclusion is minimised.
418 Interspecific competition between the sympatric riparian species in our study is likely
419 to be reduced, in part, because of the disparity between body sizes which allows for
420 different foraging strategies and the exploitation of different food resources, thus

421 facilitating co-existence through spatial niche separation (Leyequien, E. et al. 2007).
422 Furthermore, temporal niche separation, as exhibited by nocturnally foraging northern
423 lapwings, may also enable co-existence.

424 Patterns of random co-occurrence were relatively prevalent amongst river bird
425 communities. There are several reasons why such patterns might be observed. First,
426 random patterns of co-occurrence may indicate a strong influence of the filtering of
427 species from the regional species pool which may be greatest at locations with lower
428 productivity and reduced competitive exclusion (Houseman, G. R. and Gross, K. L.
429 2006). Variability in river flows exerts a strong disturbance regime that can limit
430 productivity in aquatic-riparian environments which, in turn, prevents competitive
431 exclusion (Bunn, S. E. and Arthington, A. H. 2002, Ledger, M. E. et al. 2012, Poff, N.
432 L. R. et al. 1997). Consequently, the natural disturbance regime of rivers may enhance
433 ecological filtering from species pools into local communities via heightened abiotic
434 filtering which maintains productivity at relatively low levels. In support of this
435 theory, the percentage of co-occurrence patterns that were random was higher at river
436 locations with greater river flow variability than at locations with more stable river
437 flow regimes (Figure A1). Secondly, patterns of random co-occurrence could also be
438 caused by the operation of multiple environmental factors which cause both
439 aggregation and segregation of species distributions, as it has been shown
440 experimentally that contrasting environmental processes might counterbalance each
441 other to co-produce patterns of random species co-occurrence (García-Baquero, G.
442 and Crujeiras, R. M. 2015). Finally, patterns of random co-occurrence could also arise
443 as a consequence of imperfect detection of some species which leads to false absences
444 in the species presence/absence matrix (MacKenzie, D. I. et al. 2004). However, we

445 aimed to minimise the potential for bias caused by species detection probability by
446 only using survey locations that were visited on several occasions.

447 In summary, co-occurrence patterns were primarily driven by shared
448 environmental responses. We found limited evidence for behaviour-driven
449 assemblage patterns in bird communities at a relatively large spatial scale.
450 Consequently, by underestimating the prevalence of shared environmental responses
451 studies based solely on analyses of null model matrices or probabilistic models may
452 overstate the influence of species interactions on community structure. However, we
453 also found that pluralistic models of community assembly may be more appropriate
454 for some avian taxa and that the high disturbance regimes of rivers may enhance
455 random ecological filtering of species into avian assemblages. Therefore, our results
456 still highlight the necessity to consider biotic interactions in the modelling of species
457 distributions, especially in environments where gradients of disturbance exist and
458 facilitative mechanisms such as interspecific attraction may operate to promote
459 positive associations amongst some species. Our analyses also highlight the value of
460 long-term and large-scale bird monitoring programmes for the collation of data that
461 allow for macro-ecological studies of community-level interaction strengths.

462

463 **Acknowledgements**

464 We would like to thank Michael McCarthy, Miguel Matias, Joseph Veech and two
465 anonymous referees for reviewing and providing comments on previous versions of
466 this manuscript, and Nick Golding for assistance with the JSJM code. We also extend
467 gratitude to the BTO for access to WBBS datasets, Mark Hulme and John Marchant
468 for preparing raw data, and the many BTO volunteers who collected WBBS data
469 during surveys between 1998 and 2012 (inclusive), with funding for the survey

470 provided by the Environment Agency and the BTO. National River Flow Archive
471 (NRFA) data were provided by the Centre for Ecology & Hydrology (CEH). This
472 research was made possible by financial support to AR from a National Environment
473 Research Council (NERC) studentship (NE/J500240/1).

