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

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Abstract

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

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

Introduction

Species distributions are determined by a range of factors, including climate, land cover, landscape barriers, dispersal ability and species interactions (MacArthur, R. H. 1972). Mechanistic models of community assembly predicate that the impacts of these biotic and abiotic factors on the trait composition of communities manifest through assembly rules (i.e. biological filters) and the ability of species to tolerate local conditions (i.e. environmental filters) (Belmaker, J. and Jetz, W. 2013). Environmental filters restrict community membership to species possessing a particular set of functional traits (Petchey, O. L. et al. 2007). Conversely, a number of positive (e.g. mutualisms and commensalisms), negative (e.g. competition) and neutral models of species interaction may describe overlapping patterns in species distributions (Araújo, M. B. and Rozenfeld, A. 2013). Such interactions may leave imprints on species distributions that are detectable at large spatial scales (Baselga, A. et al. 2012, Gotelli, N. J. et al. 2010, Heikkinen, R. K. et al. 2007); both positive and negative interactions can be discernible across scales of hundreds of kilometres (Araújo, M. B. and Rozenfeld, A. 2013). However, positive/negative associations can result from species having similar/dissimilar habitat requirements as well as from direct or indirect interactions (Ovaskainen, O. et al. 2010), meaning (dis)similarity in habitat preference is a legitimate ecological explanation for why two species might have positive (or negative) association. Consequently, disentangling the relative roles of environmental and biotic factors in community assemblage processes *and* understanding their link to spatial patterns in species distributions is a considerable challenge and is a prominent unresolved issue in ecology (Barnagaud, J. Y. et al. 2014, Kraft, N. J. B. et al. 2014, MacArthur, R. and Levins, R. 1964, MacArthur, R. H. 1958, Peron, G. and Altwegg, R. 2015).

Associations between species have particularly pervasive impacts on bird populations, where interspecific competition may influence the distribution, habitat choice, abundance and productivity of species (Cody, M. L. 1974), and interactions between them have been detected in the distributions of species at large spatial scales (Gotelli, N. J. et al. 2010, Heikkinen, R. K. et al. 2007, Robertson, O. J. et al. 2013). Community-wide patterns of spatial segregation in the Danish avifauna could not be attributed to heterogeneity in the distribution of habitat or differences in habitat utilisation, suggesting that the large-scale operation of species interactions (e.g. interspecific territoriality and conspecific attraction) can cause behaviour-driven assembly patterns (Gotelli, N. J. et al. 2010). However, it has been suggested that habitat variability, disturbance regimes and food availability structure bird

communities at finer spatial scales, with geomorphic landforms and climatic envelopes becoming more important in determining neighbourhood associations at coarser scales (Börger, L. and Nudds, T. D. 2014, Gotelli, N. J. et al. 1997, Kroll, A. J. et al. 2014, Mattsson, B. J. et al. 2013).

Considering the impact of both environmental and biotic effects, there are four prevalent hypotheses that explain the distribution of heterospecifics (Mattsson, B. J. et al. 2013): (1) a null hypothesis that species are distributed entirely randomly and patterns of species occurrence do not conform to variability in habitat condition or the distribution of heterospecifics (Hubbell, S. P. 2001); (2) the environmental filtering hypothesis where community structure relates to variability in abiotic factors (e.g. disturbance) with species partitioned according to abiotic constraints (MacArthur, R. H. 1958). Community membership will therefore be restricted to those species possessing a particular set of functional traits (Keddy, P. A. 1992, Petchey, O. L. et al. 2007, Weiher, E. and Keddy, P. A. 1995) and one might expect species occurrences to be highly correlated with environmental variables; (3) the interspecific interaction hypothesis, where species distributions are primarily influenced by the occurrence of heterospecifics and species either aggregate in patches occupied by heterospecifics or segregate to occupy empty patches. Individuals may cluster with heterospecifics because of the benefits of group membership in terms of increased vigilance, reduced predation risk and enhanced assessment of habitat quality (Ward, P. and Zahavi, A. 1973). Conversely, segregation may occur due to mechanisms such as competitive exclusion (MacArthur, R. and Levins, R. 1967). In this interspecific interaction hypothesis we would expect to find irregular distributions of species that are poorly explained solely by environmental variables; (4) a pluralistic hypothesis in which species not only interact and aggregate/segregate according to the distribution of heterospecifics but they do so in a manner reflecting the patchiness of habitats that promote fitness. These hypotheses can be termed ‘surrogate hypotheses’ as they are assessed through an examination of patterns in data rather than by controlled experimentation (Araujo, M. B. and Luoto, M. 2007) and provide a strong analytical framework in macro-ecological studies where the manipulation of experimental conditions is not possible (Gotelli, N. J. and McGill, B. J. 2006).