474

475 **References**

- 476 Araújo, M. B. and Luoto, M. 2007. The importance of biotic interactions for
477 modelling species distributions under climate change. — *Global Ecology and*
478 *Biogeography* 16: 743-753.
- 479 Araújo, M. B. and Rozenfeld, A. 2013. The geographic scaling of biotic interactions.
480 — *Ecography* 37: 406-415.
- 481 Araújo, M. B. et al. 2011. Using species co-occurrence networks to assess the impacts
482 of climate change. — *Ecography* 34: 897-908.
- 483 Barnagaud, J. Y. et al. 2014. Habitat filtering by landscape and local forest
484 composition in native and exotic New Zealand birds. — *Ecology* 95: 78-87.
- 485 Baselga, A. et al. 2012. Global patterns in the shape of species geographical ranges
486 reveal range determinants. — *Journal of Biogeography* 39: 760-771.
- 487 Bayliss, A. C. and Davies, H. N. 2003. Evaluation of the Mapping and Assessment of
488 Urban and Suburban Areas. Final Report, R&D Project FD 1919. Report to
489 Defra/Environment Agency. 35 pp.
- 490 Belmaker, J. and Jetz, W. 2013. Spatial scaling of functional structure in bird and
491 mammal assemblages. — *American Naturalist* 181: 464-478.
- 492 Belmaker, J. et al. 2012. Global patterns of specialization and coexistence in bird
493 assemblages. — *Journal of Biogeography* 39: 193-203.
- 494 Börger, L. and Nudds, T. D. 2014. Fire, humans, and climate: modeling distribution
495 dynamics of boreal forest waterbirds. — *Ecological Applications* 24: 121-141.
- 496 Boulangeat, I. et al. 2012. Accounting for dispersal and biotic interactions to
497 disentangle the drivers of species distributions and their abundances. —
498 *Ecology Letters* 15: 584-593.
- 499 Bunn, S. E. and Arthington, A. H. 2002. Basic principles and ecological consequences
500 of altered flow regimes for aquatic biodiversity. — *Environmental*
501 *Management* 30: 492-507.
- 502 Cody, M. L. 1974. *Competition and the Structure of Bird Communities*. — Princeton
503 University Press.
- 504 Devictor, V. et al. 2007. Functional homogenization effect of urbanization on bird
505 communities. — *Conservation Biology* 21: 741-751.
- 506 Diamond, J. M. 1975. Assembly of species communities. — In: Diamond, M. L. C. J.
507 M. (ed), *Ecology and Evolution of Communities*. Harvard University Press,
508 pp. 342-444.
- 509 García-Baquero, G. and Crujeiras, R. M. 2015. Can environmental constraints
510 determine random patterns of plant species co-occurrence? — *Ecology and*
511 *Evolution Early View*:

- 512 Gelman, A. et al. 2008. A weakly informative default prior distribution for logistic
513 and other regression models. — *The Annals of Applied Statistics* 1360-1383.
- 514 Gelman, A., Yu-Sung, S., Yajima, M., Hill, J., Pittau, M.G., Kerman, J., Zheng, T.,
515 Dorie, V. 2014. arm: Data Analysis Using Regression and
516 Multilevel/Hierarchical Models. R package version 1.7-07. — Available at
517 <http://CRAN.R-project.org/package=arm>.
- 518 Gotelli, N. J. et al. 1997. Co-occurrence of Australian land birds: Diamond's assembly
519 rules revisited. — *Oikos* 80: 311-324.
- 520 Gotelli, N. J. et al. 2010. Macroecological signals of species interactions in the Danish
521 avifauna. — *Proceedings of the National Academy of Sciences of the United*
522 *States of America* 107: 5030-5035.
- 523 Gotelli, N. J. and McGill, B. J. 2006. Null versus neutral models: what's the
524 difference? — *Ecography* 29: 793-800.
- 525 Griffith, D. M., Veech, J.A. & Marsh, C.J. In press. co-occur: Probabilistic species co-
526 occurrence analysis in R. — *Journal of Statistical Software*
- 527 Heikkinen, R. K. et al. 2007. Biotic interactions improve prediction of boreal bird
528 distributions at macro-scales. — *Global Ecology and Biogeography* 16: 754-
529 763.
- 530 Houseman, G. R. and Gross, K. L. 2006. Does ecological filtering across a
531 productivity gradient explain variation in species pool-richness relationships?
532 — *Oikos* 115: 148-154.
- 533 Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*.
534 — Princeton University Press.
- 535 Junk, W. J. et al. 1989. The flood pulse concept in river-floodplain systems. —
536 *Canadian Special Publication of Fisheries and Aquatic Sciences* 106: 110-127.
- 537 Keddy, P. A. 1992. Assembly and response rules - 2 goals for predictive community
538 ecology. — *Journal of Vegetation Science* 3: 157-164.
- 539 Kraft, N. J. B. et al. 2014. Community assembly, coexistence, and the environmental
540 filtering metaphor. — *Functional Ecology Early view*:
- 541 Kroll, A. J. et al. 2014. Avian community composition associated with interactions
542 between local and landscape habitat attributes. — *For. Ecol. Manage.* 326: 46-
543 57.
- 544 Ledger, M. E. et al. 2012. Drought alters the structure and functioning of complex
545 food webs. — *Nature Climate Change* 3: 223-227.
- 546 Lehikoinen, A. et al. 2013. Rapid climate driven shifts in wintering distributions of
547 three common waterbird species. — *Global Change Biology* 19: 2071-2081.
- 548 Leyequien, E. et al. 2007. Influence of body size on coexistence of bird species. —
549 *Ecological Research* 22: 735-741.
- 550 Luck, G. W. et al. 2013. Changes in bird functional diversity across multiple land
551 uses: Interpretations of functional redundancy depend on functional group
552 identity. — *PLoS ONE* 8: e63671.
- 553 MacArthur, R. and Levins, R. 1964. Competition, habitat selection, and character
554 displacement in a patchy environment. — *Proceedings of the National*
555 *Academy of Sciences of the United States of America* 51: 1207.
- 556 MacArthur, R. and Levins, R. 1967. The limiting similarity, convergence, and
557 divergence of coexisting species. — *American naturalist* 101: 377-385.
- 558 MacArthur, R. H. 1958. Population ecology of some warblers of northeastern
559 coniferous forests. — *Ecology* 39: 599-619.
- 560 MacArthur, R. H. 1972. *Geographical Ecology: Patterns in the Distribution of*
561 *Species*. — Harper & Row.

562 MacKenzie, D. I. et al. 2004. Investigating species co-occurrence patterns when
563 species are detected imperfectly. — *Journal of Animal Ecology* 73: 546-555.

564 Marchant, J. H., Noble, D.G., Leech, D.I., Freeman, S.N. 2002. River Habitat Survey
565 and Waterways Breeding Bird Survey 1998–2000: Final Report. — British
566 Trust for Ornithology.

567 Mattsson, B. J. et al. 2013. Explaining local-scale species distributions: Relative
568 contributions of spatial autocorrelation and landscape heterogeneity for an
569 avian assemblage. — *PLoS ONE* 8: e55097.

570 McCarthy, M. A. et al. 2012. The influence of abundance on detectability. — *Oikos*
571 122: 717-726.

572 Meier, E. S. et al. 2010. Biotic and abiotic variables show little redundancy in
573 explaining tree species distributions. — *Ecography* 33: 1038-1048.

574 Monkkonen, M. et al. 1990. Numerical and behavioral-responses of migrant
575 passerines to experimental manipulation of resident tits (*Parus* spp) -
576 heterospecific attraction in northern breeding bird communities. — *Oecologia*
577 85: 218-225.