Investigation into non-random patterns of association between pairs of species has largely centred on the comparison of presence/absence matrices with null models (Gotelli, N. J. et al. 1997, Gotelli, N. J. et al. 2010, Ulrich, W. and Gotelli, N. J. 2010, Weiher, E. et al. 1998). Analyses are based on inferences as to whether an observed matrix differs from those produced by random processes or

from a known ecological mechanism. Investigations of these matrices have led to the analysis of empirical patterns in species distributions and the development of ecological hypotheses for community organisation, including the community assembly rules of Diamond, J. M. (1975). However, it is not clear if it is possible to use such approaches to discriminate between spatial patterns caused by species interaction and those caused by affinities for particular habitats. An alternative method in modelling biotic interactions is to restrict the distribution of one species by including the abundance of another as a predictor alongside environmental variables (Meier, E. S. et al. 2010). However, the abundance of heterospecifics could act as a surrogate for absent important environmental variables (Araujo, M. B. and Luoto, M. 2007). Additionally, two-species occupancy models can use species distribution data to model the probability of occurrence of species pairs and show how the detection probability of either species may change in the presence of the other (Richmond, O. M. W. et al. 2010). This approach is well suited to the analysis of the co-occurrence of subordinate (e.g. prey) species and dominant (e.g. predator) species (Robinson, Q. H. et al. 2014) but has less applicability to macro-ecological studies of multiple species distributions.

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

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

assess the importance of species interactions in determining species distributions across different guilds.

Material and methods

River bird data

Bird survey data were obtained from the British Trust for Ornithology's (BTO's) Waterways Breeding Bird Survey (WBBS), an annual large-scale national survey of birds on rivers in Great Britain.

Waterway locations for the WBBS are randomly selected according to a stratification procedure (Marchant, J. H., Noble, D.G., Leech, D.I., Freeman, S.N. 2002). First, national grid squares at 2×2 km resolution are selected at random and those without a waterway are discarded. Waterways within remaining squares are then identified according to the definition of any double blue line, with shaded in-fill, on the OS 1:25,000 Pathfinder map series. A single waterway within each square is then randomly selected, with the start and end points of the survey location determined by the observer.

Each year two visits are made to WBBS survey locations by the same observer, one in the first half of the breeding season and one in the second half; typically early April and late June, respectively. The WBBS comprises transect methodology, with survey locations divided into 10 linear transects of fixed 500 m length situated along one side of the waterway. The observer counts all birds seen or heard within 100 m of each 500 m linear transect, with the total number of transects surveyed (up to a maximum of 10) counted and recorded so that heterogeneity in survey effort may be quantified and accounted for in subsequent statistical analyses. As multiple visits to survey locations provide more reasonable estimates of species occupancy and abundance which, in turn, reduce bias associated with detection probability (McCarthy, M. A. et al. 2012), we selected WBBS survey locations with a minimum of four repeated visits between 1998 and 2011 (inclusive). In total, 100 WBBS locations were used, achieving wide coverage across mainland Great Britain (Fig.1).