578 Newbold, T. et al. 2014. Functional traits, land-use change and the structure of present
579 and future bird communities in tropical forests. — *Global Ecology and*
580 *Biogeography* 23: 1073-1084.

581 Ovaskainen, O. et al. 2010. Modeling species co-occurrence by multivariate logistic
582 regression generates new hypotheses on fungal interactions. — *Ecology* 91:
583 2514-2521.

584 Peron, G. and Altwegg, R. 2015. The abundant centre syndrome and species
585 distributions: insights from closely related species pairs in southern Africa. —
586 *Global Ecology and Biogeography* 24: 215-225.

587 Petchey, O. L. et al. 2007. Low functional diversity and no redundancy in British
588 avian assemblages. — *Journal of Animal Ecology* 76: 977-985.

589 Plummer, M. 2014. rjags: Bayesian graphical models using MCMC. R package
590 version 3-12. — Available at: <http://CRAN.Rproject.org/package=rjags>.

591 Poff, N. L. R. et al. 1997. The natural flow regime. — *BioScience* 47: 769-784.

592 Pollock, L. J. et al. 2014. Understanding co-occurrence by modelling species
593 simultaneously with a Joint Species Distribution Model (JSDM). — *Methods*
594 *in Ecology and Evolution* 5: 397-406.

595 Renwick, A. R. et al. 2012. Modelling changes in species' abundance in response to
596 projected climate change. — *Divers. Distrib.* 18: 121-132.

597 Richmond, O. M. W. et al. 2010. Two-species occupancy models: a new
598 parameterization applied to co-occurrence of secretive rails. — *Ecological*
599 *Applications* 20: 2036-2046.

600 Robertson, O. J. et al. 2013. Influence of interspecific competition and landscape
601 structure on spatial homogenization of avian assemblages. — *PLoS ONE* 8:
602 e65299.

603 Robinson, Q. H. et al. 2014. The application of occupancy modeling to evaluate
604 intraguild predation in a model carnivore system. — *Ecology* 95: 3112-3123.

605 Royan, A. et al. 2013. Avian community responses to variability in river hydrology.
606 — *PLoS ONE* 8: e83221.

607 Royan, A. et al. 2014. River birds' response to hydrological extremes: New
608 vulnerability index and conservation implications. — *Biological Conservation*
609 177: 64-73.

- 610 Sebastian-Gonzalez, E. et al. 2010. Testing the heterospecific attraction hypothesis
611 with time-series data on species co-occurrence. — *Proceedings of the Royal*
612 *Society B-Biological Sciences* 277: 2983-2990.
- 613 Ulrich, W. and Gotelli, N. J. 2010. Null model analysis of species associations using
614 abundance data. — *Ecology* 91: 3384-3397.
- 615 Vandewalle, M. et al. 2010. Functional traits as indicators of biodiversity response to
616 land use changes across ecosystems and organisms. — *Biodiversity and*
617 *Conservation* 19: 2921-2947.
- 618 Vaughan, I. P. et al. 2007. Combining surveys of river habitats and river birds to
619 appraise riverine hydromorphology. — *Freshwater Biology* 52: 2270-2284.
- 620 Veech, J. A. 2013. A probabilistic model for analysing species co-occurrence. —
621 *Global Ecology and Biogeography* 22: 252-260.
- 622 Veech, J. A. 2014. The pairwise approach to analysing species co-occurrence. —
623 *Journal of Biogeography* 41: 1029-1035.
- 624 Villarreal-Barajas, T. and Martorell, C. 2009. Species-specific disturbance tolerance,
625 competition and positive interactions along an anthropogenic disturbance
626 gradient. — *Journal of Vegetation Science* 20: 1027-1040.
- 627 Ward, J. V. et al. 2002. Riverine landscape diversity. — *Freshwater Biology* 47: 517-
628 539.
- 629 Ward, P. and Zahavi, A. 1973. Importance of certain assemblages of birds as
630 information-centers for food-finding. — *Ibis* 115: 517-534.
- 631 Weiher, E. et al. 1998. Community assembly rules, morphological dispersion, and the
632 coexistence of plant species. — *Oikos* 81: 309-322.
- 633 Weiher, E. and Keddy, P. A. 1995. The assembly of experimental wetland plant-
634 communities. — *Oikos* 73: 323-335.
- 635

636 **Tables**

637 **Table 1.** Description of the four environmental variables used in the joint species
 638 distribution model (JSDM) as predictors of the occurrence and co-occurrence patterns
 639 of 19 river bird species across mainland Great Britain. River flow variables were
 640 defined *a priori* according to Royan, A. et al. (2013) and were calculated using long-
 641 term averages between 1998 and 2011 (inclusive) with data obtained from the
 642 National River Flow Archive (NRFA). Land use data were produced by the Centre for
 643 Ecology and Hydrology (CEH) as part of the Countryside Survey 2000 and were
 644 derived from the satellite-generated Land Cover Map 2000 (LCM2000) with a
 645 resolution of 50 m. Climate data were obtained from the UKCP09 gridded
 646 observation datasets at 5 × 5 km resolution at monthly timescales and climate
 647 variables were calculated using data between January 1998 and December 2011
 648 (inclusive).

Environmental variables	Calculation	Description
<i>Climate variables</i>		
Total Breeding Season	Sum of April to July	During birds' breeding season.
Rainfall (mm)	(inclusive) rainfall between 1998 and 2011 (inclusive)	
Mean Breeding Season	Mean value of April to	During birds' breeding season.
Temperature (°C)	July (inclusive) temperature between 1998 and 2011 (inclusive)	
<i>Land use variables</i>		

Area of woodland (%)	Broadleaved/mixed woodland Coniferous woodland	Catchment that is woodland habitat
Area of arable land (%)	Arable cereals Arable horticulture Arable non-rotational	Catchment that is arable habitat
Area of grassland (%)	Improved grassland Set-aside grass Neutral grass Calcareous grass Acid grassland Bracken Fen, marsh, swamp	Catchment that is grassland habitat
Area of heathland (%)	Montane habitats Dense dwarf shrub heath Open dwarf shrub heath Bog (deep peat)	Catchment that is heathland habitat
Area of urban land (%)	A composite index based on a refined version of the data for the LCM2000 classes Suburban, Urban and Inland bare ground (Bayliss, A. C. and Davies, H. N. 2003)	Urban extent within the catchment boundary.

River flow variables

Flow Variation (m^3/sec)	Standard deviation of daily discharge.	Variability around average flow conditions.
Mean Daily Flow (m^3/sec)	Mean value of daily discharge divided by median of daily discharge.	Average flow magnitude, correcting for river size.
Three Day Maximum (m^3/sec)	Average 3-day maximum divided by median discharge.	Variability around high flows and the deviation of high flows from the median.
Three Day Minimum (m^3/sec)	Average 3-day minimum divided by median discharge.	Variability around low flows and the deviation of low flows from the median.

650 **Figures headings**

651

652 **Figure 1.** Map showing the distribution of the 100 Waterways Breeding Bird Survey
653 (WBBS) survey locations used to derive presence/absence data for 19 river bird
654 species.

655

656 **Figure 2.** Heatmap visualisation showing pairwise associations between 19 river bird
657 species calculated according to the probability model of species co-occurrence
658 (Griffith, D. M., Veech, J.A. & Marsh, C.J. In press). Significant positive (negative)
659 associations are displayed where species co-occurred more (less) frequently than by
660 chance, with an alpha threshold of 0.05.

661

662 **Figure 3.** Modelled environmental and residual correlations between pairs of all 19
663 river bird species (i.e. 171 pairs) averaged across all 100 WBBS locations. The error
664 bars display 95% confidence intervals for the mean modelled environmental and
665 residual correlations. The points are coloured blue where both environmental and
666 residual correlation are positive, and environmental correlation is stronger (i.e. closer
667 to 1), and coloured orange where both environmental and residual correlation are
668 negative, and environmental correlation is stronger (i.e. closer to -1).