We used data for 19 bird species which were selected because they are largely ubiquitous across riverine landscapes in Great Britain and sufficiently characterised diversity in river bird communities (Royan, A. et al. 2013, Royan, A. et al. 2014). Additionally, these species also possess an array of ecological traits, which provides the opportunity to study a broad range of responses to the environmental variables and interaction with heterospecifics (Newbold, T. et al. 2014, Vandewalle, M. et al. 2010), whilst the relationship between their distribution in Great Britain and key environmental

variables is well characterised (Royan, A. et al. 2013, Vaughan, I. P. et al. 2007). Our response variable was defined as the presence/absence of a bird species at each of the 100 locations. Because waterbird distributions may shift across years (Lehikoinen, A. et al. 2013), river bird occurrence data could potentially be influenced by the date of survey. Bird occurrence data may also be influenced by incomplete survey designs causing the introduction of false absences to the data set. To mitigate any potential bias arising from imperfect detection and false absences, occurrence data were therefore combined across visits to the survey locations, whereby a species was recorded as present if it was observed during surveys at any time between 1998 and 2011 (the presence/absence matrix is provided in Table A1). However, it should be noted that the inclusion of detection probabilities has no effect on the inference of population trends in widespread and abundant species (Newson, S. E. et al. 2013).

Environmental data

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

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

Land use data were produced by the CEH as part of the Countryside Survey 2000 and were derived from the satellite-generated Land Cover Map 2000 (LCM2000) with a resolution of 50 m. Land use variables quantified the percentage of the riverine catchment comprising woodland, arable, urban, heathland and grassland habitats. Climate data for each survey location were obtained from the UKCP09 gridded observation datasets at 5×5 km resolution at monthly timescales and climate variables were calculated using data between January 1998 and December 2011 (inclusive). Further details on how these data were derived can be found on the UK Met Office website

(<http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/index.html>). We calculated mean breeding season temperature (°C) and total breeding season rainfall (mm), with the breeding season defined as April to July (inclusive). We chose to use climate variables calculated during the breeding season rather than annual or winter variables as they have been shown to be better predictors of bird distributions in Great Britain (Renwick, A. R. et al. 2012).

Modelling procedure

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

We further analysed co-occurrence patterns using the JSDM developed by Pollock, L. J. et al. (2014). This hierarchical modelling approach attributes co-occurrence patterns to shared environmental responses and residual patterns of co-occurrence and so can be used to investigate the mechanisms that influence the structure and dynamics of species assemblages. For instance, evidence of strong environmental correlation would support the hypothesis for the operation of environmental filtering assembly mechanisms. Weak environmental correlation and strong residual correlation would lend support to the interspecific interaction hypothesis, although one cannot completely discount the possibility of some influence of unmeasured habitat relationships (Börger, L. and Nudds, T. D. 2014). Evidence of strong environmental correlation and also a broad range of residual correlation would provide evidence for a pluralistic hypothesis of community organisation. The null hypothesis of random community organisation would be supported if no significant positive or negative pairwise associations were detected.

Full details of the JSDM can be found in Pollock, L. J. et al. (2014) but below we summarise this approach in brief. Co-occurrence patterns were modelled using a hierarchical probit regression model in which the linear environmental predictors were related to a binary response variable using a latent variable formulation. The probability of occurrence of each species at a site is determined by the

mean of a normal distribution (the latent variable), assuming a standard deviation of one, whereby species are modelled as being present when the distribution mean is greater than zero and modelled as absent when less than zero. Associations amongst species are modelled by changing the locations of the latent multivariate normal distribution and probabilities of co-occurrence by changing the correlations of the latent distribution. The number of species being modelled determines the number of dimensions of the multivariate normal distribution. The means of the normal distribution were modelled using regression equations and a matrix of regression coefficients. Residual correlation is controlled by a matrix of correlation coefficients in the latent distribution between species. This was calculated by rescaling the variance/covariance matrix of the multivariate normal distribution by dividing the terms by the corresponding standard deviations and defining with an inverse-Wishart prior. A second correlation matrix was also calculated to account for the component of between-species correlation that is due to shared environmental responses. The model estimates posterior distributions for four parameters: correlations between species due to the environment, the residual correlation between species, regression coefficients, and the predicted probability of occurrence of a species at each site.

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

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

Results

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

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

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

Hierarchical cluster analysis revealed that the communities can be decomposed into three guilds, whereby species within each guild were likely to co-occur due to similar environmental tolerances (Fig. 5). Species within each guild displayed similar characteristics for foraging habitat and resource acquisition. These were species that forage on fast-flowing rivers (i.e. common sandpiper [*Calidris hypoleucos*], white-throated dipper [*Cinclus cinclus*], common merganser [*Mergus merganser*], grey wagtail [*Motacilla cinerea*]), those that forage on large, slow-flowing rivers (i.e. Eurasian coot [*Fulica atra*], great cormorant [*Phalacrocorax carbo*], great crested grebe [*Podiceps cristatus*], common kingfisher [*Alcedo atthis*], common moorhen [*Gallinula chloropus*], mute swan [*Cygnus olor*], Eurasian reed warbler [*Acrocephalus scirpaceus*], sedge warbler [*A. schoenobaenus*], western yellow wagtail [*Motacilla flava*]), and species that forage at riparian margins across a range of rivers (i.e. northern lapwing [*Vanellus vanellus*], Eurasian oystercatcher [*Haematopus ostralegus*], common redshank [*Tringa totanus*], common reed bunting [*Emberiza schoeniclus*], white wagtail [*Motacilla alba*], and sand martin [*Riparia riparia*]). Further analysis of the residual correlation between species within these guilds revealed additional complexities in species covariance patterns. Residual correlation was significantly higher between species within the riparian guild than between species within the slow-flowing guilds (Kruskal-Wallis: $\chi^2 = 15.70$, $p < 0.001$) (Fig. 6).

Discussion

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

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

Whilst our results corroborate the findings of some studies in suggesting that species interactions are of secondary importance relative to habitat structure and resource availability (Börger, L. and Nudds, T. D. 2014, Gotelli, N. J. et al. 1997, Kroll, A. J. et al. 2014, Mattsson, B. J. et al. 2013, Petchey, O. L. et al. 2007), they contrast markedly with others (Gotelli, N. J. et al. 2010, Heikkinen, R. K. et al. 2007, Robertson, O. J. et al. 2013, Sebastian-Gonzalez, E. et al. 2010). One reason for this might be that we focussed on bird communities on riverine systems which are highly dynamic, disturbance-prone environments in which river flow is the dominant driver of changes in ecosystem structure (Junk, W. J. et al. 1989). High levels of environmental disturbance result in rapid turnover of

biota through flow-induced spatial and temporal heterogeneities in the prevalence of key foraging and breeding habitats (Ward, J. V. et al. 2002). Perturbations in aquatic-riparian food webs also cause irregularity in ecological processes such as production and biotic interactions (Ledger, M. E. et al. 2012). Heterogeneity in external factors such as land-cover complexity and the availability of foraging habitat also exerts strong formative pressure on the structure of bird communities (Devictor, V. et al. 2007, Mattsson, B. J. et al. 2013, Robertson, O. J. et al. 2013). Consequently, in riverine systems the influence of abiotic factors in constraining bird species distributions is likely to be strengthened, with species interactions such as competitive filtering reduced to a minor role. Moreover, it is plausible that those species with the greatest exposure to abiotic disturbance are the least likely to be connected to other species in the community and so are less influenced in distribution by interspecific interaction (Araujo, M. B. et al. 2011). Evidence from bird communities indicates that when species richness is depressed by disturbance, abiotic constraints are more important than species interactions in structuring species assemblages (Belmaker, J. et al. 2012).