669

670 **Figure 4.** Network diagrams showing modelled environmental correlation (a & c) and
671 residual correlation (b & d) between 19 river bird species, where the black lines
672 represent positive correlations at $R_s > 0.5$ and $R_s > 0.7$.

673

674 **Figure 5.** A dendrogram, created by converting the matrix of species occurrences
675 across the 100 river locations into a binary dissimilarity matrix and by then using
676 hierarchical cluster analysis, to show how species occurrences cluster in a manner
677 consistent with three guilds based on foraging habitat and resource acquisition: slow-
678 flowing species, fast-flowing species, and riparian species.

679

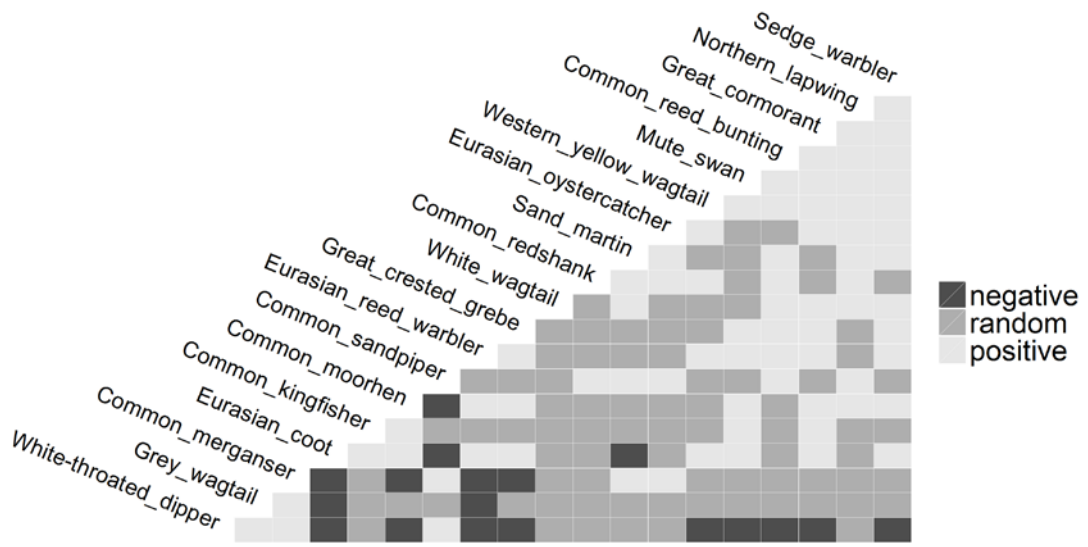
680 **Figure 6.** Box-and-whisker plots of the mean residual correlation between species
681 within three guilds based on foraging habitat and resource acquisition: fast-flowing,
682 riparian, and slow-flowing (see **Results** section for the species composition of guilds).
683 In each box the thick black line represents the median average residual correlation
684 between species and the limits illustrate the interquartile range from the first quartile
685 (i.e. 25th quantile) to the third quartile (i.e. 75th quantile). The whiskers extend to the
686 minimum and maximum values, excluding outliers.