However, the predictive performance of the JSDM varied between bird foraging guilds, with residual correlation most positive amongst riparian species. It may be the case that a few species in the community have close links to others in the community network with most species poorly connected to others, with a tendency for individualistic behaviour and partitioning (Araujo, M. B. et al. 2011). This perhaps indicates a reduced impact of environmental filtering and an enhanced influence of species interactions on riparian species distributions. Therefore, a pluralistic model of community organisation may be more appropriate for some avian taxa. Riparian species such as the common redshank, Eurasian oystercatcher and northern lapwing forage in ephemeral patches of habitat. It is plausible that competition amongst these functionally similar species for transitory food resources is likely and that this would lead to segregation (MacArthur, R. and Levins, R. 1967). Yet, co-occurrence between these species was observed to be positive, suggesting the operation of an alternative model of interspecific interaction such as heterospecific attraction. However, positive residual correlation could also be caused by an unmeasured variable for habitat quality which might influence species distributions. It is possible that the habitat, river flow and climate variables used to model species distributions did not fully capture variability in ephemeral habitat patches, which are utilised by species such as the Eurasian oystercatcher and northern lapwing. It is also possible that an enhanced influence of interspecific interaction might have been detected by using abundance rather than presence data as there is some

evidence that mechanisms underlying abundance variations occur at community scales where species interaction is greatest (Boulangeat, I. et al. 2012).

Heterospecific attraction can lead to positive patterns of co-occurrence as species preferentially select patches of habitat already occupied by heterospecifics, whereby individuals may use the presence of other species as an indicator of patch quality (Monkkonen, M. et al. 1990). Such patterns have previously been observed in some waterbird species including riparian waders (Sebastian-Gonzalez, E. et al. 2010). Facilitative processes like heterospecific attraction are thought to be more prevalent in disturbed environments by increasing the average fitness of individuals of a species that could not survive in isolation (Villarreal-Barajas, T. and Martorell, C. 2009). However, this requires intraspecific to be stronger than interspecific competition, allowing for niche partitioning (MacArthur, R. and Levins, R. 1967), or for resources to be sufficiently abundant that competitive exclusion is minimised. Interspecific competition between the sympatric riparian species in our study is likely to be reduced, in part, because of the disparity between body sizes which allows for different foraging strategies and the exploitation of different food resources, thus facilitating co-existence through spatial niche separation (Leyequien, E. et al. 2007). Furthermore, temporal niche separation, as exhibited by nocturnally foraging northern lapwings, may also enable co-existence.

Patterns of random co-occurrence were relatively prevalent amongst river bird communities. There are several reasons why such patterns might be observed. First, random patterns of co-occurrence may indicate a strong influence of the filtering of species from the regional species pool which may be greatest at locations with lower productivity and reduced competitive exclusion (Houseman, G. R. and Gross, K. L. 2006). Variability in river flows exerts a strong disturbance regime that can limit productivity in aquatic-riparian environments which, in turn, prevents competitive exclusion (Bunn, S. E. and Arthington, A. H. 2002, Ledger, M. E. et al. 2012, O'Callaghan, M. J. et al. 2013, Poff, N. L. R. et al. 1997). Consequently, the natural disturbance regime of rivers may enhance ecological filtering from species pools into local communities via heightened abiotic filtering which maintains productivity at relatively low levels. In support of this theory, the percentage of co-occurrence patterns that were random was higher at river locations with greater river flow variability than at locations with more stable river flow regimes (Figure A1). Secondly, patterns of random co-occurrence could also be caused by the operation of multiple environmental factors which cause both aggregation and segregation of species distributions, as it has been shown experimentally that contrasting environmental

processes might counterbalance each other to co-produce patterns of random species co-occurrence (García-Baquero, G. and Crujeiras, R. M. 2015). Finally, patterns of random co-occurrence could also arise as a consequence of imperfect detection of some species which leads to false absences in the species presence/absence matrix (MacKenzie, D. I. et al. 2004). However, we aimed to minimise the potential for bias caused by species detection probability by only using survey locations that were visited on several occasions.

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

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Table Legend

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

Environmental variables	Calculation	Description
<i>Climate variables</i>		
Total Breeding Season Rainfall (mm)	Sum of April to July (inclusive) rainfall between 1998 and 2011 (inclusive)	During birds' breeding season.
Mean Breeding Season Temperature (°C)	Mean value of April to July (inclusive) temperature between 1998 and 2011 (inclusive)	During birds' breeding season.
<i>Land use variables</i>		
Area of woodland (%)	Broadleaved/mixed woodland	Catchment that is woodland habitat
	Coniferous woodland	
Area of arable land (%)	Arable cereals	Catchment that is arable habitat
	Arable horticulture	
	Arable non-rotational	
Area of grassland (%)	Improved grassland	Catchment that is grassland habitat
	Set-aside grass	
	Neutral grass	
	Calcareous grass	
	Acid grassland	

	Bracken	
	Fen, marsh, swamp	
Area of heathland (%)	Montane habitats	Catchment that is heathland
	Dense dwarf shrub heath	habitat
	Open dwarf shrub heath	
	Bog (deep peat)	
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.
<i>River flow variables</i>		
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.

Figure Legends

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



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

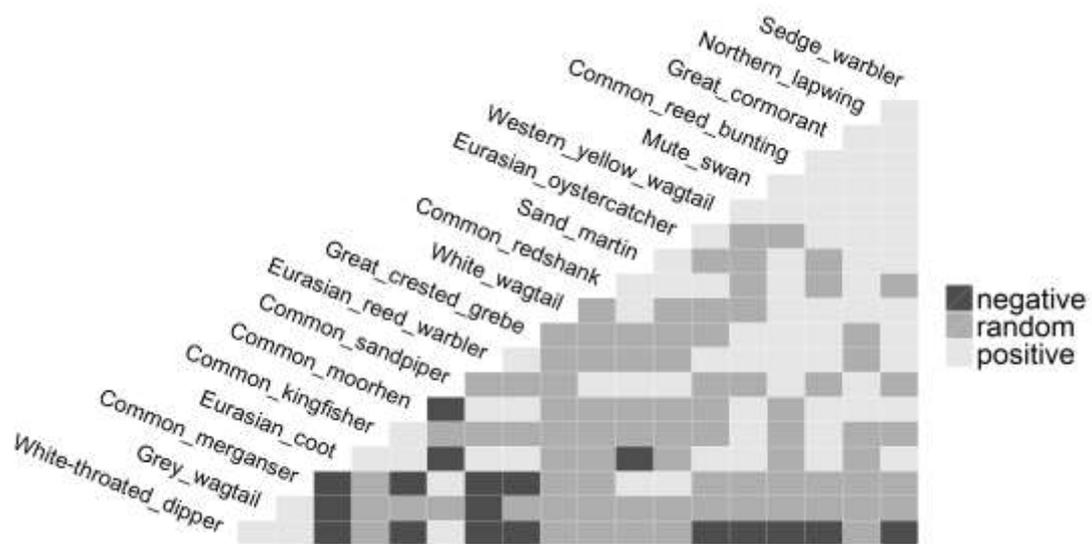


Figure 3. Modelled environmental and residual correlations between pairs of all 19 river bird species (i.e. 171 pairs) averaged across all 100 WBBS locations. The error bars display 95% confidence intervals for the mean modelled environmental and residual correlations. The points are coloured blue where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