687



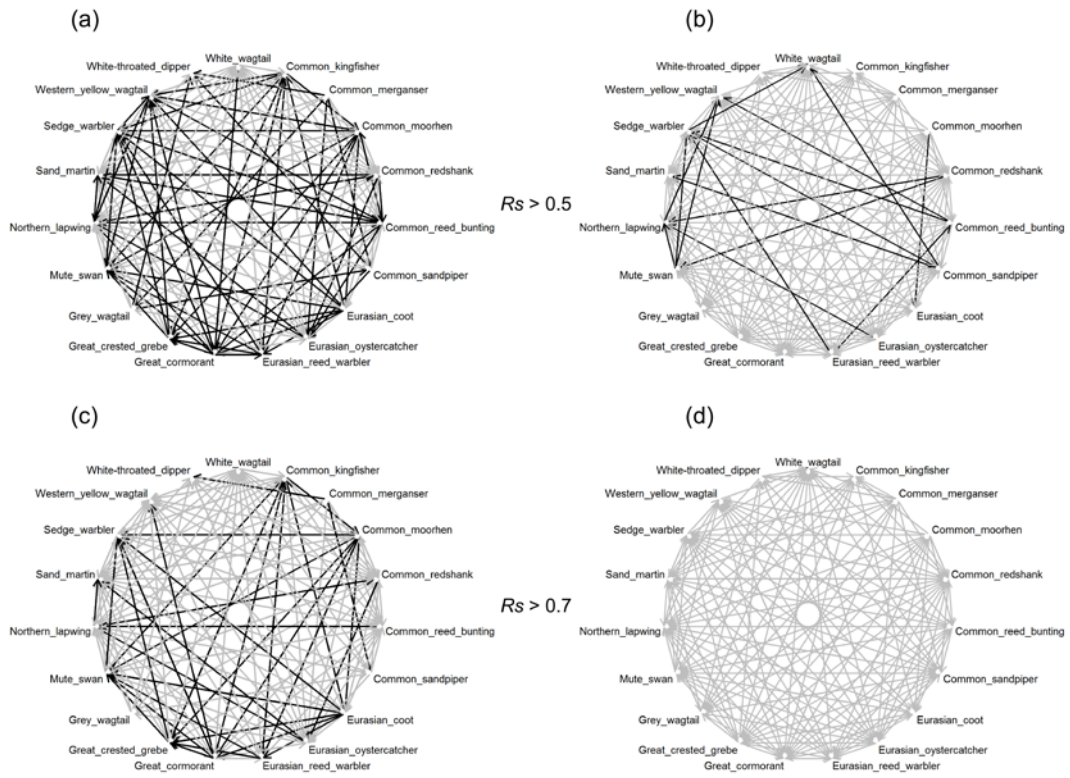
688 Figure 1

689 Figure 2
690



691
692

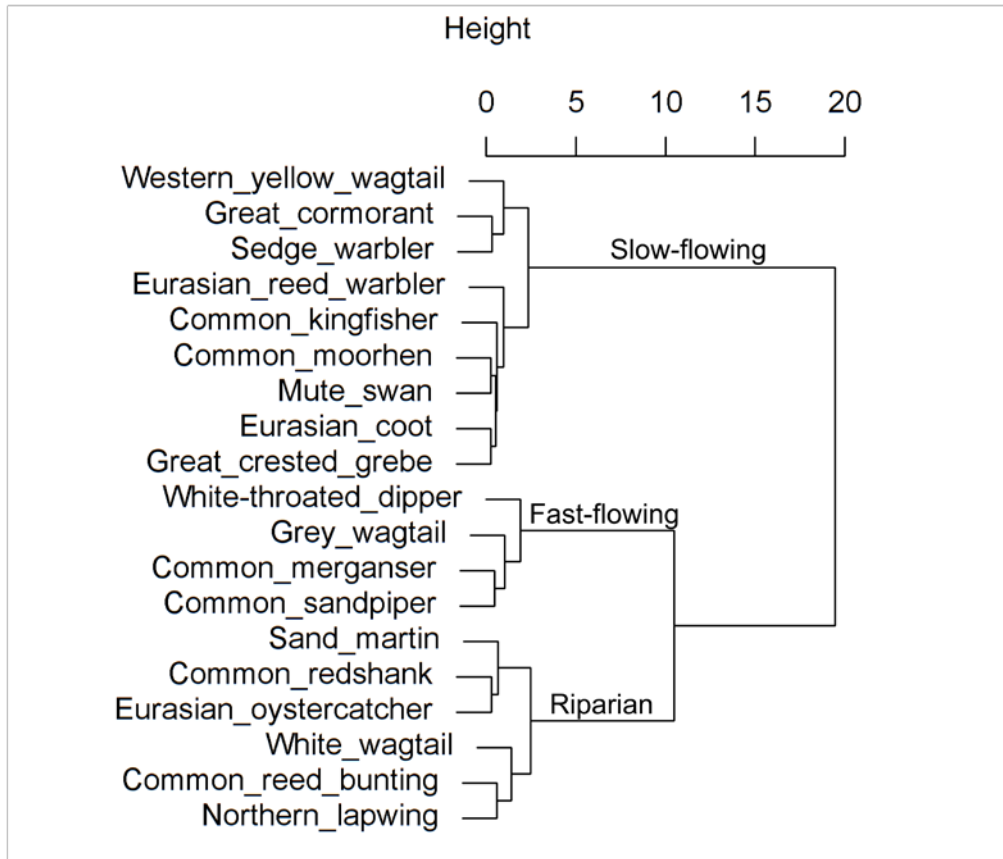