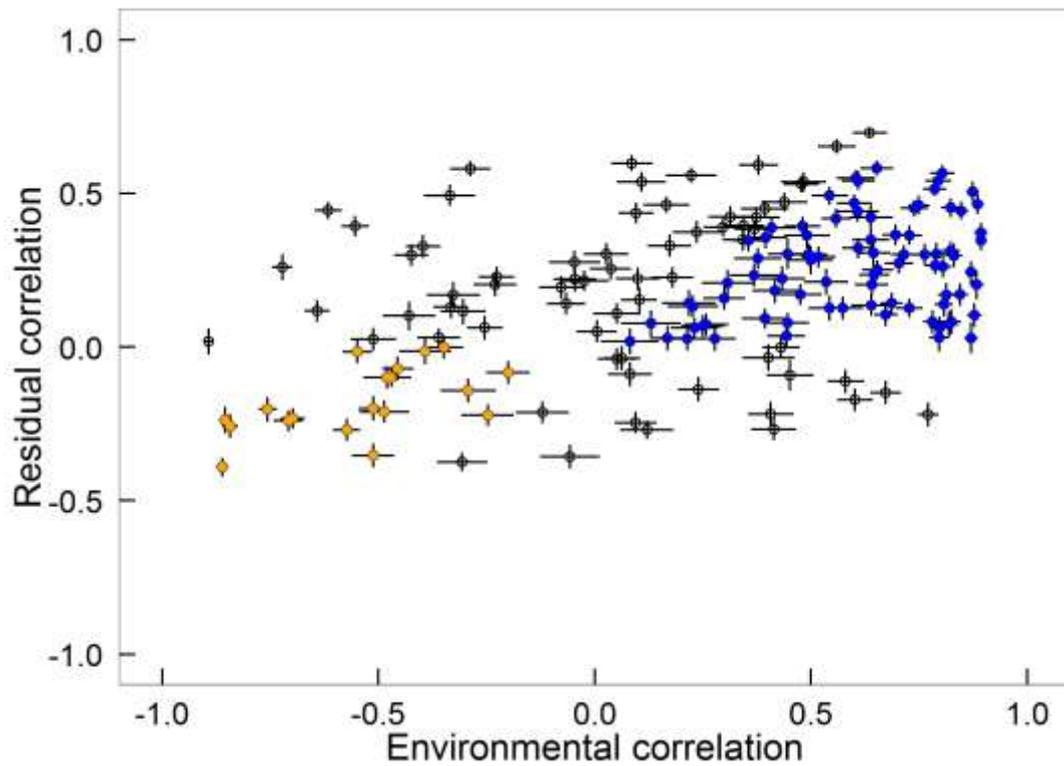


Figure 4. Network diagrams showing modelled environmental correlation (a & c) and residual correlation (b & d) between 19 river bird species, where the black lines represent positive correlations at $R_s > 0.5$ and $R_s > 0.7$.

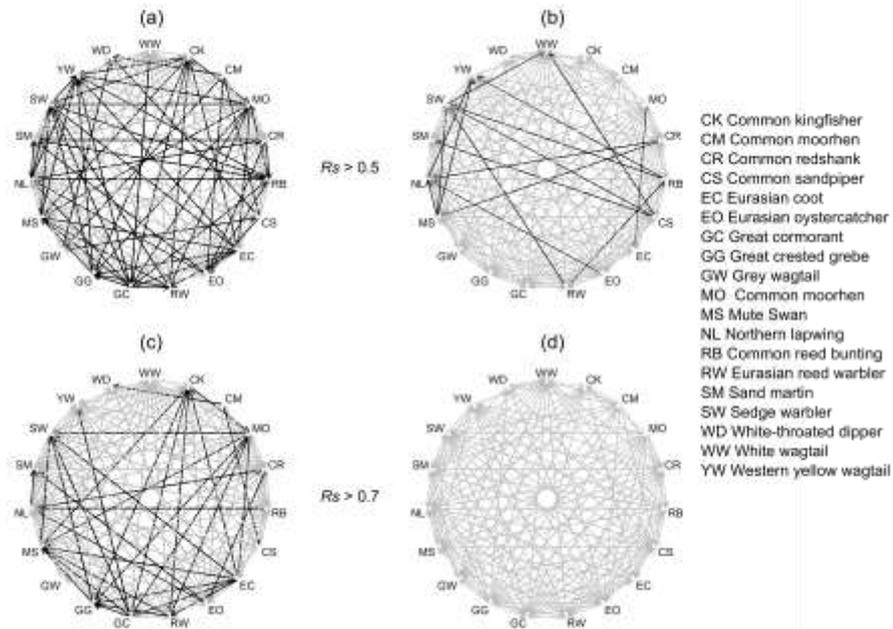


Figure 5. A dendrogram, created by converting the matrix of species occurrences across the 100 river locations into a binary dissimilarity matrix and by then using hierarchical cluster analysis, to show how species occurrences cluster in a manner consistent with three guilds based on foraging habitat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

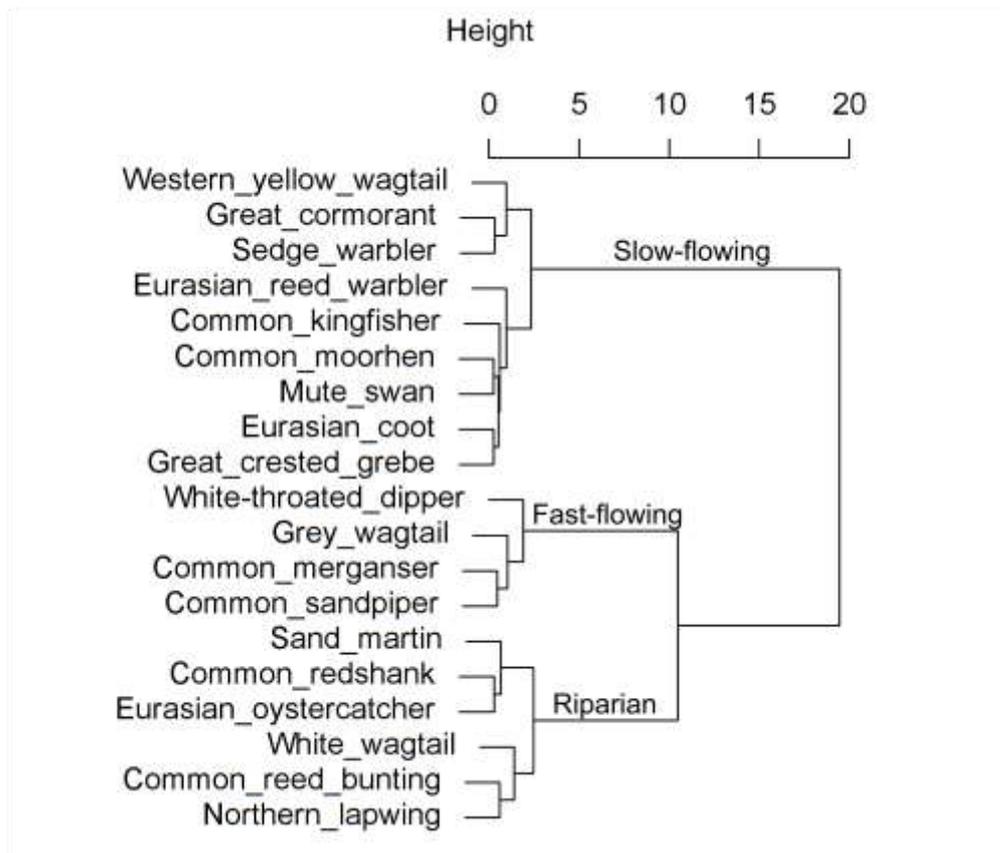


Figure 6. Box-and-whisker plots of the mean residual correlation between species within three guilds based on foraging habitat and resource acquisition: fast-flowing, riparian, and slow-flowing (see **Results** section for the species composition of guilds). In each box the thick black line represents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