693 Figure 3
694
695



696
697

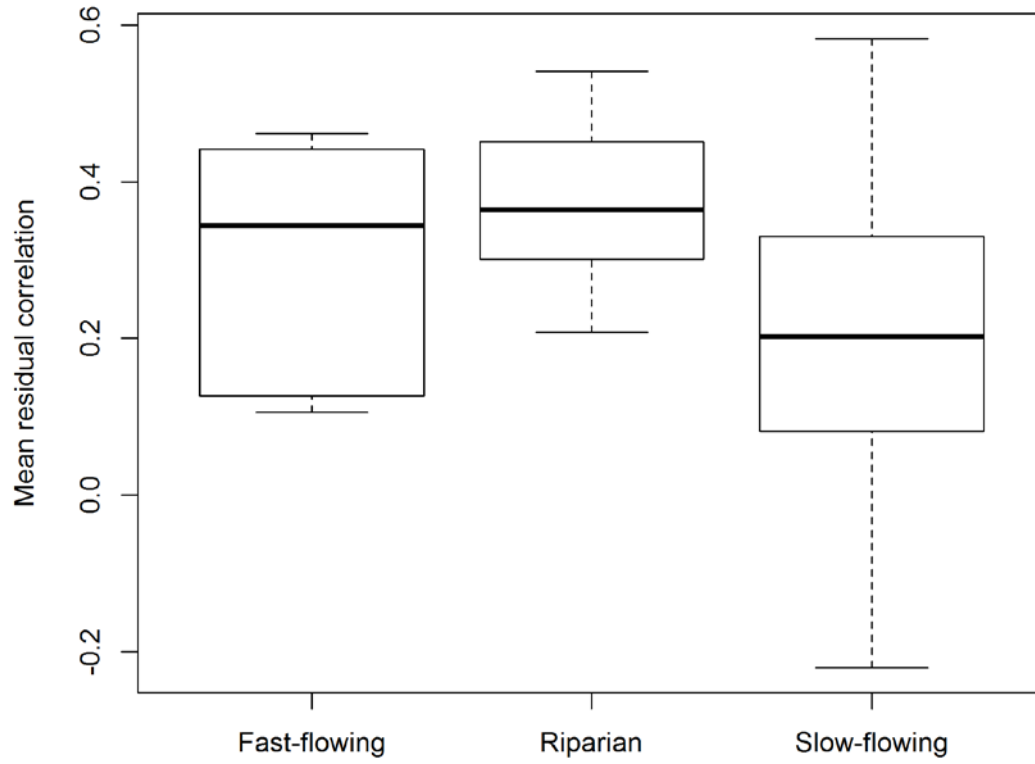
Figure 4

698 Figure 5
699



700

701 Figure 6
702



703
704

705
706